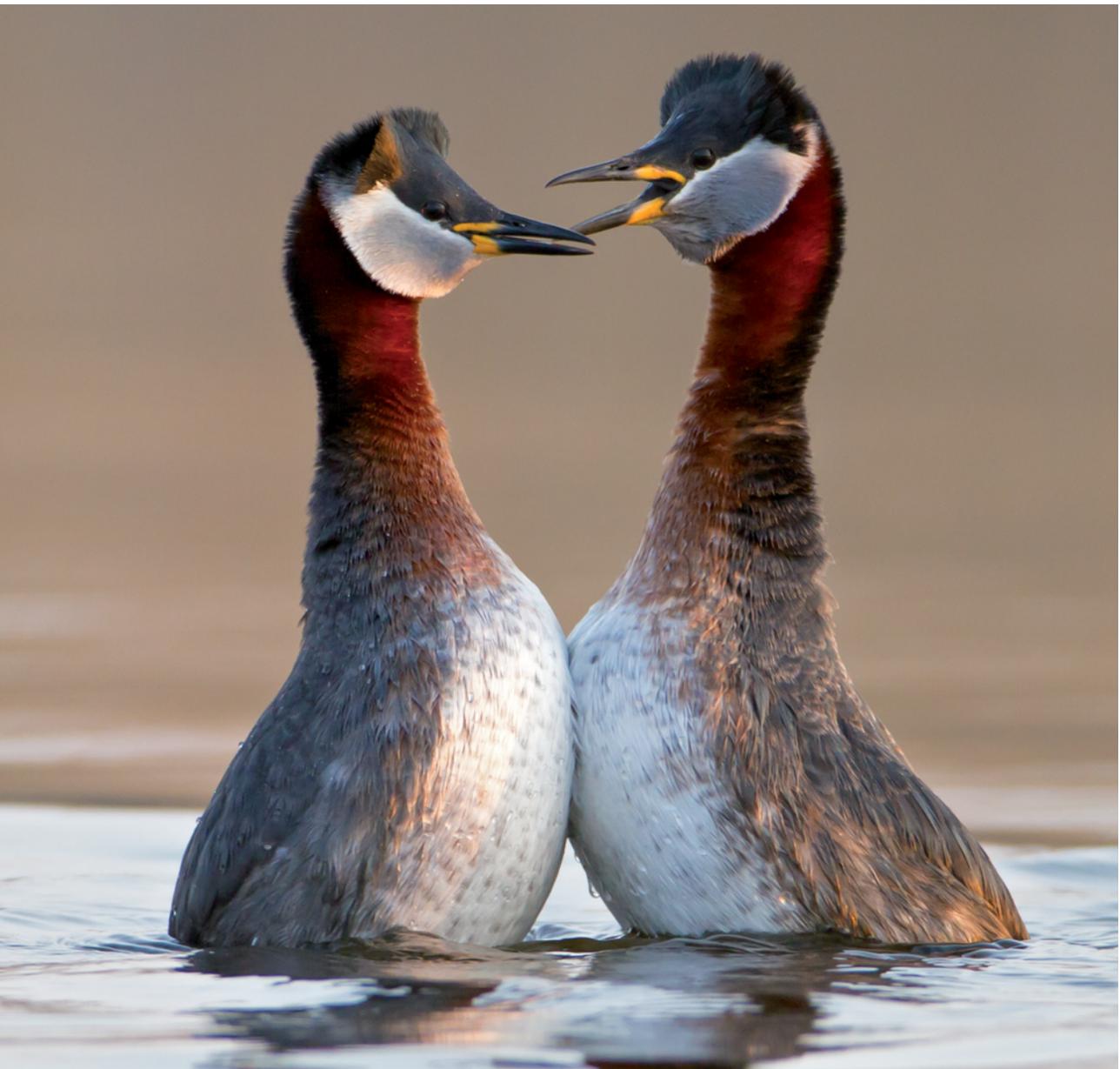


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The Red-necked Grebe - a Monograph of a Vociferous Inhabitant of Marshy Lakes

Jan Johan Vlug

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Preface and Acknowledgements

In 1964 Ulrich Wobus published his monograph “Der Rothalstaucher” (“The Red-necked Grebe”). He lived in the former German Democratic Republic. Every spring, from a base in Oberlausitz (Upper Lusatia) in eastern Germany, he studied the interesting courtship behaviour and harsh-sounding territorial Song and display-call of this bird. Wobus called the Song “uööh-Gebrüll” - “Gebrüll” in German denotes a harsh bellowing sound. For that reason the title of my monograph is “The Red-necked Grebe – a Monograph of a Vociferous Inhabitant of Marshy Lakes”. In the 103 pages of his publication, Wobus laid the foundations of what we know about the Red-necked Grebe. However, since then, much new material has been collected and new theories have been advanced, so it is both surprising and impressive that even today Wobus’s monograph remains the standard account of this fascinating and beautiful grebe.

In this special issue of “Corax”, by integrating old and new information from many sources in the field of ornithology, I have tried to advance general understanding of the Red-necked Grebe and other grebe species, especially in the areas of ecology, breeding and behaviour. I have found much valuable information in the works of P Axelsson, R K Berndt, D Buitron, K D de Smet, J Fjeldså, J R Jehl Jr, C L Kevan, J Kloskowski, A Konter, B Koop, J A Munro, G L Nuechterlein, I A Ohanjanian, T Piersma, M E Riske, K E L Simmons, F Spletzer, R W Storer, B E Stout, T Wheeler, U Wobus and many others. The chief part of whatever merit my paper may possess has been derived from studying the admirable works of Jon Fjeldså.

This monograph is intended primarily as a reference work for students interested in the biology of grebes and other waterbirds. After an introductory chapter, which gives some general background information, the text is arranged in 16 chapters dealing with topics such as systematics, origins, habitat, interspecific competition, population trends, threats, movements, food, behaviour and breeding. With this treatment, some topics inevitably arise in more than one chapter. Because I considered every chapter as an independent unit, I had to accept the repetition of some themes.

This publication would not have been possible without the hard work of Nina Vivanco (Edinburgh, Scotland), who spent countless hours checking the language and contents of the manuscript. Any errors that may remain are entirely my own.

I am greatly indebted to the generosity of six bird photographers who have allowed me to use some of their best work as illustrations. The many images that enliven the book were provided by Thorsten Runge (Kiel, Germany), André Konter (Echternach, Luxemburg), Harm Niesen (Bergen, Netherlands), Gaby and Rolf Berndt (Kiel, Germany) and Natasha Paklina (Enkhuizen, Netherlands).

The beautiful drawings were made by my beloved Rineke (C M Vlug-Kempen), who tragically died prematurely.

I have benefited from discussions with Paul Axelsson (Ystad, Sweden), Rolf Berndt, André Konter, Bernd Koop (Plön, Germany) and Janusz Kloskowski (Poznań, Poland). Rolf, Bernd, Birgit Mohwinkel (Hohenfelde, Germany) and Martin Rieck (Bellin, Germany), heavily supported me and often accompanied me on field trips.

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I am also very grateful to the executive committee of the “Ornithologische Arbeitsgemeinschaft für Schleswig-Holstein und Hamburg” (Ornithological Study Group in Schleswig-Holstein and Hamburg), which allowed me to publish this monograph as a special issue of the ornithological journal “Corax”. I could not have published this paper without the kind help of the members of this committee.

Finally, my wife Irina deserves the most thanks, for patiently accepting my absences during the many field trips to Germany, as well as the hours that I spent working in my study.

Alkmaar, March 2018

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Photo: T Runge (Schleswig-Holstein)

1. Introduction

The members of the grebe family Podicipedidae are strictly aquatic, and during the breeding season they usually occupy lakes or pools, often with ample amounts of floating, emergent or underwater vegetation. They have representative species on all continents except Antarctica. Grebes are unique and unusual in many ways, including their habit of feather-eating, their courtship behaviour in which all of the displays up to and including mounting are performed by either sex, and the building of floating nests, which makes it possible for a grebe to live its whole life without going on land (Storer 2004). The structure of their feet is different from all other living lobe-toed birds. Compared with most other birds, grebes have their legs displaced to the rear end of the body, and out to the sides. This placement of the feet causes instability and clumsiness on land but provides efficient propulsion during swimming and diving (Fjelds  2004).

The grebes are the only family of the order Podicipediformes, and taxonomically they do not appear to be very closely related to any other group. Historically Gaviiformes (divers or loons) and grebes have been regarded as closely related, due to their similarity to each other. However, this similarity is due to convergent evolution and many morphological and molecular data have usually failed to support the holophyly of a proposed diver/grebe clade (e. g. Hackett *et al.* 2008). Instead, molecular, morphological, oological and cladistic analyses strongly support sister group relationship between grebes and flamingos Phoenicopteridae (Van Tuinen *et al.* 2001, Mayr 2004, Manegold 2006). Scientists, using mitochondrial and nuclear markers, calibrated the divergence of flamingos and grebes at 32.6 million years ago (early Oligocene) (Torres *et al.* 2014).

Nowadays, seven genera of grebes are recognized. The divergence of these extant grebes was calibrated at 8.7 million year ago (late Miocene) based on *Thiornis sociata*, a grebe from the late Miocene of Spain (Torres *et al.* 2014). The most diversified genus is *Podiceps*, with eight species, and these are normally divided into two main subgroups. The first, the “crested” subgroup, is composed of the Red-necked, Great Crested and the Slavonian (Horned) Grebes, three species that are often sympatric. The second, the “eared” subgroup, consists of five closely related species (Black-necked Grebe and rel-

atives). Using genetic data from mitochondrial markers, Ogawa *et al.* (2015) estimated that the last common ancestor of the Red-necked Grebe and the Slavonian Grebe existed around 3.38 million years ago (Pliocene). We must assume that the divergence of the Red-necked Grebe and the Great Crested Grebe also occurred at the same time or somewhat earlier or later.

Although the 22 recent species form a minute fraction of the world’s avifauna, a series of ornithologists has been drawn by grebes’ spectacular courtship behaviour to study these birds. It began with Julian Sorell Huxley, grandson of the zoologist Thomas Henry Huxley, the latter known as Darwin’s bulldog for defending natural selection. Julian Huxley’s detailed study of the courtship behaviour of Great Crested Grebes at Tring reservoir, made in just two weeks during the Easter vacation of 1912 (Huxley 1914), was a milestone in the study of animal behaviour (Birkhead *et al.* 2014). This pioneering work led a series of enthusiasts to study the behaviour repertoire of grebes. Three of them were Ken (K E L) Simmons, who published a high number of articles on the behaviour of the Great Crested Grebe, Bob (R W) Storer, who investigated many aspects of a number of grebe species and Ulrich Wobus, who published in 1964 his monograph on the Red-necked Grebe. In this last mentioned publication, the foundations of our present knowledge of the behaviour and ecology of *Podiceps grisegena* were laid. Authors such as Kenneth (K D) de Smet, Jon Fjelds , Cora (C L) Kevan, Janusz Kloskowski, Andr  Konter, Gary (G L) Nuechterlein, Frank Spletzer, Bonnie (B E) Stout, Han (J J) Vlug and many others used the pioneering studies of Huxley, Simmons, Storer and Wobus. Some of them paid special attention to the study of the Red-necked Grebe.

However, there are still many unanswered questions. Almost nothing is known about the causes of population trends and population regulation, life span, survivorship and other demographic factors. There is not much information about ecology and behaviour on the wintering grounds, moults, summering, pair formation, mate fidelity, territorial attachment and numerous other topics. Many questions could be answered by colour-banding, wing tags, radio transmitters, satellite-tracking and similar methods, but it is very difficult to catch Red-necked Grebes and, until now, not much has been done to enable individual identification and keeping track of the movements of the birds and their life histories.

2. Names and Classification

2.1 Vernacular Names

The Red-necked Grebe has received numerous colourful and apt local names, which almost always refer to the distinctive plumage and sometimes to the voice. Of course, the great majority of “official” or standardized vernacular names by which the Red-necked Grebe is known in the language of the countries where it occurs, derive from local stock. Each common name, needless to say, identifies the species only to a limited number of people and can lead to confusion.

2.1.1 Names of the European Red-necked Grebe

Most of late 18th- and 19th-century British naturalists already called the species “Red-necked Grebe” (for example John Latham 1787, Thomas Bewick 1804, 1826, William Yarrell 1843, 1884/1885). This English name emphasizes the conspicuous chestnut colour of the neck, just as for example the German (“Rothalstaucher”) and the Dutch (“Roodhalsfuut”) names.

Many common names bring the mouse-grey colour of chin, throat or sides of head (“cheeks”) to our notice, such as the Swedish “Gråhakedopping”, the Danish “Gråstrubet Lappedykker” and the French “Grèbe jougris”. Johann Andreas Naumann (1802, p. 438 of Volume 3) called the species “graukehlige Taucher” (“grau” = grey, “kehlige” = throated, “Taucher” = grebe) and “graukehlige Haubentaucher” (“Haubentaucher” = Great Crested Grebe), but also “kastanienhalsige Taucher” [“kastanien (braun)” = chestnut (brown), “halsig” = necked]. William MacGillivray (1852) mentioned the name “Red-necked Grebe” as well as “Grey-cheeked Grebe” in Volume 5 of his work “A History of British Birds”.

The French name is of importance as the scientific name is based on it (see 2.2.2). On page 241 of Volume 8 (and p. 374 of Volume 15) of “Histoire Naturelle des Oiseaux”, Buffon (1781*a, b*) used the names “le grèbe à joues grises” and “le jougris” (“joue” = cheek, “gris” = grey). The Dutch naturalist C J Temminck (1815, 1820) called the Red-necked Grebe “Grèbe jou-gris”.

The English word grebe is derived from French “grèbe”, whose origin is unknown. It may be another of the many bird names to have arisen out of a generalized term for a seabird, or it may be a corruption of the Breton word

“krib”, meaning “crest” and probably referring to the Great Crested Grebe (Leahy 1983). However, we cannot exclude the possibility that the French name “grèbe” is an onomatopoeic word, referring to the call of the adult (Great Crested) Grebe (Eigenhuis 2004).

2.1.2 Names of the East Asiatic-North American (or North Pacific) Red-necked Grebe

The Red-necked Grebes from Europe, Asia and North America were originally seen as belonging to one species and bore the same name. J J Audubon (1844), for one, still applied the name Red-necked Grebe to the North American birds in the 1840s (see Fig. 1). After J Reinhardt (1854) published a paper on birds collected in Greenland, the North American (and East Asiatic) Red-necked Grebe was considered to be a separate species and was named Holboell’s Grebe (see 2.2.3). In the 1950s the name Red-necked Grebe for North American birds was restored.

2.2 Scientific Names

2.2.1 First Scientific Names and Descriptions of the Red-necked Grebe; Development of Binomial and Trinomial Nomenclatures

The Italian naturalist Ulisse (Ulyssis) Aldrovandi (1603, 1637) published an illustration of a Red-necked Grebe on page 254 in his work “Ornithologiae, Tomus Tertius ac postremus”. It seems that he considered the Red-necked and the Great Crested Grebes (illustration on p. 255) to be two “varieties” of one single species (description on page 253, *cf.* Buffon 1781*a*, p. 236 and 1781*b*, p. 365) because he called the Red-necked Grebe *Colymbus maior cristatus* and the Great Crested Grebe *Colymbus maior cristatus alter* (Latin “alter” = the other) (see Fig. 2). However, today’s species concepts are quite different from those of 400 years ago, and the first person to produce a biological species definition was John Ray (1686, *cited in* Mayr 1982). He did so in Volume 1 of his “Historia Plantarum – De Plantis in Genere”.

In another work, John Ray (1678, “The Ornithology of Francis Willughby”) gave an account of “The grey or ash-coloured Loon of Dr. Brown” (p. 340) and showed an illustration [Tab. 61: *Colymbus seu Podiripes (sic) cinereus*]. Possibly, this ash-coloured bird was a Red-necked Grebe, but it can not be excluded that it was a Great Crested Grebe in winter plumage (*cf.* Bewick 1804,



Fig. 1: “Podiceps rubricollis - Red-necked Grebe”, in Audubon (1844).



Fig. 2: “Colymbus maior cristatus”, in Aldrovandi (1603).

p. 145, 1826, p. 153, and 1885, p. 164). Probably, Ray's description (p. 339) of "The greater crested or copped Doucker of Aldrovand" concerned a Red-necked Grebe in breeding dress. Almost hundred years later the German naturalist Jacobi Christiani Schaeffer (Schäffer) (1774) described some characteristics of grebes (Genus 30 *Colymbus* – "La Grebe" – "Seehahn") and printed a picture (Tabula 29) of a standing Red-necked Grebe in nuptial plumage, but he gave no species names and did not describe the features of the Red-necked Grebe. Seven years after Schaeffer, Buffon (1781*a, b*) treated the Red-necked Grebe in his "Histoire Naturelle, Générale et Particulière" and mentioned a few characteristics of the species. However, he only gave a French name to the bird (see 2.2.2).

Binomial Nomenclature

The early ornithologists such as Aldrovandi (1603, 1637) often named the birds with (long) descriptive Latin sentences until the Swedish botanist and pioneer of taxonomy Carolus Linnaeus (Carl von Linné) originated his simplified system. It was in 1758, in the 10th edition of his work "Systema Naturae per Regna tria Naturae", Volume 1, that Linnaeus first consistently applied binomial (or binominal) nomenclature to the animal kingdom. This was not his invention, as many other naturalists such as Gesner (Gessner) (1555) used a similar system. However, Linnaeus was the first to develop a system of rules, seeking to standardize the work of naturalists (Chansigaud 2009). Many immediately realized the advantages offered by this clear and unambiguous system. The 10th edition of the aforementioned work is the basis for our present system of zoological nomenclature. In the binomial system all species are given two names: the second name identifies a species considered to be unique in nature; the first name assigns it to a genus. Linnaeus (1758) did not mention the Red-necked Grebe but named three other species of grebes. One of them was the Great Crested Grebe which received the name *Colymbus cristatus*.

Trinomial Nomenclature

Linnaeus and the early taxonomists were essentialists and believed that each species is characterized by its unchanging essence ("eidos"), separated from all other species by a sharp discontinuity. Essentialists did not know how to deal with variation. When individuals were found that differed strongly from the norm of the species, they were considered a different species; when

they differed only slightly, a "variety" (Mayr 1982). The German pastor Christian Ludwig Brehm became notorious for binomially naming every minor variation he could find in birds so that they appeared as species and did not make a distinction between individual and geographical variations (Stresemann 1951, Walters 2003). Brehm (1831, pp. 956-8) distinguished three "species" of the Red-necked Grebe in Germany and its adjoining countries, especially because he found small differences in bill shape and size (see 2.2.4). He believed that, as a rule, only members of the same "species" paired together (Stresemann 1951, Walters 2003). Hermann Schlegel (1844) was not happy with the vast increase of binomials and was the first to adopt trinomial (trinomial) nomenclature routinely for geographical bird races, though the practice did not come into general use until many years later (Walters 2003, Birkhead *et al.* 2014). Where a species is divisible into subspecies (races), the binomen constituting the name of the species is for each of them extended by a third term, the subspecific name; the trinomen thus formed is the name of the subspecies (Campbell and Lack 1985). The subspecific name *Podiceps rubricollis major* was conferred on the "Japanese" Red-necked Grebe by Temminck and Schlegel (1850) (see 2.2.3, and Fig. 3).

Priority and Chaos in Classification

The basic principle of zoological nomenclature is priority. Accordingly, the valid name of a taxon (species, subspecies, etc.) is basically the oldest available name that has been applied to it since 1758. It must be noted, however, that in practice, scientific naming has fallen short of the ideal, for reasons partly inevitable and partly arising from human wilfulness and negligence. Many naturalists in the 18th and 19th centuries were eager to name as many new species as possible and succumbed to the craze of species description. Numerous errors were made, and multifarious synonyms demonstrate that chaos in classification was enormous (see 2.2.4).

2.2.2 Formation of the Current Scientific Name of the Nominate Subspecies

Four naturalists played an important part in the formation of the current scientific name of the Red-necked Grebe: Buffon, Daubenton, Boddaert and Latham.

Le Jougris and *Colymbus grisegena*

Georges-Louis Leclerc, Comte de Buffon, one of the giants of the French Enlightenment, published a massive,



Fig. 3: “*Podiceps rubricollis major* - le grèbe à joues grises du Japon”, in Temminck and Schlegel (1850).

classic work in the history of the natural sciences, his “*Histoire Naturelle, Générale et Particulière*”. In the zoological volumes, unfortunately, the work’s relevance to modern science is severely restricted by the fact that Buffon refused to adopt his contemporary Linnaeus’s invaluable system of binomial nomenclature (1758). He opted instead to use a common name – in French, of course. After 1758, Buffon (1781*a, b*) was probably the first naturalist to describe the Red-necked Grebe (see 2.2.1) and called the species “le jougris” (see 2.1.1); he named the Great Crested Grebe “le grèbe cornu”.

Buffon produced his work with the assistance of many colleagues such as Louis Jean-Marie d’Aubenton (Daubenton), who conceived the idea of publishing a set of coloured plates of specimens from the royal collections in his care. Among the collected specimens were a number of grebes from Europe, Asia and the Americas. Daubenton commissioned the artist François Nicolas Martinet to produce the plates and began issuing them in 1765 in cahiers, but in 1767 he withdrew from the project; Buffon and Daubenton’s cousin Edmé Louis

Daubenton continued issuing the plates under the title “*Planches Enluminées*” for the planned section on birds. The complete “*Planches*” consists of 42 cahiers (d’Aubenton 1765-83?) (Zaharek and Overstreet 2001).

In 1783, an identification key to the “*Planches Enluminées*”, the “*Table des Planches Enluminées*” (*sic*), assigning binomial scientific names to Daubenton’s plates, was provided by the Dutch naturalist Pieter Boddaert. Some authors felt that Boddaert’s work was too sloppy, and his nomenclature too lax for his names to be accepted. Nevertheless, they have been recognized and a considerable number of current scientific names are credited to Boddaert (Walters 2003). On page 55 of his list, Boddaert (1783) gave the Red-necked Grebe the name *Colymbus grisegena*. He based *grisegena* on “Le Jougris” of plate 931 from “*Planches Enluminées*” (Latin “*griseus*” = grey, and “*gena*” = cheek; *grisegena* erroneously spelled *griseigena* by many authors). This plate, produced by Martinet, shows a standing Red-necked Grebe in breeding plumage (in Buffon 2008 plate 931 is reproduced as plate 853 on page 571). As Linnaeus

(1758, 1766), Brisson (1760, Volume 6), Klein (1760), Brännich (1764), Berkenhout (1769), Schaeffer (1774), Pennant (1776) and other authors in the period from 1758 (10th edition of “Systema Naturae”) to 1783 did not mention or name the Red-necked Grebe, and Buffon (1781a, b) did not give scientific names, Boddaert’s *grisegena* is the oldest accepted scientific specific name of the species [the description of *Colymbus vulgaris* (Latin “vulgaris” = common, ordinary) (I A Scopoli 1769, p. 78, species No. 102) is not reliable (cf. Hartert 1912-21)].

***Colymbus* and Colymbidae, Podiceps and Podicipedidae. Generic and Family-group Names of Grebes and Divers**

The generic name *Colymbus* derives from Greek “kolumbis”, a waterbird mentioned by Aristophanes, Aristotle, Dionysius, and other authors (Jobling 1995). In the Renaissance *Colymbus* reappears in “Historiæ Animalium” of the famous Swiss naturalist Conrad Gesner (Gessner). In the Volume on birds (Volume 3, 1555, “Qui est de Avium Natura”), he called the Great Crested Grebe *Colymbus major* (“*De Colymbis maioribus*”, pp. 133-5), and so did Georg Horst (1669) in the revised edition of this work (“Vogelbuch”, first part, pp. 112-4) (see also Springer and Kinzelbach 2013). As already mentioned Aldrovandi (1603, 1637) also used the name *Colymbus* (see 2.2.1, and Fig. 2).

An association of the grebes and divers (loons) began with the early classifications. Linnaeus (1758, pp. 135-6) included not only the grebes (*Colymbus cristatus*, *C. auritus* and *C. Podiceps*) but also the divers (*C. arcticus*) in *Colymbus*, one of the genera in his order Anseres. The majority of taxonomists after Linnaeus agreed that both groups are closely associated and thus their taxonomic histories have been intertwined. Morten Thrane Brännich (1764), the founder of Danish faunistic zoology, placed the divers (for instance *C. immer* and *C. Stellatus*) and the grebes (*C. cristatus* and *C. auritus*) together in the genus *Colymbus* of Linnaeus.

Pygopodes, or Pygopodidae, was a name often given to a family, order, or cohort of aquatic birds, which included at one time or another ducks, geese, swans, divers, grebes, auks, penguins, tubenoses, and/or the Cretaceous toothed divers, the Hesperornithes, depending on whose classification scheme it was (Fjeldså 2004). The family Pygopodes (“Steißfüßer”) of the German naturalist Jo-

hann Karl Wilhelm Illiger (1811) included the grebes, divers, guillemots, puffins and razorbills. The genus *Colymbus* (“Plongeurs”) in “Le Règne Animal” of the French comparative anatomist Georges Cuvier (1817, Volume 1, pp. 507-10) comprised the grebes (“les Grèbes”: *Col. cristatus*, *Col. cornutus*, *Col. subcristatus* and *Col. minor*), divers (loons), guillemots (murre) and true guillemots (tysties) (Cuvier 1817). The family Colymbidae of Friedrich Boie (1826, column 980), an ornithologist who lived in Schleswig-Holstein, contained the divers, grebes, penguins and auks. Thomas Henry Huxley (1867, pp. 457-8), the well-known British biologist and supporter of Charles Robert Darwin, united the divers and grebes in the family Colymbidae, which with the Laridae, Procellariidae, and Alcidae composed his Cecomorphae.

Max Fürbringer (1888, pp. 1541-2, p. 1565), a German anatomist known for his anatomical investigations of all types of vertebrates, was specialized in avian systematics and morphology. His suborder Podicipitiformes comprised three genera: the Colymbo-Podicipites (divers and grebes), the Hesperornithes and the Enaliornithes. Robert Wilson Shufeldt (1892) had the same opinion and considered the divers and grebes to be one group, perhaps derived from a *Hesperornis*-like ancestor. In 1914 he wrote: “Taken collectively, the loons and grebes form a natural Supersuborder of birds, created to contain the Suborder *Pygopodes*, which latter is represented by two families, namely the *Colymbidae* or Grebes, and the *Gaviidae* or Loons” (Shufeldt 1914). Hans Gadow (1893), the founder of modern classification, also found divers and grebes similar and placed them as two suborders (Colymbi and Podicipedes) in his order Colymbiformes near the beginning of his sequence. Richard Bowdler Sharpe (1891, 1899) assigned the two groups to adjacent orders (Podicipediformes and Colymbiformes).

Not all taxonomists were convinced of a close relationship. Leon Gardner (1925) found that the tongue of divers differs from that of grebes, although they have similar food habits. Max Stolpe (1935) examined the structure and functions of muscles (myology) and skeleton (osteology) of the hind limbs of divers and grebes and concluded that the facts support the hypothesis that both groups are not more closely related than each is to some other group of swimming bird. His observations and conclusions had a major influence on subsequent

ideas about the relationship between these birds. Most authors accepted his discoveries as conclusive evidence that the similarities between divers and grebes are due to convergence (Sibley and Ahlquist 1990) (see 8.3 for more details).

Taxonomists, more than ever before, realized that the names *Colymbus* and Colymbidae could not be used for both groups. However, there was much confusion about what the correct generic and family-group names should be. Did the names *Colymbus* and Colymbidae belong to the grebes or to the divers? The cause of this uncertainty was a doubt about the designation of the type species, i.e. the species chosen to serve as the basis for naming and describing the genus *Colymbus*. G R Gray (1855), E Hartert (1912-21) and E D van Oort (1922) assumed that Linnaeus described the Black-throated Diver as type species of his genus *Colymbus*, and so this name could not be a correct one for grebes. Many authors did not agree and supposed that the genus *Colymbus* Linnaeus 1758 is typified by *Colymbus cristatus* (Great Crested Grebe).

As early as 1787 John Latham, British ornithologist, physician and a founder of the Linnean Society, provided the grebes with the generic name *Podiceps* on page 294 of Supplement 1 to his work “A General Synopsis of Birds” (Latham 1787). Although Linnaeus used *Podiceps* in 1758 (p. 136), he applied it to a species, *Colymbus Podiceps* (today *Podilymbus podiceps*), and not to a whole genus. John Ray (1678, “The Ornithology of Francis Willughby”) already used the related name *Podicipes* [p. 340: *Colymbus sive Podicipes minor*, and Tab. 61: *Colymbus seu Podiripes (sic) cinereus*]. *Podiceps* comes from Latin “podex”, “podicis” = vent or anus; and “pes” = foot, because the feet of grebes are placed at the rear of the body.

During a long period, *Colymbus* as well as *Podiceps* were used simultaneously as generic name for grebes. The German ornithologist Johann Friedrich Naumann (1838), in “Naturgeschichte der Vögel Deutschlands”, adopted *Colymbus* and called the Red-necked Grebe *Colymbus rubricollis* (see Fig. 4), and Carl R Henricke (1903), who revised this work, also used the name *Colymbus* (*Colymbus griseigena*). Temminck (1815, 1820) and MacGillivray (1852) applied *Podiceps* and named the species *Podiceps rubricollis* and so did John Gould (1873) in Volume 5 of his magnificent illustrated

“The Birds of Great Britain”. Far into the 1950s, the majority of ornithologists in the New World gave the generic name *Colymbus* to the typical grebes, and thus the East Asiatic-North American Red-necked Grebe was called *Colymbus holboelli(i)griseigena* (see 2.2.3).

As it had been found impossible to reach agreement on the correct use of the names Colymbidae and *Colymbus* (and the name of the order Colymbiformes), there was a widespread feeling among ornithologists that they should be entirely suppressed, in favour of the names next in priority in the divers and grebes (and already partially current). Thus, in 1956, the generic name *Podiceps* given by Latham (1787) to the grebes, has been placed on the Official List of Generic Names in Zoology with the Name No. 993 by the International Commission on Zoological Nomenclature. The generic name *Gavia* Forster 1788 and the family-group name Gaviidae Coues 1903 have been assigned to the divers (Storer 1979).



Fig. 4: “*Colymbus rubricollis* - Rothhalsiger Lappentaucher”, in Naumann (1838).

Nowadays, the family-group name of grebes is Podicipedidae, derived from Podicipinae of C L Bonaparte (1831, p. 62). Podicipedidae has been placed on the Official List of Family-Group Names in Zoology in 1972, and the family-group name Podicipitidae, likewise derived from Podicipinae of Bonaparte (1831), has been rejected (Melville 1972, Storer 1979).

Podiceps grisegena

Thus the present scientific name of the Red-necked Grebe is *Podiceps grisegena*. As was stated above, Latham (1787) coined the generic name *Podiceps* and Boddaert (1783) the specific name *grisegena*. It was not until the second half of the 19th century that the present name was used regularly, usually as *Podiceps griseigena*, for instance by Degland and Gerbe (1867), Dresser (1878), Giglioli (1886) and Reiser (1894) (all these authors cited in Hennicke 1903), and Yarrell (1884/1885). During the largest part of the 19th century the species was better known as *Podiceps (Colymbus) rubricollis*.

Podiceps ruficollis* and *Podiceps (Colymbus) rubricollis

In his "A General Synopsis of Birds" (3 Volumes, 1781-85) John Latham described many new species. In Volume 3 (part 1, p. 288), he gives an account of the Red-necked Grebe (Latham 1785). However, he made no attempt to supply scientific names. He hastened to rectify this and, in 1787, he compiled a list of the birds of Great Britain provided with binomial nomenclature. In this list, which was placed at the end of the "Supplement to the General Synopsis of Birds", he coined the generic name *Podiceps* (see above). He named the Red-necked Grebe *Podiceps Ruficollis* (Latin "rufus" = red) and commented "But lately discovered in this kingdom" (Latham 1787, p. 294). However, the scientific naming of Johann Friedrich Gmelin appeared to be more influential. In 1788-93, this German professor produced his own edited 13th edition of Linnaeus's "Systema Naturae" (the volumes concerning birds were published in 1788-89), in which he added a great many new species, plundered from the accounts of Latham among other writers (Walters 2003). Gmelin (1789, Volume 1, part 2, pp. 590-2) described the Red-necked Grebe more than once, under different names. He did not mention the name *Podiceps Ruficollis* of Latham (1787) and used, among other names, *Colymbus rubricollis* (Latin "ruber" = red, and "-collis" = necked). In 1790 Latham issued a summary of "A General Synopsis of Birds", entitled "Index Ornithologicus". On page 783 (Volume 2) he called the Red-

necked Grebe *Podiceps rubricollis* (Latham 1790, cf. Johanneau 1809, p. 333). Among the large number of other naturalists adopting the name *Colymbus (Podiceps) rubricollis* were two Dutch naturalists: Coenraad Jacob Temminck (1815) named the species *Podiceps rubricollis*, Lath. in Manuel d'Ornithologie (p. 465), and Cornelius Nozeman (1770-1829) described the Red-necked Grebe as *Podiceps (Colymbus) Rubricollis* in Volume 5 (1829, pp. 435-6, plate 221) of his work "Nederlandsche Vogelen". In Naturgeschichte der Vögel Deutschlands, Volume 9 (1838, p. 720, plate 243), the German scientist and founder of scientific ornithology in Europe Johann Friedrich Naumann (1838) also called the species *Colymbus rubricollis*. Linn. (see Fig. 4). Another German ornithologist, Eugen Ferdinand von Homeyer (1837, p. 78), used the name *Podiceps rubricollis* Lath.

Subspecific Names and Type Locality

A single specimen, or individual bird, on which the original scientific description of a species or subspecies is based, is the type specimen. The place where it was collected is the type locality or "terra typica". Unfortunately, Daubenton, and consequently Boddaert, gave no locality for the Red-necked Grebe, but France has been designated as such in 1912 (Witherby *et al.* 1947). The subspecies that contains the population from the type locality is called the nominate subspecies. As the type specimen of the Red-necked Grebe of Pieter Boddaert was of European origin, European and West Asiatic birds belong to the nominate subspecies *Podiceps grisegena grisegena* (Boddaert).

2.2.3 Formation of the Scientific Name of the East Asiatic-North American (or North Pacific) Subspecies

In the first half of the 19th century, the East Asiatic-North American Red-necked Grebe was not treated as a separate species and had the same name as the West Asiatic-European Red-necked Grebe (cf. 2.1.2). In Volume 2 ("The Birds", p. 411) of their work "Fauna Boreali-Americana" (1829-37), William Swainson and John Richardson (1831) used the name *Podiceps rubricollis*. They wrote: "No specimen of this bird being obtained on the last expedition," In "A Manual of the Ornithology of the United States and of Canada", Thomas Nuttall (1834) also considered the North American Red-necked Grebe as the same species as the European *Podiceps rubricollis*, Lath. Temm. He remarked: "The Red-Necked Grebe, like most of the other species, retires to the hyperboreal regions of both con-

tinents to pass the breeding season, delighting in the seclusion of the desolate wilderness, penetrating in the present continent, as far as the remote inland shores of Great Slave Lake, where they were observed by Captain Franklin's adventurous party, in the month of May." In 1840-44, the great artist, explorer and ornithologist John James Audubon published a more accessible and revised edition of his famous work "The Birds of America". In Volume 7 (p. 312) of this edition he also mentioned the American Red-necked Grebe *Podiceps rubricollis*, Lath. (Audubon 1844) (see Fig. 1).

***Podiceps rubricollis major*, Subspecific Status**

Philipp Franz Balthasar von Siebold, a German physician, collected an enormous number of zoological specimens during his stay in Nagasaki 1823-29, among them grebes. In 1833-50 he published his splendid "Fauna Japonica". This work was compiled by three scholars of the Dutch Leiden Museum, and was the first material written in a Western language (French) on Japanese fauna. Coenraad Jacob Temminck and Hermann Schlegel wrote the work on birds ("Aves", 1844-50). They called the "Japanese" Red-necked Grebe ("le grèbe à joues grises du Japon") *Podiceps rubricollis major* (1850, p. 122, plate No. 78B, type locality Japan; pp. 122-3 description) (Latin "maior" = greater) (see Fig. 3). It was the first time in history that a population of Red-necked Grebes received a subspecific status. Nowadays, East Asiatic and North American birds are considered as belonging to one and the same subspecies. And so, Temminck and Schlegel (1850) actually assigned the subspecific name to Red-necked Grebes of this enormous area. Unfortunately, the name *major* could lead to confusion as Pieter Boddaert (1783, p. 24) called a South American species of grebe *Colymbus* (nowadays *Podiceps*) *major* (cf. *Podiceps major* in Gray 1846, Mlíkovský 2010b).

***Podiceps Holböllii*, Specific Status**

Shortly after Temminck and Schlegel (1850), the subspecific status was raised to specific status. Johannes Reinhardt (1854), a Danish naturalist, gave the North American (and East Asiatic) Red-necked Grebe a name in "Videnskabelige Meddelelser for Aaret 1853" (p. 76). Unlike earlier naturalists, he considered it to be a separate species and called it *Podiceps Holböllii*. The type locality is Julianehaab (Julianehåb) district, South Greenland. The name *Holböllii* refers to Carl Peter Holböll (Holboell, Holbøll), Danish zoologist and governor of South Greenland in 1820s (Terres 1980).

Spencer F. Baird *et al.* (1858, pp. 892-3: The Red-necked Grebe *Podiceps griseigena*, Gray) wrote: "The American bird has been separated from the Red-necked Grebe of Europe by Reinhardt, under the name of *holböllii*, principally on account of its being somewhat larger. On comparing specimens obtained here with European specimens of "*rubricollis*," ours appear somewhat larger, and generally with a longer bill; but in this family individuals vary much in size. ... Writers differ as to their being specifically distinct, and as I am not able to make out satisfactorily that they are so, shall for the present consider them the same."

John Gould (1873, Red-necked Grebe *Podiceps rubricollis* in Volume 5) stated: "In Greenland there is a bird of this form, which is so similar to the *Podiceps rubricollis* that they have been considered identical by some, while others have regarded it as distinct, and have assigned to it the specific designation of *P. Holböllii*. Among my MSS. I find a note to the following effect: - "American specimens agree with European, except in being somewhat larger." Dr. Baird, who calls it *Podiceps griseigena*, evidently considers the bird identical with ours. It is likely, however, the American and Greenland birds may be the same, and distinct from the true *P. rubricollis*, in which case the name of *P. Holböllii*, assigned to it by Reichenbach, should be retained."

Colymbus holboellii* and *Podiceps (Colymbus) griseigena holboellii

Although taxonomists and ornithologists after Reinhardt widely accepted the specific status for the North Pacific birds, many of them did not use the generic name *Podiceps* and named the species *Colymbus holboellii* (or *Colymbus holboelli*, or *Colymbus Holboellii*) (e.g. Baird *et al.* 1884, Forbush 1912, Bent 1919, Taverner 1928). In the 1930s the birds lost their specific status and were considered to be a subspecies of the Red-necked Grebe, at first with the name *Colymbus griseigena holboellii*, and from the 1950s on *Podiceps griseigena holboellii* Reinhardt.

Mlíkovský (2010b) asserts that, following the provisions of the ICZN (1999), the spelling *holboellii* is to be corrected to *holbollii*. In his opinion, frequently used *holboellii* is an incorrect subsequent spelling because Carl Peter Holböll was a Danish, not a German naturalist.

2.2.4 Synonyms

Besides the above mentioned synonyms such as *Podiceps rubricollis* and *P. ruficollis* (see 2.2.2 and 2.2.3), the Red-necked Grebe received more scientific specific names. These synonyms were created, for example, when the Red-necked Grebe was mistakenly redescribed by an author under the impression that he was dealing with a species without scientific name. Sometimes, an author was aware of an existing name, but simply neglected it. In addition to this, some authors confused the Red-necked Grebe with the Slavonian (Horned) Grebe. Other naturalists described grebes in breeding, winter and juvenile plumage as separate species, or considered a bird with a small variation as belonging to a new species. In such cases, the law of priority holds that the first specific name is the valid one and the new synonym is discarded. Well-known synonyms for the Red-necked Grebe were coined by Jacquin and Pallas.

Colymbus (Podiceps) subcristatus

In the presence of the Austrian naturalist Joseph Franz Edlen von Jacquin a Red-necked Grebe was shot in Sankt Georgen am Längsee in Austria on 21 April 1769. Later, one year after Boddaert (1783) coined the name *Colymbus grisegena*, Jacquin (1784, pp. 37-40)

described the bird as *Colymbus subcristatus* (Latin “sub” = somewhat, and “cristatus” = crested) (see Fig. 5). J F Gmelin (1789, p. 590) and G Cuvier (1817) adopted this name. J M Bechstein (1809) cited Jacquin (1784) but changed the generic name into *Podiceps* (*Podiceps subcristatus*). C J Temminck (1815, 1820) also called the species *Podiceps subcristatus* and added “Jacq. Vög. p. 37. t. 18. figure très exacte”. Other authors using the name *Podiceps subcristatus* were Kaup (1836), Thienemann *et al.* (1838), Keyserling and Blasius (1840) and crown prince Rudolf of Austria (von Oesterreich *et al.* 1879, p. 83).

Colymbus cucullatus and *Colymbus naevius*

The German zoologist Peter Simon Pallas became a professor at the St Petersburg Academy of Sciences in 1768. Between 1769 and 1774 he led an expedition to Siberia and between 1793 and 1794 a second one to southern Russia collecting natural history specimens. Pallas published many books, but his most important contribution to ornithology was the “Zoographia Rosso-Asiatica”, on which he laboured for 15 years. The year 1811 has been fixed as the publication date for Volumes 1 and 2 of that work (Zoological Citation Sources 2004). In Volume 2, Pallas (1811) distinguished two “species” of Red-necked Grebes. On page 355 he mentions *Colymbus cucullatus*



Fig. 5: “*Colymbus subcristatus* - der kastanienhälsige Taucher”, in Jacquin (1784).

(“In Rossiae et Sibiriae lacubus non infrequens, praesertim per campos Ischimenses et Barabenses copiosior”) (Latin “cucullatus” = hooded) and on page 356 *Colymbus naevius* (“In australibus circa Volgam observata, sed rarissima”) (Latin “naevius” = spotted).

Other Synonyms of Specific Names

Other synonyms are:

1. *Colymbus Parotis* Sparrman (1786, fasc. I. Plate 9 shows a standing immature Red-necked Grebe with head-stripes) (Greek “parotis” = situated near the ear)
2. *Colymbus Griseus* Coxe (1789, p. 355; Latin “griseus” = grey)
3. *Colymbus Longirostris* Bonnaterre 1790 (Latin “longus” = long, and “-rostris” = billed) (see Bonnaterre 1790, and Bonnaterre 1823, p. 54: “Le Grebe au long bec” - *C. Longirostris*)

Brehm (1831, pp. 956-8) distinguished three “species” of the Red-necked Grebe in Germany and its neighbouring countries (see 2.2.1):

1. *Podiceps rubricollis*, Lath. (“der dänische graukehlig Steissfuss” = the Danish Grey-throated Grebe) (German “Steiß” = vent or anus, and “Fuß” = foot)
2. *Podiceps subcristatus*, Bechst[ein] (“der kurz-schnäblige graukehlig Steissfuss” = the Short-billed Grey-throated Grebe)
3. *Podiceps canogularis*, Br[ehm] (Latin “canus” = grey, and “-gularis” = throated) (“der schmalschnäblige graukehlig Steissfuss” = the Slender-billed Grey-throated Grebe)

Hartert (1912-21) gives for the (East Asiatic-)North American Red-necked Grebe following synonyms:

1. *Podiceps cooperi* Lawrence 1858 (Cooper, American naturalist) (see *Podiceps cristatus*, Lath. in Baird, Cassin and Lawrence 1858, p. 893, and *Podiceps Cooperi* Lawrence in Coues 1862, p. 230)
2. *Podiceps affinis* Salvadori 1865 (Latin “affinis” = related, allied)

Synonyms of Generic Names

Synonyms of generic names were coined by Kaup (1829) and Oken (1839) and are cited by Coues (1862), Gray (1871), Gould (1873), Coues (1882), Seebohm (1885), Sharpe (1899), Thorburn (1917), Hartert (1912-21), Hellmayr and Conover (1948), Knopfli (1956), Vlug and Fjeldså (1990) and other ornithologists:

1. *Lophaithyia* (*Lophaethyia*) *griseigena* (Greek “lophos” = crest, and “aithuia”, a seabird mentioned by Aristotle, Hesychius, and other authors, Jobling 1995). Kaup (1829, p. 72) created the generic name *Lophaithyia*
2. *Pedetaithya* (*Pedeaithyia*, *Podetaithyia*) *subcristata* (*subcristatus*, *grise(i)gena*, *Holbölli*) (Latin “pes, pedis” = foot). Kaup (1829, p. 44) gave the Red-necked Grebe the generic name *Pedetaithya*
3. *Podicipes griseigena*. Oken (1839, column 673) coined the name *Podicipes*

3. General Description and Taxonomic Characters of Grebes and Detailed Treatise of the Plumages and Bare Parts of the Nominate Subspecies of the Red-necked Grebe

3.1 General Description and Taxonomic Characters of Grebes (see also 8.3 for characteristics distinguishing grebes from divers)

3.1.1 Size and Sexual Dimorphism, Especially in Red-necked Grebes

The species of grebes vary from c. 23 cm to c. 76 cm in extended length (from the tip of the bill to the tip of the tail) (Simmons 1985). In adult Red-necked Grebes (nominate *griseigena*) the extended length is 40-50 cm; their body-length is 22-30 cm and their wingspan 77-85 cm (Cramp *et al.* 1977), which means that *Podiceps griseigena* is a medium-large grebe.

Although there are no obvious structural differences between the sexes in Podicipedidae, males average somewhat larger than females and also have slightly longer and deeper bills. Kloskowski *et al.* (2006) discovered that males in Red-necked Grebes from Poland were significantly larger than females in all body measurements they used in their research. Owing to considerable overlap in measurements, however, the sexes cannot be accurately separated by biometrics at the population scale. Sexual dimorphism was most pronounced in bill length (see 7.3 for more details).

Like the sexes in other Podicipedidae, the Red-necked Grebe males and females are similar in plumage. However, the females are often a little duller (Cramp *et al.* 1977, Llimona and Del Hoyo 1992, Walser and Barthel 1994), which is especially visible in the cheek pattern of breeding Red-necked Grebes. There is one caveat: birds

are sensitive to UV (ultraviolet) light, and it is possible that there are differences between the male and female grebes in the degree of UV reflectance.

3.1.2 *The Diving Equipment of Grebes*

Red-necked Grebes are, as other Podicipedidae, almost exclusively aquatic and specialized foot-propelled diving birds. The feet are placed laterally at the rear end of the body, where they can be rotated freely. The skeleton of grebes is dense, which means that they sit low on the water. However, in contrast to the skeleton of divers which almost totally lacks pneumatization, the skeleton of grebes shows pneumatization of the long appendicular bones and some parts of the skull (Llimona and Del Hoyo 1992, Fjelds  2004).

The streamlined body is well suited for coping with the upward pressure of the water and its resistance to rapid movement. The front of the body is laterally compressed and rather pointed, so it easily penetrates the water (Llimona and Del Hoyo 1992). The lateral position of the legs, and a strong development of the hind limb musculature, adds much to the width of the posterior body resulting in streamlining combined with stabilizing breadth (Fjelds  2004).

The joints of the tibiotarsus and toes are extremely flexible (see 3.1.8). Flexibility, together with the position of the lobed feet far aft, confers a large manoeuvrability while swimming under water. Although several other diving birds can achieve higher top speeds under water, they can scarcely measure up to the grebes when it comes to manoeuvrability. However, grebes are clumsy on land (Storer 1960, Fjelds  2004).

3.1.3 *Plumages and Their Functions*

The study of the arrangement of (contour) feather tracts (pterylae) and (contour) featherless tracts (apteria) such as the dorsal and ventral apteria has considerable potential for systematic studies. So, the dorsal apterium in grebes is limited to the back, and in divers *Gavia* to the neck (Stolpe 1935). The feathering of the under parts of grebes is continuous, except for the ventral apterium, which is narrow anteriorly but broadening on the belly. Mature down is not only present on the pterylae but also on the apteria (Palmer 1962).

Another characteristic of taxonomic value is that the feathers of grebes have an aftershaft ("double feather"). Its shaft is short, and the barbs spread out (Chandler 1916).

The first plumage of natal down (neoptiles) in grebes is short but dense, each down comprising a rosette of c. 12 barbs with barbules to the tip (Fjelds  2004). This plumage has a distinctive design of clearly marked dark bands, particularly on the head and neck, in all genera except *Aechmophorus* (Llimona and Del Hoyo 1992). The pattern may have a camouflage (somatolytic) effect, but it may also provide visual signals, for instance by emphasizing the patches of bare facial skin, which represent important care-soliciting signals (Fjelds  2004).

The adult grebes' plumage is extremely waterproof and offers the skin good protection against water and the cold. It is also very thick, and each bird has from c. 14,000 to more than 20,000 feathers (Campbell and Lack 1985, Piersma 1988a, Llimona and Del Hoyo 1992, Fjelds  2004). The subcutaneous fat deposits of grebes are probably too thin (0.64 cm in *Podiceps cristatus*) to act as an effective insulator and the fat layer might be more significant as an energy resource during periods of food deprivation (De Vries and Van Eerden 1995). As a result only the feathers are effective in reducing thermoregulatory costs.

The ventral plumage of grebes is particularly dense, smooth, satiny and fur-like. Chandler (1916) describes the structure of this plumage (of *Aechmophorus*) in detail. The feathers are inserted perpendicular to the contour of the body, with the terminal portion sharply turned to lie flat on the contour, this arrangement resulting in an unusually dense plumage. The feathers are peculiar in having the barbs (rami) set conspicuously wide apart on the shaft. The barbules (radii) are of a very unusual type, flattened for about half their length and then filamentous, the flattened portion being spirally twisted. Only every second, sometimes every third, barbule reaches across to the neighbouring barb, the intervening ones being twisted so as to lie nearly parallel to the barb and ventral to it. On the outer portion of the more distal barbs this peculiar structure is lost and the barbules become elongate, slightly flattened, and less twisted, and develop on their distal ends a double series of barbicels (hamuli), the ventral ones are curved and hook-like. At the same time the barbs and barbules become ribbed in such a way as to become strongly reflex-

tive, and they give a shiny, silky appearance. The result of this peculiar structure is a very much curved, loose, open vaned-feather, which added together gives the thick silky ventral plumage so characteristic of grebes (Chandler 1916, p. 301).

The plumage is particularly fluffy on the sides, flanks, and rear of the body, where the outer three-quarters of each feather are modified as described above. The modified outer portion of the plumage becomes wet through absorption of water within the coils of parallel barbules. This increases the specific gravity when the bird is submerged and reduces turbulent flow and thereby reduces the drag and increases the diving ability. The insulating ability is maintained as the surface tension of water trapped in these barbule coils may form a skin-like barrier preventing penetration of water to the air space beneath (Fjeldså 2004).

The flight-feathers (primaries and secondaries) are rather short and curved and, when folded, fit closely to the body, hidden under the contour plumage (Cramp *et al.* 1977, Johnsgard 1987). In flight, the wing-beats are rapid because of the high loading (Simmons 1985).

Grebes are usually diastataxic (i. e. the fifth secondary is absent) and have 17-22 secondaries (*Podiceps grisegena* 20, *Podiceps cristatus* 22) (Snow 1967). The 12 primaries are numbered from the carpal joint (“wrist”) outwards (descendantly), and numbers 10 and 11 are the outermost functional and longest ones. In the nominate subspecies of the Red-necked Grebe primary 10, rarely primary 11, is the longest, primary 11 is often equal or 2 mm shorter, primary 9 is 1-4, primary 8 9-13, primary 7 15-20, primary 6 23-29 and primary 1 56-67 mm shorter. Primary 12 is minute and hidden by the coverts. Primaries 9-11 in *P. grisegena* have emarginated inner, primary 9 and 10 also emarginated outer webs; the outer web of primary 11 is narrow (Cramp *et al.* 1977). Seven of the 12 primaries are carpometacarpal (see 3.1.7). The upper medial wing coverts of grebes are variably enlarged and partially cover the innermost secondaries, presumably providing additional structural support (Johnsgard 1987).

The tail is a small tuft of six feathers of a rather decomposed, semiplumous kind (intermediate between contour feather and down), of which only the central feathers are distinctly longer than the surrounding body plumage. Pycraft (1907) stated that in the Red-

necked Grebe the vanes of the tail-feathers are quite degenerate, being made up of a series of long, weak barbs, which have quite lost the power of interlocking. The function of the tail may have been reduced from one of steering to one of signalling, as indicated by the bright colour of the under-tail coverts and the habit of cocking the tail in certain situations. Fjeldså (2004) wrote: “Nobody seems to have speculated over the reasons for the loss of a typical tail in grebes. Diving birds have short tails, overall, except for cormorants (Phalacrocoracidae) and ruddy ducks (Oxyurini), which can use their tails as hydrofoils when diving. The latter function is unnecessary in grebes because of the way in which the feet work under water. The feet trail behind the body in flight, like in rails and various wading birds, and could possibly play the role as “tail” during aerial manoeuvres.”

Grebes undergo a marked seasonal change in plumages. In breeding plumages they develop special colours, markings or plumes above, while outside the breeding season their coloration is drab.

3.1.4 Head and Skull

The skull of grebes is rather small, and schizognathous (the maxillopalatines do not meet each other or the vomers in the midline, so that there is an extensive longitudinal cleft in the bony palate), a palatal condition which may reflect phylogeny (Sibley and Ahlquist 1990). A basipterygoid process is absent in grebes (Palmer 1962) (a number of other bird taxa have basipterygoid processes, which form a short region of contact between the basitemporal region of the skull and the pterygoids). Furthermore, it is noticeable that the lachrymal (lacrymal) bones are never fused to the nasal bones (Soldaat 2004), that a zygomatic process is present (a projection of the temporal bone) (Wiki 2004) and that occipital fontanelles (fonticuli) are lacking in adult grebes (Palmer 1962, Mayr 2004).

Supraorbital grooves in grebes are hardly visible or absent, which is related to the weak development and position of the supraorbital nasal glands (“salt glands”) (Stolpe 1935, Palmer 1962, Fjeldså 2004, Soldaat 2004). The olfactory bulbs (lobes), which are attached to the anterior poles of the cerebral hemispheres (fore-brain), are large in grebes (Fjeldså 2004), which suggests that they have a well developed sense of smell.

3.1.5 Bill

The bills of grebes are highly variable: from long, stout, and diver-like, long and pointed, to short and sturdy (Cramp *et al.* 1977). Red-necked Grebes have a pointed, straight, rather stout and relatively long bill, which has in the males of the nominate subspecies *grisegena* a length of *c.* 40 mm and in the females *c.* 37 mm (from the implantation of the feathers to the tip of the upper mandible) (Cramp *et al.* 1977).

The nares (nostrils) in grebes are holorrhinal, i.e. the posterior margin of the *bony* aperture of the nostrils is rounded (Cracraft 1982, Campbell and Lack 1985, Sibley and Ahlquist 1990). The nares in grebes are pervious, i.e. with an incomplete nasal septum; hence the opening extends through from side to side (Sibley and Ahlquist 1990, Payne 2000). The head feathers do not extend to the external nares, which are narrow slits in the rhamphoteca (outer covering of the bill) (Cramp *et al.* 1977, Johnsgard 1987).

The bills are prokinetic, a form of upper jaw mobility in which rotation takes place about a region of flexible bone at the junction of upper jaw and neurocranium (Campbell and Lack 1985, Fjelds  2004). The hind process of the lower mandible in grebes is short or absent (Stolpe 1935, Sibley and Ahlquist 1990).

The tongues are small with a single caudal row of spinous processes, which is one of the characteristics distinguishing grebes from divers (Sibley and Ahlquist 1990, Wiki 2004).

3.1.6 Trunk and Neck: Skeleton, Musculature, Carotid, Uropygial Gland, Stomach Morphology, and Caeca

The trunk of *Podiceps grisegena* is rather long and slender compared with small grebes. But compared with other diving birds, the body of Red-necked Grebes and other Podicipedidae is relatively short. This may be related to the rather small, narrow and curved wings, which can be easily accommodated when tucked into the plumage at rest (Fjelds  2004).

Neck

The flexible and slender neck of the Podicipedidae is much longer than the length of the body skeleton; it has 17-21 cervical vertebrae (in the Red-necked Grebe we find 19, and in the divers only 14 or 15 cervical vertebrae)

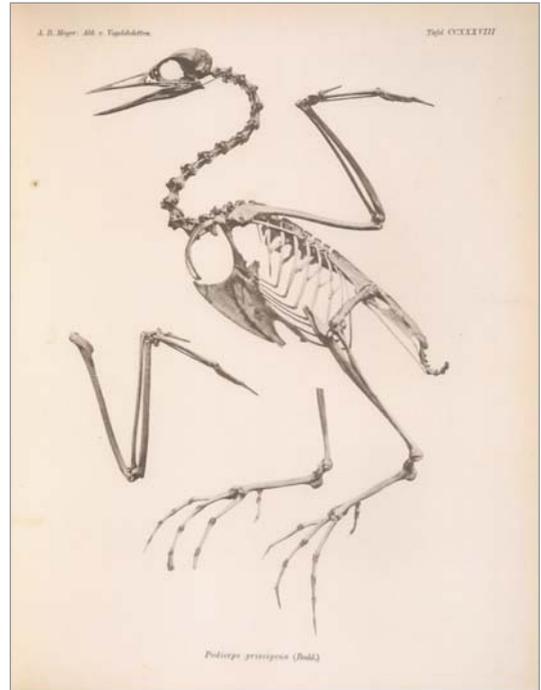


Fig. 6: Skeleton of a Red-necked Grebe (nominate subspecies), in Meyer (1889-97).

Fig. 6: Skelett eines Rothalst chers (Nominatform), in Meyer (1889-97).

(Meyer 1889-97, Stolpe 1935) (see Fig. 6). The upper neck has a very tight-fitting skin to the great irritation of taxidermists, who have to cut up the neck skin when preparing specimens (Fjelds  2004).

In grebes, only the left carotid artery is present, a characteristic that has been used in taxonomy (the bicarotid condition is the most prevalent in birds) (Stolpe 1935, Wiki 2004).

Pectoral Girdle and Sternum

The coracoids, paired bones of the pectoral girdle, are long (Palmer 1962). The mean total length of the coracoid (distance from the acrocoracoid to the apex lateralis) in *Podiceps grisegena grisegena* males (*n* = 18) is 40.7 mm and in females (*n* = 22) 38.9 mm (Bocheński 1994). The procoracoid is vestigial and the ventral and dorsal lips of the coracoid groove are strongly developed (Fjelds  2004, Mayr 2004).

The sternum (breast bone) of the Podicipedidae is short compared with other diving birds and has one median

and one pair of lateral notches behind (Palmer 1962, Soldaat 2004). The mean sternal length (the longest mid-line measurement, from the bottom of the notch in the metasternum to the mid-point of the labium) in *Podiceps grisegena grisegena* males ($n = 17$) is 52.6 mm and in females ($n = 22$) 50.1 mm (Bocheński 1994). The sternum in grebes lacks a robust spina externa rostri (Wiki 2004). The notched metasternum does not project beyond the level of the free ends of the posterior lateral processes (Fjeldså 2004).

The sterno-tracheal musculature of grebes is asymmetrical, which is another of the many anatomical differences between grebes and divers (Stolpe 1935, Sibley and Ahlquist 1990).

The majority of grebes maintain the necessary architecture and minimum of pectoral (flight) musculature for direct, rapid flight. In Great Crested Grebes, for example, the *pectoralis major* muscle constitutes only 4 percent of the total body weight (in alcid 7-9 percent) (Kartashev 1960, cited in Johnsgard 1987).

Dorsal Vertebrae

In most adult grebes the spinous processes of 4-5 dorsal (thoracic) vertebrae are fused into a strong, vertical ridge of bone (notarium) to which the large back muscles attach (Stolpe 1935, Storer 1982, Mayr 2004). The majority of Red-necked Grebes have 4 fused and 2 unfused thoracic vertebrae. In the Podicipedidae the weight of the hind limbs and their musculature may have been a factor in the development of the notarium (Storer 1982).

Pelvic Girdle

Although the pelvis and synsacrum of all grebes are laterally compressed (Palmer 1962, Cracraft 1982), they show a considerable variation in form. The small grebes have a quite short, broad pelvis, but the Red-necked Grebe and the other longer and slender grebes have a narrower one. The mean total length of the synsacrum in *Podiceps grisegena grisegena* males ($n = 16$) is 72.0 mm and in females ($n = 21$) 68.9 mm; the mean pelvis width (distance from the right to the left processus praepubicus) in males ($n = 17$) is 17.7 and in females ($n = 21$) 17.6 mm (Bocheński 1994). In the synsacrum 17-18 vertebrae are ankylosed (fused) (Mayr 2004, Wiki 2004).

In grebes the pelvis has a very long post-acetabular part (part of the ilium after the hip joint socket). It is essentially as long as that of *Gavia*, suggesting a similarly im-

portant muscular role for the leg muscles originating on the posterior pelvis, while the pre-acetabular pelvic length in the Podicipedidae is substantially longer than in divers (Johnsgard 1987). The post-ilia (back part of the ilia) meet in the mid-dorsal line above the neural spines of the synsacrum (Cracraft 1982, Fjeldså 2004).

Pelvic-hind Limb Muscles

A number of pelvic-hind limb muscles of grebes and other bird groups have been used in taxonomy. Anatomists have set up a formula in which the presence of (components of) these muscles was denoted using letters as symbols. In general, the presence of "formula" muscles is regarded as a primitive state, and their loss as derived; large complements occur among groups regarded as phylogenetically old, while groups of more recent origin mostly show a reduced complement (Campbell and Lack 1985). ACEFMNXY is probably typical of most passerines, while drastic reduction occurs in Podicipedidae. Grebes, which have specialized pelvic muscles, have the formula BCX (and flexor tendons types 2 and 4) (Hudson 1937, Sibley and Ahlquist 1990). This means that they possess *Musculus iliofemoralis*, *M. iliotrochantericus medius* (*M. ilio-trochantericus*) and *M. flexor cruris lateralis, pars pelvica* (*semitendinosus*). Absent in the Podicipedidae are *Musculus ambiens*, *M. femoro-caudalis* (*M. caudofemoralis*), *Fibularis* (*Peroneus*) *brevis* and the accessory *semitendinosus* (*M. flexor cruris lateralis, pars accessoria*) (Hudson 1937, Sibley and Ahlquist 1990, Mayr 2004).

The *Musculus sartorius* (*M. ilio-tibialis medialis*) in grebes (and in divers) has an isolated insertion on the medial side of the head of the tibia (Sibley and Ahlquist 1990). The described muscle is an offshoot of the reptilian *ilio-tibialis* and not homologous with the mammalian *sartorius* (Thomson 1964) (other hind limb muscles and the deep flexor tendons are treated in 3.1.8).

Tail

The caudal (tail) vertebrae are vestigial and the pygostyle (the fusion of the final few caudal vertebrae) is reduced to a small rod. The corpus of the pygostyle is perforated caudoventrally (Wiki 2004).

Uropygial Gland

Podicipedidae have a well developed tufted and bilobed uropygial gland (oil gland) (Simmons 1985, Sibley and Ahlquist 1990). Besides making the feathers flexible, the secretion seems to play an important role in plumage

hygiene, since some of its constituents possess bacteriostatic and fungistatic properties (inhibiting the multiplying of bacteria and the growth of fungi) (Campbell and Lack 1985). Grebes are the only avian group so far investigated where the uropygial gland secretions contain paraffin, even in high concentrations (50–60%). The specific function of paraffin in grebe preen oils has not been studied, but waterproofing would seem the most plausible function (Fjeldså 2004).

Stomach Morphology

Jehl (2017) described the stomach morphology of Podicipedidae. The stomach of a grebe is a large, tripartite organ. The anterior section is a thick-walled and highly glandular proventriculus, which does not hold food but generates secretions that initiate its breakdown. The proventriculus is separated from the larger but thinner-walled gizzard by a narrow constriction (isthmus gastricus). The koilin lining of the gizzard is largely undifferentiated, as is typical in gizzards that serve primarily as a holding chamber. Food is churned and liquified in the gizzard before being refluxed through a small slit into a small accessory chamber, the pyloric pouch (= pyloric stomach), before entering the duodenum. A pyloric pouch occurs in a variety of birds (e.g. flamingos, herons, cormorants) and functions to prolong the duration of digestion. The pouch in grebes, however, is small and never holds food. A large proventriculus, relatively thin-walled gizzard with an undifferentiated lining, pyloric pouch, and absence of grit show that the grebe stomach is modified for chemical digestion (Jehl 2017).

Caeca

Caeca are appendices of the intestinal tract, blind diverticula like the human appendix. In some taxonomic groups they are absent or there is only a single caecum. Grebes possess paired caeca, but they are short.

3.1.7 Wing Skeleton and Musculature

The primaries are supported by a relatively thin and (compared with divers) relatively short carpometacarpus-phalanges component (seven of the 12 primaries are carpometacarpal). The secondaries are supported by a long and fairly weak ulna (Palmer 1962, Johnsgard 1987). The mean total length of the ulna (distance from the olecranon to the crest of the condylus medialis) in *Podiceps grisegena grisegena* ($n = 47$) is 89.1 mm (Bocheński 1994). The humerus of grebes has a low deltoid (triangular) crest, like a long ridge (Fjeldså 2004).

The mean total length of the humerus (distance from the caput humeri to the condylus radialis) in the nominate subspecies of the Red-necked Grebe ($n = 47$) is 98.0 mm (Bocheński 1994).

The pectoral musculature of grebes as already stated, is relatively poor developed (see 3.1.6).

3.1.8 Legs and Toes

In all grebes, the legs have a changed position – compared with other birds – from pointing down to lying in a plane parallel with the surface of the water. During swimming, the femora stand right out to the side, in an almost fixed position (Fjeldså 2004). The femora and the tibiotarsi (“tibias”) lie nearly in the frontal plane passing through the acetabula (hip joint sockets), and all but the distal ends of the tibiotarsi lie within the main body mass. The femur is short, stout and distinctly curved and has a double, hinge-like articulation with the acetabulum and the anti-trochanter (Storer 1960). The mean total length of the femur (distance from the trochanter major to the condylus lateralis) in males of *Podiceps grisegena grisegena* ($n = 18$) is 42.6 mm and in females ($n = 21$) 42.0 mm; the mean total length of the tibiotarsus (maximum distance from the tip of the processus cnemialis to the condylus distalis lateralis) is 112.4 mm in males ($n = 15$) and 108.1 mm in females ($n = 19$) (Bocheński 1994). The tibial bridge is tendinous (Fjeldså 2004).

The patella (“kneecap”) in grebes is large, pyramidal, vertically elongated, with a loose terminal sesamoid, and positioned behind a long bony extension on the tibiotarsus. The patella and this extension of the tibia together form the large cnemial crest to which the powerful extensor muscles of the leg are attached (divers have no patella and in these birds the cnemial crest is formed by an enormous extension of the tibia alone) (Stolpe 1935, Storer 1960, Sibley and Ahlquist 1990, Feduccia 1999, Fjeldså 2004).

The feet are large and used for propulsion and steering. Because of the position of the feet far aft, coupled with a considerable ability to rotate the tibiotarsus, grebes can move their feet above, below, or on a level with the body when under water. Hence steering can be accomplished on the propulsive strokes and thus with a minimal loss of energy (Storer 1960).

The hypotarsus in grebes is complex with canals and grooves and possesses medial and lateral cristae (ridges or crests), which surround the flexor tendon canal (Wiki 2004).

The tarsometatarsus (“tarsus”) is markedly flattened laterally and has two serrated ridges along the rear edge (except in young birds), formed by projecting knobs or spines on a double row of small scutes along this edge of the tarsus. These spines may possibly play a role in cutting plant stalks when the grebe has to work its way through dense masses of submergent water-weeds (Fjeldså 2004). The mean total length of the tarsometatarsus (distance between the medial edge of the facies articularis medialis and the trochlea metatarsi III or IV) in males of *Podiceps grisegena* ($n = 15$) is 56.8 mm and in females ($n = 18$) 54.8 mm (Bocheński 1994).

Probably the most peculiar and unique structures of grebes are their broadly lobed toes (see Fig. 7). The three front toes have only a rather small connecting basal membrane (web), and instead, each toe has at its distal end a very large, wide asymmetric and stiff (not soft and pliable) swimming lobe, of which the medial (inner) part is much broader than the lateral (outer) part (Stolpe 1935, Fjeldså 2004).

Because of a special construction of the proximal hinge joints of the toes, the toes rotate *c.* 90° or more (up to 120°) as they are spread and stretched. They therefore form a large broad and stable paddle when the foot is pushed back. During the recovery (forwards) stroke, grebes rotate the toes while flexing them so that the

larger medial lobes trail and the smaller lateral lobes fold against the underside of the toe (divers flex the toes without rotating them). By this construction (together with the very strong flattening of the tarsi and bony elements of the toes), maximum power production can be combined with minimal drag during the return stroke, analogous with the rotation of the primary flight feathers of large birds during flight (Stolpe 1935, Fjeldså 2004) (see also 15.1.3).

The hind toe (first toe or hallux) is raised above the level of the other toes and is vestigial (Simmons 1985). The outer toe of *Podiceps g. grisegena* is the longest one and *c.* 108% of the length of the middle toe (but the lobes of the middle toe are somewhat broader, Hennicke 1903); the inner toe is *c.* 83% and the hind toe only *c.* 25% of the length of the middle one (Cramp *et al.* 1977). The skeleton of a Red-necked Grebe, measured by Meyer (1889-97), showed the following toe (digit) lengths: digit I 16 mm, digit II 52 mm, digit III 61 mm and digit IV 67 mm. The nails of the Podicipedidae are wide and flat, pectinated on the middle toe (Simmons 1985).

For a description and measurements of the skeleton of *Podiceps grisegena* see Meyer (1889-97), Volume 2, pp. 118-9 and plate CCXXXVIII (see Fig. 6), and Bocheński (1994).

Hind Limb Musculature

In grebes the muscles of the lower extremities are highly developed and may compose about 15-19 percent of the weight (Hartman 1961, *cited in* Johnsgard 1987). The



Fig. 7: Toes of a juvenile Red-necked Grebe. Photo: A Konter (Luxembourg)

Fig. 7: Zehen eines juvenilen Rothalstauchers.

pelvic-hind limb muscles have the formula BCX (see 3.1.6 for details).

The *pars interna* of *Musculus gastrocnemius* is two-headed (Sibley and Ahlquist 1990, Wiki 2004). The origin of this muscle, the principal muscle in the power stroke when swimming, is switched from the femur to the cnemial crest (Fjeldså 2004).

Two characters of taxonomic value are that the *Musculus fibularis longus* does not branch to *Musculus flexor perforatus digiti III*, and that the tendon of *Musculus flexor digitorum longus* is enclosed within an osseous canal of the hypotarsus (Mayr 2004, Wiki 2004).

Grebes show deep flexor tendons type 4 of Gadow (and of George and Berger), which means that the entire tendon of *Musculus flexor hallucis longus* fuses with the tendon of *Musculus flexor digitorum longus*. The combined tendon trifurcates below and sends branches to digits II, III, and IV; no branch goes to the hallux. This pattern is not only found in tridactyl birds, but also in those in

which the hallux is small (Hudson 1937, Sibley and Ahlquist 1990).

3.2 Plumages and Bare Parts in the Nominate Subspecies of the Red-necked Grebe (see 4.3, chapter 7 and 8.1 for a description of the plumages, bare parts and other characteristics of *Podiceps grisegena holboellii*; see illustrations of both subspecies in Fjeldså 2004, plates 5, 6, 7 and 8)

3.2.1 Adult Breeding

In this chapter and in 3.2.2 the described adult Red-necked Grebes *Podiceps grisegena grisegena* are old, i.e. in their third calendar year or older (see Fig. 8). Younger birds in their first winter and first summer plumage are distinguishable from older birds by some characteristics and are discussed in 3.2.5 and 3.2.6.

Adults already occasionally show their breeding (nuptial) plumage at a very advanced stage around the turn of the year, and almost all of them possess a complete breeding plumage in March (Walser and Barthel 1994).



Fig. 8: Adult Red-necked Grebe in breeding plumage. Photo: H Niesen (Netherlands)

Fig. 8: Adulter Rothalstaucher im Brutkleid.



Fig. 9: Head of an adult Red-necked Grebe in breeding plumage. Photo: H Niesen (Netherlands)

Fig. 9: Kopf eines adulten Rot-halstauchers im Brutkleid.

Head Plumage (see Fig. 9)

The glossy deep black crown (down to the eye level) ends in a double black tuft (crest) of elongated feathers, which may be spread as a broad occipital fan. The crown may show a metallic green sheen. The chin, throat and the sides of the head (cheeks) are ashy or mouse grey, conspicuously bordered with white. The grey feathers of the sides of the head may almost touch at the occiput (T Runge).

Wobus (1964) and other authors used differences in the cheek pattern (the extent, demarcation and intensity of the grey colouring) of the partners of a breeding pair to distinguish them in the field. When the feathers of the crests, cheeks and throat are ruffled they give the head a large and thick appearance (Hennicke 1903; see photographs in Hammond and Everett 1980, p. 31, and in Simmons 1989, p. 5) (see Fig. 70, 78 and 81).

The classical breeding plumage of the Red-necked Grebe shows an additional subtype. After a partial summer moult, in which a new feather generation is formed, the cheeks become more whitish with dark smudges and the white demarcations of the throat and cheeks disappear (eclipse plumage). The bird looks dull and is not as beautiful as at the beginning of the breeding season (Fjeldså 2004; T Runge). Piersma (1988a) described the eclipse plumage in the Great Crested Grebe as a peculiar “autumnal head plumage” which is showed during and after the wing moult. In this species

it looks like a pale adult breeding plumage with shorter crest and tippets.

Neck and Chest Plumage

The front and sides of the neck are chestnut (deep reddish-brown, burnt sienna); the chest (part of the bird between fore-neck and breast) is paler with a bronze gloss. The neck has a blackish dorsal line (Cramp *et al.* 1977, Fjeldså 2004). The feathers of the neck can be spread out, so that the neck seems heavy and thick (see photographs in Hammond and Everett 1980, p. 31, and in Simmons 1989, p.5) (see Fig. 72).

Body Plumage

The upperparts of the body are dark brown or sooty black with slightly paler (brown-grey) feather margins. The sides and flanks are pale grey with very little buff (the sides of the breast have a variable amount of rufous), and are strongly suffused with sooty feather-tips. The belly is silky white, often mottled dark (grey) (see Fig. 10 and 11). The vent is pale grey. The tail-tuft consists of downy, black feathers, and is partly white below (Cramp *et al.* 1977, Fjeldså 2004).

Wing Plumage

The brown-grey primaries have black shafts. They contrast sharply with the white of many secondaries (first wing-patch) and the leading edge of the inner wing (marginal and lesser upper wing-coverts) (second wing-



Fig. 10: Flying adult Red-necked Grebe in breeding plumage with a silky white belly. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 10: Fliegender adulter Rothalstaucher im Brutkleid mit seidenartigem, weißem Bauch.



Fig. 11: Adult Red-necked Grebe in breeding plumage, settling down on the eggs. The belly is mottled dark. Photo: T Runge (Schleswig-Holstein)

Fig. 11: Adulter Rothalstaucher im Brutkleid, sich auf den Eiern niederlassend. Der Bauch ist dunkel gesprenkelt.

patch). The two white wing-patches are not connected (see Fig. 42).

The colour of the outermost secondary is similar to that of the primaries. The next 2 or 3 secondaries are increasingly spotted white and are followed by *c.* 10 which are mainly white with basally black shafts. The following *c.* 3 secondaries are brown-grey with white or rufous at the base. The innermost secondaries are brown-black like the mantle.

The upper wing-coverts are brown-grey, near the body brown-black, but the marginal upper wing-coverts and part of the lesser upper wing-coverts are white. The under wing-coverts and axillaries are white (Cramp *et al.* 1977).

Bill

The bill is black with a bright or deep yellow patch at the base of the upper and lower mandible (see Fig. 9). This patch becomes paler and more extensive after midsummer (from July onwards), with yellow reaching the tip especially on the lower mandible (Walser and Barthel 1994) (see Fig. 102).

Lores

Red-necked Grebes have a very narrow strip of skin on the lores (from the upper mandible to the eye) (Henricke 1903). This bare skin is present all year round.

Eye

The eye in grebes and other birds is very large and only the dark pupil and surrounding iris are visible; much more of the eyeball lies under the skin. The iris in the adult Red-necked Grebes (in all seasons) is completely warm or dark brown, not red as is often stated. The iris usually has a light-coloured outer ring of yellowish or gold, to be sure, but this outer ring is normally concealed and therefore invisible. Adult birds usually have an inconspicuous eyelid-ring, but in a few birds the eyelid is somewhat lighter coloured and rarely it even may have a yellowish colouring at some places, so that it seems as if the adult birds possess an iris ring. In fact, only young birds have a visible yellow iris ring (see 3.2.4, 3.2.5 and 3.2.6) (Brooks 1932, Cramp *et al.* 1977, Walser and Barthel 1994).

Feet and Toes

The feet are black to dark grey-green on the outside and underside. The inside and upper side of the toes are pale



Fig. 12: Adult Red-necked Grebe in non-breeding plumage. Photo: H Niesen (Netherlands)

Fig. 12: *Adulter Rothalstaucher im Winterkleid.*

yellow to greenish-grey, and are sometimes mottled brown (Cramp *et al.* 1977). There are no descriptions of seasonal changes in the colours of the feet and toes.

3.2.2 Adult Non-breeding

Adult Red-necked Grebes show their complete non-breeding (winter) plumage only a relatively short period, namely from mid-October to the end of December (Walser and Barthel 1994) (see Fig. 12).

Head Plumage

The bird in winter has a dark grey crown extending to the eye level. The sides of the head are white or whitish and behind the eye is a dusky (or mouse-grey) patch (ear-coverts). The crown and the cheeks are less contrasting than they are in the breeding plumage. The whitish or pale buff throat and the light (white or whitish) crescent extending upwards behind the ear-coverts contrast diffusely against the dusky ear-coverts (Cramp *et al.* 1977, Svensson *et al.* 2000).

Neck Plumage

The neck is variable, especially the fore-neck which varies from pale grey to nearly white; the sides of the

neck are pale grey. A faint shade of reddish-brown or rust-colour may be present. The neck contrasts more or less with the above-mentioned light crescent and whitish throat. The hind-neck is dark grey-black, blending into the paler sides (Cramp *et al.* 1977, Walser and Barthel 1994, Stout and Nuechterlein 1999, Svensson *et al.* 2000).

Body Plumage

The upper-parts of the bird are dark grey, but the feathers of the mantle and the scapulars have paler edges. The underside of the trunk is white. The chest, sides and flanks and sometimes the breast and belly are mottled grey. The chest (part of the bird between fore-neck and breast) and breast are often the whitest parts. The vent is washed pale grey (Cramp *et al.* 1977, Svensson *et al.* 2000).

Wing Plumage

The wing of the non-breeding adult is similar to that of the breeding adult, but the innermost secondaries and their coverts are greyer (Cramp *et al.* 1977).

Bill

The bill is paler than in the breeding adult, blue-grey, greyish black or brownish black at the tip, and pale yellow.

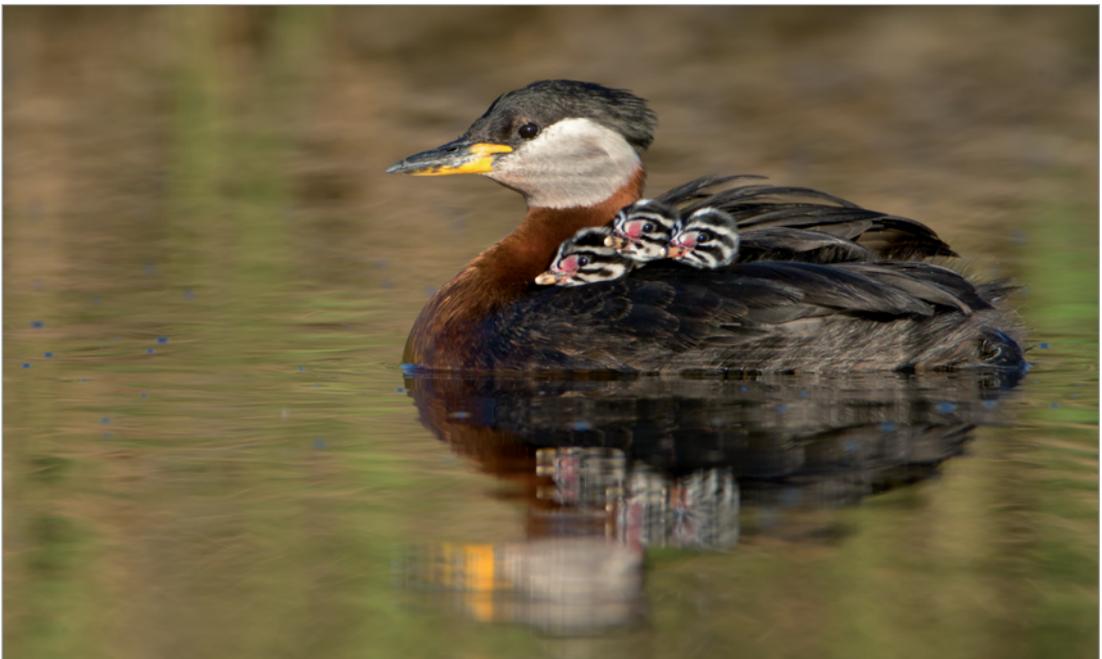


Fig. 13: Adult Red-necked Grebe with three downy young. Photo: T Runge (Schleswig-Holstein)

Fig. 13: Adlerer Rothalstaucher mit drei Dunenjungem.

low at the base. The dirty yellow may reach the tip especially on the lower mandible (Cramp *et al.* 1977, Walser and Barthel 1994).

Eye

The iris in the adult non-breeding birds is warm or dark brown as in the breeding birds.

3.2.3 Downy Young (Hatchlings)

(based mainly on Storer 1967, Fjeldså 1977b, Stout and Nuechterlein 1999, Harrison and Castell 2002) (see Fig. 13, 100, 101 and 102).

The newly-hatched young of Red-necked Grebes average 98 mm in total length, and weigh 17-23 g (Fjeldså 1977b). The small young are covered with soft, dense, but very short, straight down. They have a striped pattern.

Down of the Head

The head has a pattern of white, buffish white or creamy white stripes, alternated with bold, black bands and blotches. This pattern is arranged almost as in Slavonian and Great Crested Grebes. As in the other *Podiceps* species, the pattern varies among individuals, and is possibly used by the parents to identify the young.

The crown is largely black and is characterized by a central white crown-stripe behind the bare crown-spot. The rear part of the central white crown-stripe lies between the ends of the white neck stripes which form the borders of the dark mid-dorsal stripe, and the front part of the central white crown-stripe lies anterior to the ends of these white neck stripes. The central white crown-stripe is narrow especially at the rear. The two bordering dark crown-stripes are much wider. Next to these wide dark crown-stripes are two lateral white stripes which originate on the neck, run forward, diverging as they reach the crown and then converging to join on the forehead. Next is a black eye-stripe which runs from above the bare lores and through the eye, bending sharply down on the cheek (often after an interruption) and running to the throat. A short, thick, black stripe runs from behind the bill onto the cheek. A smaller, irregular cheek-stripe originates behind the base of the lower mandible. The chin and throat are white, sometimes with irregular stripes and spots (see illustrations in Harrison and Castell 2002, p. 38, and in Fjeldså 2004, plate 8).

Down of the Neck

The fairly long, sinuous neck has creamy white or buffish white stripes, alternated with seven dark stripes, one mid-dorsal and three pairs of lateral stripes. The black lateral stripes may be broken about halfway. The most ventral pair of the dark lateral stripes is the most variable: they may fuse into a single mid-ventral stripe anteriorly (near the lower throat), they may meet in a V, they may be joined by a crossbar, or they may not meet (see illustration in Fjeldså 2004, plate 8).

Down of the Body and Wings

The basic pattern on the body consists of nine wide, dark stripes on the back and sides. Of these, the central one is the narrowest. These dark stripes are divided by very faint, narrow, pale brownish (or deep grey) lines that fade as the chick grows. The stripes on the flanks are broken up into many spots. The down on the wings is nearly black, with some lighter splotches. The under parts are white (see illustrations in Fjeldså 1977b, p. 199, and in Fjeldså 2004, plate 8).

Bare Parts

The *grisegena* chicks have bare skin on the lores, and a bare spot on the anterior crown. The last mentioned is vestigial. These naked skin patches flush at intervals from pale flesh-coloured (or pink) to scarlet (or red).

The conical bill is buffish-pink or pink with a white tip and possesses two vertical blackish crossbars around both mandibles, one near the base and one near the tip. The large whitish egg tooth near the tip of the upper mandible is retained for a long time and gradually disappears during the first two weeks rather than breaking off. The gape is red.

The iris is brown or olive-brown.

The tarsi and toes are medium-grey to dark grey or black. There is a variable amount of pale-yellow to greenish-grey or olive-grey splotching, especially on the inside and the upper side of the toes. A correlation between the amount and distribution of colour and age, if any, is uncertain.

3.2.4 Juvenile

The juvenile Red-necked Grebes have a plumage that bears a remote resemblance to the breeding plumage (see



Fig. 14: Juvenile Red-necked Grebe. Photo: T Runge (Schleswig-Holstein)

Fig. 14: Jugendkleid eines Rothalstauchers.



Fig. 15: Head and neck of a juvenile Red-necked Grebe. Photo: A Konter (Luxembourg)

Fig. 15: Kopf und Hals eines juvenilen Rothalstauchers.

Fig. 14). The natal down adheres to the feather-tips and is lost by abrasion.

Head Plumage (see Fig. 15)

The crown (down to the eye level) is dark brown or dark brown-grey. The sides of the head are whitish with two prominent dark (brownish black or brown to brownish grey) stripes, resembling the hatchling pattern. The uppermost of these dark stripes runs from the eye almost horizontally or somewhat slanting over the side of the

head and bends behind the ear coverts downwards, ending at the side of the head or running further to the side of the tawny-buff upper-neck, where it is only vaguely visible. The second stripe begins under the eye or at the base of the upper mandible and runs a little diagonally downwards. Near the base of the lower mandible a long dark spot or short line is visible.

The stripe pattern shows variations. The dark stripes may be clearly demarcated from the whitish sides of the head, or they may have no distinct boundary. They also vary in size and in length. They are sometimes so wide that very little room is left for the whitish sides of the head. At first, the stripes usually show a strikingly brownish black colour, and subsequently they may be rather brown to brownish-grey (Walser and Barthel 1994; see photographs and illustrations in Ornithologische Mitteilungen 34(2) 1982, Jonsson 1992, p. 41, Walser and Barthel 1994, p. 106, Svensson *et al.* 2000, p. 19, and in Konter 2004a, p. 11).

In autumn and early winter the head stripes are lost by abrasion and moult. The stripe running from the eye is often still visible in January (Walser and Barthel 1994).

The chin and the throat of juveniles are white (Cramp *et al.* 1977).

Neck and Chest Plumage

The fore-neck, the sides of the neck and the chest are tawny-buff or reddish-brown, paler than in the breeding adult and so a dull reflection of the attractive summer plumage (Cramp *et al.* 1977, Svensson *et al.* 2000). Because juveniles and adults share the reddish-brown neck, young birds especially in late autumn and early winter are sometimes misidentified as “adults with remnants of breeding plumage”, however in the majority of young birds the rest of the neck colour and the pattern of the head-stripes are still well visible from October to December, which is exactly the period in which the winter plumage of old birds shows the least reddish-brown colour (Walser and Barthel 1994). The hind-neck of juveniles is brown-grey.

Body Plumage

The back of the juveniles gives a uniform dark brown or sooty brown impression. The pale feather fringes are inconspicuous and hardly visible. There are remains of down to the long feathers. The under parts of the body

of juveniles are white and the vent is grey (Cramp *et al.* 1977, Fjeldså 2004).

The sides and flanks differ from those of the adults in breeding plumage. In juveniles they are whitish, interspersed with pale dark spots or broken lines (in adult breeding plumage the sides and flanks are darker, see 3.2.1) (Cramp *et al.* 1977, Walser and Barthel 1994, Fjeldså 2004; see photographs in Walser and Barthel 1994, p. 106 and 111, and in Pffor and Limbrunner 1980, p. 32 and 33).

Wing Plumage

The wings, according to Cramp *et al.* (1977), are as in the adult birds, but usually have less white in the secondaries. However, the amount of white on the secondaries forming the white wing-patch is highly variable. In juveniles there is also a highly variable amount of white on the marginal, lesser, median, and greater upper wing-coverts, forming the white patch of the leading edge of the inner wing. A relationship between the extent and pattern of the white patches and age or sex is possible but not yet determined (Stout and Nuechterlein 1999).



Fig. 16: First winter plumage of a Red-necked Grebe. The iris still shows a yellowish outer ring. Photo: H Niesen (Netherlands)

Fig. 16: Erstes Winterkleid eines Rothalstauchers. Die Iris zeigt noch immer einen gelblichen Außenring.

Bill

In juvenile birds the colour of the bill is pale yellowish. The pale yellowish colour extends diffusely towards the tip. There is no clear-cut bright yellow patch at the base of the bill. The tip may be somewhat greyish or greyish yellow, but is never black (Cramp *et al.* 1977, Harris *et al.* 1990, Walser and Barthel 1994, Svensson *et al.* 2000; see photographs in Walser and Barthel 1994, p. 106).

Eye

The iris of the juvenile has a clearly visible yellow outer ring, not becoming completely dark brown before the summer of the second calendar year (Walser and Barthel 1994) (see Fig. 14 and 15).

3.2.5 First Winter

The complete first winter plumage of Red-necked Grebes is rarely visible before December, the winter plumage of older birds rarely after January. Both are very similar (Walser and Barthel 1994) (see Fig. 12 and 16).

Head Plumage

First winter birds have a brownish black cap. The whitish crescent extending upwards behind the ear-coverts, visible in the majority of older winter birds, is often (but not always) lacking in first winter birds. The chin, throat and sides of the head (cheeks) may be whitish and contrasting with the dark cap. But in many first winter birds the sides of the head (behind the eye and below the cap) have a faded brownish colour, often so dark, that it is not possible to draw a dividing line between the sides of the head and the cap. The brownish (or greyish) colour of the cheeks may contrast with the whitish chin and throat region. Many older winter birds show extensive whitish head-sides which extend to the eye level. This means that they may have a larger whitish area on the cheeks than most first winter birds. However, the first and following winter plumages show overlap in the extension of white (or whitish) on the cheeks and the presence of a white crescent behind the ear-coverts so that these features are not reliable to determine the age of the birds (Walser and Barthel 1994; see photographs in Walser and Barthel 1994, p. 107 and 115).

First winter birds often have a more rounded cap and occiput, which are not as flat and angular as in older winter birds (Walser and Barthel 1994).

Bill

The colour of the bill is highly variable and changes during winter and therefore does not allow safe ageing. The observation of a Red-necked Grebe in winter with a bill with an extensive, pale yellowish colouring gives a clear indication that the observed bird is in his first winter. However, the tip turns greyish or brownish black in the course of the season and so becomes similar to that of older winter birds (Walser and Barthel 1994).

Eye

First winter birds can only be aged reliably by their iris which still shows a pale (yellowish) outer ring (Walser and Barthel 1994) (see Fig. 16).

3.2.6 First Summer

Immatures start the moult into their first summer plumage later than older birds and often do not complete it before May or even later (older birds usually in March). Red-necked Grebes in April (or later) in which the conspicuous head- and neck colouring is still largely lacking are probably always birds in their second calendar year (Walser and Barthel 1994).

Head, Neck and Chest Plumages

The first summer plumage is very difficult to distinguish from the summer plumage of older Red-necked Grebes. First summer birds often have a dull brownish black crown and hind-neck and usually do not show the glossy deep black or metallic green sheen of the older birds. The reddish-brown feathers of the neck and chest are on average paler and less red than in older birds (Walser and Barthel 1994; see photograph in Walser and Barthel 1994, p. 118).

Bill

The yellow on the base of the bill is often paler and less deep than in older grebes. It is usually also less extensive than in older birds, this may especially be the case on the lower mandible (Walser and Barthel 1994).

Eye

The pale iris ring (rather brownish yellow than yellow) is still present in first summer birds (see photographs in König 1967, p. 17, and in Walser and Barthel 1994, p. 118), but it darkens in the course of the summer (Walser and Barthel 1994).

3.2.7 Aberrant Plumages and Pigmentation

The correct identification of aberrations in plumages presupposes a good knowledge of the pigments ordinarily occurring in the species or the family of birds investigated. Probably, the pigmentation in grebes is largely melanin-based. Their integument (plumage, skin, scutes, ramphotheca of the bill etc.) colouration is due to either one or a combination of both melanin colour pigments, eumelanin and phaeomelanin (Konter 2015). Abnormalities are often genetically determined, or the result of causes such as disease, temporary food deficiencies, sun bleaching, hormonal disorders, staining by different substances in the water of the breeding and wintering lakes, and ageing (Campbell and Lack 1985, Konter 2015). The genetically determined leucism and dilution are often confused with non-genetically caused progressive greying, an age-related cause of aberration leading over time to more and more white feathers in the plumage (Konter 2015).

There are a number of reports of Red-necked Grebes with aberrant pigmentation such as albinism, leucism, dilution, brown, ino, and progressive greying (e.g. Henricke 1903, Chernel de Chernelháza 1907, Drechsler 1955, Knopfli 1956, Walkmeister 1956, Sage 1962, Scholl 1974, Stout and Nuechterlein 1999, Thiede 2005, Konter 2015). Weller (1959), King (1973, 1975), Thiede (2005) and Konter (2015) brought the records of aberrant plumages in grebes together. Considering the conspicuousness and wide distribution of most grebes it is surprising that more aberrantly pigmented birds have not been observed. Konter (2015) found data of only 32 aberrantly pigmented Red-necked Grebes (22 in the subspecies *grisegena*, and 10 in *holboellii*). The conclusion to be drawn is that abnormal plumages in Red-necked Grebes and other Podicipedidae are rare.

Konter (2015) described the following *genetically* caused aberrations in Red-necked Grebes:

1. Albinism. Entirely white plumage; pale flesh pink to yellowish orange bill with no dark parts; yellowish orange to flesh pink feet; serous red eyes.
2. Leucism. Feathers affected all white; bill and feet either as in albinism if leucism is total, or normally pigmented or as in albinism if leucism is partial; dark brown eyes not affected.
3. Dilution. Eumelanin-based plumage pale grey; phaeomelanin-based plumage with pale chestnut

hues; bare parts possibly not affected; phaeomelanin not present in non-breeding plumage.

4. Brown. Eumelanin-based plumage pale brown to beige; phaeomelanin-based plumage unaffected; pale yellow bill; yellowish feet; dark eyes not visibly affected.
5. Ino. Eumelanin-based plumage pale brown to beige; phaeomelanin-based plumage with light rusty yellowish tint (neck and flanks); feet and beak flesh coloured; iris pinkish, in dark ino less visible effect; in non-breeding plumage no phaeomelanin present.

It is said that individuals showing abnormal plumages are usually at a disadvantage and short-lived, mainly because their greater conspicuousness makes them more liable to predation. In addition, reduced pigmentation weakens the feather structure, causing accelerated abrasion and wear, particularly of flight feathers, and it is also possible that, in the wild, the reproduction of aberrant individuals is problematic as they are generally at a disadvantage (Campbell and Lack 1985, Konter 2015). Albinistic grebes (individuals with no production of melanin pigments at all, neither for feathers nor bare parts and eyes) have short survival expectations (Konter 2015). However, individual grebes with other aberrant plumages can be observed over a period of several years which suggests that the negative effects are not as great as expected (*cf.* Thiede 2005). Scholl (1974), for example, observed a “partially albinistic” (according to Konter 2015 a progressive greying or partially leucistic) Red-necked Grebe near Kiel in northern Germany in 1970, 1971 and 1974. It bred successfully in at least two years. Another Red-necked Grebe, with almost no pigmentation (dilution), was reported from Allskog, South Sweden. It was present there almost every year from 2000 to 2010 (P Axelsson). An aberrantly plumaged (brown) *grisegena* was seen on a lake, Pfaffensee, in Hessen (Hesse), Germany, in 2011, 2012 and 2013. Despite several attempts to find a partner in all three years, the bird was unable to establish a stable pair bond and to breed (Konter 2015).

In the context of genetic determination, the records of Weller (1959), Scholl (1974), Dittberner (1996) and Konter (2015) may be interesting.

During field work in the Delta Marsh in southern Manitoba, two juvenile “albino” (according to Konter 2015 completely leucistic) Red-necked Grebes were seen

with a normal coloured adult (probably one of the parents) during July, 1954. One of the juveniles was collected and was found to be an “incomplete albino”. Its irises were brown and the bill and feet were yellow, though the plumage lacked any colouration. The bird was nearly fully-grown, with the body plumage complete and primaries breaking from their sheaths (Weller 1959).

Scholl (1974) (see above) observed a “partially albinistic” Red-necked Grebe breeding successfully in at least two years. Because he did not mention the colour of the chicks, we have to conclude that they were normal coloured.

A pair of Red-necked Grebes (undoubtedly normal coloured) reared a “partially albinistic” (according to Konter 2015 diluted) chick near Landin (Brandenburg, Germany) in 1984. The young bird was white, with the exception of the normal red(dish-brown) neck and the characteristic head-stripe pattern of juvenile birds (Dittberner 1996).

On 12 June 2002, Berger and Hoffmann (*cited in* Konter 2015) filmed a young Red-necked Grebe at Zichow, Uckermark, Germany. The chick was almost completely white and was accompanied by a normal coloured sibling and normal parents. Brown was a plausible causal mutation (Konter 2015).

In 2005, Young and Karlson (*cited in* Konter 2015) photographed a pale Red-necked Grebe in the company of a normally plumaged partner and two normal chicks at Tunkwa Lake, British Columbia. Rather than albinism, a form of pastel dilution may explain the appearance of this grebe.

4. Comparison of the Nominate Subspecies of the Red-necked Grebe with *Podiceps grisegena holboellii*, other Grebes and Divers in the Field

4.1 Comparison with Divers

Due to the lack of true rectrices, grebes appear to be virtually tailless. Having a “tailless” appearance combined with a long, slim neck distinguishes grebes from all other waterbirds apart from divers *Gavia*. However, divers are larger in size, have a thicker and distinctly shorter neck, and have, although short and inconspicuous, normal tail-feathers (see also 4.3).

4.2 Comparison of the Nominate Subspecies of the Red-necked Grebe with Great Crested and Slavonian Grebes

4.2.1 Size and Shape

The size of Red-necked Grebes is intermediate between Slavonian and Great Crested Grebes. At close range Red-necked Grebes are unlikely to be confused with the slightly larger and longer-necked Great Crested Grebes, although at longer distances or in poor light, the differentiation requires attention to character as well as plumage. *P. grisegena* is distinct, with a shorter, stouter bill, a deeper head shape (often showing a round crown in winter), a thicker, less elongated neck, a bulkier body and often a small “powder puff” rear end – all contributing to the stocky silhouette and lack of serpentine appearance often suggested by *P. cristatus* (Cramp *et al.* 1977, Svensson *et al.* 2000).

4.2.2 Plumage

Breeding Red-necked-Grebes are unmistakable, but birds in non-breeding plumage are, especially at longer distances, not recognized so easily. They are perhaps as likely to be confused with Slavonian (Horned) as with Great Crested Grebes, particularly with those Slavonian Grebes that show dark shading on the neck, and also with Slavonian Grebes that have started to acquire the chestnut neck feathering during spring. Like *P. auritus*, the winter Red-necked Grebe has a dark cap down to the eye, but the cheeks of *P. grisegena* tend to be dingier and greyer; the neck, although variable, is usually a rather dark brownish-grey (Harris *et al.* 1990).

Compared with the Great Crested, the non-breeding Red-necked Grebe looks dull and scruffy. The head and fore-neck of *P. cristatus* are much more extensively white than in *P. grisegena*, with white before and above the eyes. *P. grisegena* has a dark crown extending to the eye level and lacks a white superloral line (Harris *et al.* 1990, Svensson *et al.* 2000).

4.2.3 Bill

The Red-necked Grebe of the nominate subspecies has an essentially black, rather dagger-like bill, which is shorter and sturdier than in *P. cristatus*, but the diagnostic feature is the bright yellow patch at the base, which is usually prominent, even at long range. On the breeding

adult Red-necked Grebe, the yellow is restricted to a well-defined, clear-cut patch at the base of the bill, whereas on juveniles and winter birds it extends more diffusely towards the tip (Harris *et al.* 1990, Walser and Barthel 1994). Great Crested Grebes have a long, slender, pink(ish) bill with a dark culmen. The Slavonian Grebe has a short, weak, black(ish) bill, often with a pale tip (Cramp *et al.* 1977, Svensson *et al.* 2000).

4.2.4 Iris

The dark-brown iris of adult Red-necked Grebes is unlike the red or orange-pink iris of the other European *Podiceps* species (Cramp *et al.* 1977, Walser and Barthel 1994, Svensson *et al.* 2000).

4.2.5 Behaviour

Red-necked Grebes are less sociable than Great Crested Grebes and are often encountered singly. On the breeding waters they tend to be more cover-loving and live more secretly than Great Crested Grebes and the other *Podiceps* species. Frequently, they lurk just inside the cover of emergent vegetation. However, birds on the breeding grounds often reveal their presence by their remarkable, loud, diver-like sound, a roaring, wailing, howling, or hooting “uööh...”. The calls are uttered by one bird or by a pair in duet, during the night as well as the day, often from cover (Cramp *et al.* 1977, Jonsson 1992, Beaman and Madge 1998).

When feeding in deep winter lakes and at sea, Red-necked Grebes are more inclined to “spring-dive” than Great Crested Grebes, with an initial leap well clear of the surface, entering at an acute angle, rather like the Shag *Phalacrocorax aristotelis*. Slavonian and Black-necked Grebes tend to spring forward with a quick, dapper action; Great Crested Grebes usually submerge smoothly, without leaping (Harris *et al.* 1990, Svensson *et al.* 2000, Vlуг 2002a).

The Flight of the Nominate Subspecies

In flight, the silhouette of the Red-necked Grebe of the nominate subspecies lacks the abnormally elongated appearance of the Great Crested Grebe and is a more compact and chubbier bird (see Fig. 37 and 41). The wings are situated at the mid-point of the body, and the Red-necked Grebe thus looks more in balance and harmony with equal body mass in front of, and behind, the wings. The silhouette can be likened to a

miniature Black-throated Diver *Gavia arctica*. *Podiceps grisegena* never looks as long-necked as the Great Crested Grebe as the neck is shorter, thicker and of even width. The head merges with the neck, so lacking the “light bulb” impression of a flying Great Crested Grebe, and the bill is shorter. It usually keeps the head and neck level, but it can hang its neck down, albeit never as much as *P. cristatus* (see Fig. 42). The body is held completely still in flight, as if it were threaded on an invisible skewer, with the wings working hard to maintain speed. The head and neck are held stable relative to the body, unlike the Slavonian Grebe (Blomdahl *et al.* 2007). The bird gives a darker general impression than *P. cristatus*, because it has a darker neck and less white on the upper wing. The less variegated upper-wing pattern makes the flight action look more regular, but the flight is virtually identical to the Great Crested Grebe with respect to wingbeats and movements. The dangling feet are always prominent (Cramp *et al.* 1977, Svensson *et al.* 2000, Blomdahl *et al.* 2007; see photographs in Blomdahl *et al.* 2007, p. 42 and p. 47). The flying Red-necked Grebe is particularly distinctive in its breeding plumage (the cheeks are grey, conspicuously bordered with white and the neck is deep reddish brown), and appears cleaner and more colourful than it does in its drab non-breeding plumage (compare with the flight of *Podiceps grisegena holboellii*, 4.3).

4.2.6 Downy Young (Hatchlings)

The Red-necked Grebe chicks closely resemble young Slavonian Grebes, but Red-necked Grebe chicks have a black bar, at least indicated on the proximal part of the lower mandible. The light stripes on the back of *P. grisegena* chicks are washed with a pale brownish tone whereas they are nearly white in *P. auritus* (Storer 1967, Fjeldså 1977b).

Red-necked Grebe chicks also resemble hatchlings of the Great Crested Grebe, but the downy young of the Red-necked Grebe are darker than Great Crested Grebe chicks. The white of the crown stripe of the *P. grisegena* chick is narrower especially at the rear and the pair of the bordering dark stripes is wider. The bare crown patch of small young of the Red-necked Grebe is vestigial, in Great Crested Grebes it is much larger (in *P. auritus* the size is smaller than in *P. cristatus*, but larger than in *P. grisegena*) (Fjeldså 1977b, Harrison and Castell 2002).



Fig. 17: Adult Red-necked Grebe *P. g. holboellii* in breeding plumage. Photo: A Konter (Canada)

Fig. 17: Adler Rothalstaucher *P. g. holboellii* im Brutkleid.



Fig. 18: Red-necked Grebe *P. g. holboellii* in its first breeding plumage. Photo: A Konter (Canada)

Fig. 18: Rothalstaucher *P. g. holboellii* im ersten Brutkleid.

4.3 Comparison of the Nominate Subspecies with East Asiatic-North American (or North Pacific) Red-necked Grebes

Birds of the subspecies *holboellii* are remarkably larger than the Red-necked Grebes of the nominate subspecies, with longer bills (often with a drooping appearance) (see Fig. 17). In the breeding birds of the race *holboellii* the yellow colour of the bill extends more distally on the lower mandible, the upperparts are not so dark (but greyer), the grey cheeks have a lighter colour and also the chestnut colour of the neck is not as intense as in nominate birds (Storer 1996, Stout and Nuechterlein 1999, Fjelds  2004; see photographs in Armstrong 1983, p. 18, Farrand 1983, p. 45, and in Matthews 1990, p. 182) (see Fig. 17 and 18). Fjelds  (2004) believes that American birds in first winter plumage differ from nominate birds by a dark grey face, but there is much variation in this characteristic and a considerable overlap between the two subspecies (see photograph in Farrand 1983, p. 45, and drawings in Palmer 1962, p. 64, and in Sibley 2000, p. 26).

P. g. holboellii is a large grebe (the largest North American Podiceps), exceeded in size in North America only by Western *Aechmophorus occidentalis* and Clark's *A. clarkii* grebes. The appearance of an adult in non-breeding plumage is reminiscent of a small diver *Gavia* in winter. *P. g. holboellii* is best distinguished from divers (loons) by its smaller size, the greyish fore-neck, the white (or whitish) crescent extending upwards behind the ear-coverts, and (in flight) the white patches on the wing (Stout and Nuechterlein 1999).

The Flight of *Podiceps grisegena holboellii*

The flight of the subspecies *holboellii* is almost the same as in the nominate race. Behrens and Cox (2013) wrote that the birds in flight give an oddly and somewhat awkwardly proportioned impression. Although they are diver like in structure, they lack the sleek elegance of divers and always retain some of the clumsiness that characterizes grebes in flight. The heavy body often shows a Great Northern Diver-like *Gavia immer* bulging belly, whereas the neck is long and skinny. The modestly peaked head blends into the neck in flight and does not stand out. The large feet project past the tail and are so oversized that they appear to be covered in heavy gloves. Both the neck and feet are slightly drooped, creating a hunchbacked appearance. The wings are located slightly ahead of the centre of the body and are long and slim,

like a diver's, but they angle back more at the wrist and have blunter tips.

Further Behrens and Cox (2013) wrote that the steady flight of *holboellii* is driven by wingbeats that are fairly even and shallow. Although the beats may actually be slower than those of divers, they have an awkward twitching quality that makes them seem frantic. In this respect, the Red-necked Grebe flies more like a Red-throated Diver *Gavia stellata* than like the other divers, but the frantic quality of its wingbeats exceeds even that of a Red-throated Diver. The flight speed exceeds that of *Podiceps auritus* but is slower than in divers. The birds usually fly just above the water.

5. Moults

5.1 Time and Functions of Body-moulting

The body moult in Red-necked Grebes and other Podicipedidae is an almost continuous process, although there are moments at which it is at its strongest. Most body feather tracts show least moult in midwinter, and it is possible that each individual stops its body moult (except for the flanks) for a short time in this period. The almost continuous moult may particularly reflect the need for keeping the plumage constantly waterproof. It has been suggested that the maintenance of moulting the flank feathers throughout the winter is to provide the grebes with a continuing resource of feather material which contribute substance to the stomach content, enabling the formation of pellets that can be ejected (Piersma 1988a, Piersma and Van Eerden 1989). Another important function of the moult is to provide a gradual change in the strength of different signal functions (such as nuptial plumes) in the course of the annual cycle (Fjelds  2004).

5.2 Moulting in Adult Birds

5.2.1 From Adult Breeding Plumage to Adult Non-breeding Plumage (Adult Post-breeding or Post-nuptial Mould)

The post-breeding moult leads to an inconspicuous winter plumage. It is complete and far more intensive than the pre-breeding moult. During the post-breeding moult all the remiges and other wing-feathers, including the coverts, are shed simultaneously so that the birds are unable to fly.

The best period for moulting is summer because of its optimal thermal conditions (Piersma 1988a). As a rule this is not possible for nesting adult birds. Wing moulting and breeding of Podicipedidae typically occur at separate times during the annual cycle because these events are energetically incompatible (but observations of Otto and Strohmeier 1985 indicate that wing moult does occur, albeit uncommonly, among nesting Pied-billed Grebes *Podilymbus podiceps*). Red-necked and other grebes that have been prevented from breeding, failed and non-breeding birds are in a position to begin the post-nuptial moult in an earlier and better period than birds with nests or chicks (Vlug 1996, 2002a). There is a record of a non-breeding Red-necked Grebe in Switzerland which had already shed his remiges at the beginning of May (Winkler 1987). Red-necked Grebes with eggs or young have to delay their moult and they are only later able to leave the breeding site and visit the moulting areas (see 5.4). Juveniles moult less intensively than adults and do not shed the remiges (see 5.3.1), so they do not need to leave their birthplace in a hurry.

Thus, there is much individual variation in the timing of the post-nuptial moult in Red-necked Grebes. The simultaneous moult of the flight feathers usually takes place in August, September, and early October (Kuročkin 1985, Walser and Barthel 1994, Stout 1995, Vlug 1996, 2000, Stout and Cooke 2003). On 10 August 1996 Koop (*cited in* Vlug 2000) recorded at least 12 Red-necked Grebes in wing moult on a fish-pond in Schleswig-Holstein, Germany.

At Chaleur Bay, Quebec/New Brunswick, Canada, on 30 September 1974, Canadian Wildlife Service biologists examined 195 oiled Red-necked Grebes, and all were in wing moult. Surveys at the Gulf of St. Lawrence from 19 to 23 September 1994 found 136 Red-necked Grebes at Chaleur Bay, 136 at Baie Verte, Nova Scotia/New Brunswick, Canada; and 52 at other locations. At each site, individuals in wing moult were detected. At Boundary Bay, British Columbia, Canada, on 10 September 1998, ten of 14 birds seen wing-flapping had noticeably incompletely grown remiges (Stout and Cooke 2003).

Stout (1995) studied moulting Red-necked Grebes at various bays and shoreline areas around Manitoulin Island, Lake Huron, Ontario. In 1994, the Manitoulin moulters were in the early stages of wing moult when the surveys began on 20 August. Wing-flap observations indicated that most birds in a site were at the same moult

stage. By early October 1994, the Manitoulin moulters were in the late stages of moult, with wing moult largely complete and the body plumage approaching the full winter dress.

There are no records of wing-moulting Red-necked Grebes in winter, but a study of Humple *et al.* (2013) revealed that remigial moult is relatively common among non-breeding *Aechmophorus* grebes during autumn and winter in coastal California, Oregon and Washington.

It seems that the wing-moulting process of *griseogena* begins at about the same time as in *cristatus*. The first Great Crested Grebes of Lake IJsselmeer do not lose their primaries until early August (Piersma 1988a).

The simultaneous wing-feather moult may be explained by the high wing loading of grebes. Even the loss of one flight feather will probably greatly affect the flight capabilities and so it is best to complete the moult as fast as possible (Piersma 1988c).

Not much is known about the wing-moult duration in individual Red-necked Grebes. Köhler and Köhler (2006) observed a flightless Red-necked Grebe in Bavaria from 17.07. to 11.08.2003 (26 days). It is assumed that each bird of this species is usually flightless for about 2-3 weeks or a few days more (Vlug 1996; B Stout). Piersma (1987, 1988a) calculated that it takes an individual Great Crested Grebe about 17 days to complete the wing moult. In Black-necked Grebes, field estimates have shown that it lasts approximately 30 days for remiges to be replaced and this has been verified by observations on a captive bird which required 35 days (Storer and Jehl 1985).

Great Crested and probably Red-necked Grebes eat little halfway through the wing moult, possibly to minimize the risk of damaging the growing flight feathers underwater. Growing feathers are soft and break easily. Breaking one or more (growing) flight feathers may have dramatic implications for a grebe: only if feathers break at their bases will they be replaced immediately. If not, new feathers will only grow during the next year's wing moult. During the simultaneous moult all flight feathers grow concurrently, and hence form a large and fragile surface. If grebes in wing moult (have to) unfold their wings when underwater, the density of water can cause the flight feathers to break. For this reason, it is safer to dive and forage as little as possible in this period (Piersma 1988c).

In *Podiceps nigricollis* (Jehl 1988, Cullen *et al.* 1999), in *Podiceps cristatus* (Piersma 1988c) and probably in Red-necked Grebes, the pectoral muscles atrophy during the post-breeding moult. This phenomenon appears to be widespread in grebes. The large decrease in breast muscle mass in (Great Crested) Grebes just after the shedding of the flight feathers is not correlated to a fast, but to a sudden reduced exercise level of the breast muscles. This does not exclude the possibility that some of the catabolized breast muscle protein is used in the feather synthesis. The muscles are later built up again, probably aided by exercise, as the birds show much increased rates of wing-flapping at the end of the wing moult (Piersma 1988c).

The post-nuptial moult of the head and neck is almost continuous, with high intensities during late summer and early autumn (Piersma 1988a). The classical breeding plumage of Red-necked, Slavonian and Great Crested Grebes shows an additional subtype during mid- or late summer. This eclipse plumage is formed by a new feather generation. The longest ornamental plumes are shed and replaced by a plumage with shorter plumes of similar colour (Piersma 1988a, Fjeldså 2004). So, although a Red-necked Grebe will still have the principal characters of the breeding plumage, it looks dull in mid- and late summer.

Red-necked Grebes which are at least one year old possess a complete winter plumage from mid-October to the end of December (Walser and Barthel 1994).

5.2.2 From Adult Non-breeding Plumage to Adult Breeding Plumage (Adult Pre-breeding or Pre-nuptial Moult)

The breeding plumage develops by a partial moult, presumably of the feathers of the entire body, but mainly of the head, neck, breast, flanks and tail, and of the innermost secondaries and innermost greater wing-coverts (but not the rest of the wing) (Witherby *et al.* 1947, Cramp *et al.* 1977, Fjeldså 2004).

Old birds (birds in their third calendar year and older) already occasionally show their breeding plumage at a very advanced stage around the turn of the year, and almost all of them possess a complete breeding plumage in March (Walser and Barthel 1994).

5.3 Moulting in Young Birds

5.3.1 From Downy Young to First Winter Plumage

The first plumage of natal down – or neoptiles – has a complex pattern of dark and light stripes and spots. The natal down is soon pushed out by longer down, which actually comprises the soft terminal filaments of later feathers. This plumage is also distinctly striped on the head and neck (Fjeldså 2004). In autumn and early winter the downy head striping of the young Red-necked Grebes is lost by abrasion and moult. The stripe running from the eye is often still visible in January (Walser and Barthel 1994).

The post-juvenile moult is partial. The feathers of the head, neck and rest of the upperparts, chest and flanks are involved, but the juvenile remiges are retained. The replacement of the body-feathers is gradual (Cramp *et al.* 1977, Stout and Nuechterlein 1999). The post-juvenile moult takes place during the period September to late January. The first complete winter plumage is rarely shown before December and may occasionally be seen in April. The majority of the birds possess this plumage from January to March (Walser and Barthel 1994).

5.3.2 From First Winter Plumage to First Summer Plumage

Immatures start the moult into their first summer plumage later than older Red-necked Grebes and often do not complete it before May or even later. Birds in April (or later) which largely lack the striking head- and neck colouring are probably always birds in their second calendar year (Walser and Barthel 1994).

5.4 Moulting Habitat

Most breeding sites, in particular small, shallow ponds and lagoons, do not offer favourable conditions for the post-nuptial moult of *griseigena*. As already mentioned (see 5.2.1), during this moult the birds are unable to fly for a longer time and they especially need safety, which is not usually found in the breeding waters. If the birds are disturbed frequently, they lose a lot of energy. They have to leave the breeding grounds to moult elsewhere.

The simultaneous (flightless) wing moult of the Red-necked Grebe in Europe usually takes place in tidal waters, and only a small number of birds undergo the post-breeding moult on inland waters. The most impor-

tant moulting areas are probably in the shallow bays of the Baltic Sea (Vlug 1996). In two marine areas near the island of Sjælland (Zealand), Denmark, large numbers of Red-necked Grebes were observed in the moulting season, at the end of August/early September. In 1990, an estimated number of 1,500 grebes were moulting here. The birds were observed 2-8 km from the nearest shore in water of a depth of 3-20 m, the majority in 8-15 m deep water (Pihl 1995) (see 9.2 for more details).

In North America, important moult sites have been identified not only in marine waters, but also on large inland lakes (Stout and Nuechterlein 1999). An estimated 1,300 Red-necked Grebes completed their autumn moult around Manitoulin Island, Lake Huron, in 1994. The moulting sites were scattered around the island in large bays and near small islands. Within the moult areas, the grebes usually remained between 100 and 2,000 m from the shoreline. The moult sites around Manitoulin Island had water depths of 3-55 m, were somewhat sheltered (large bays and/or lee sides of islands) and had a varied underwater topography (i. e. deep areas near shallow areas, forming shelves, holes, etc.). The moulting Red-necked Grebes were present in loose flocks of 1-40 birds per flock at each site (Stout 1995, Stout and Cooke 2003) (see 9.2 for more details).

Red-necked Grebes in Boundary Bay, Pacific coast of British Columbia (e. g. 22 September 1998 2,229 birds), were undergoing body moult, and some birds were in wing moult or had incompletely grown remiges (regrowth). They were typically found in shallow portions of the sub tidal zone (< 13 m deep at low tide) but also used the intertidal zone on high tides (Stout and Cooke 2003).

6. Voice

6.1 Calls of the Adults

The Red-necked Grebe is a highly vocal species on the breeding grounds. Its voice is varied and, in the breeding season, often used. The birds are mostly silent during the rest of the year.

The voices of the North American *holboellii* closely resemble those of the nominate *griseogena*, but it is quite conceivable that there are differences.

The following description of the different calls is mainly based on Wobus (1964), Cramp *et al.* (1977) and Stout

and Nuechterlein (1999). Cramp *et al.* (1977), Stout and Nuechterlein (1999) and Bergmann *et al.* (2008) give sonograms.

6.1.1 Song and Display-call (Whinny-braying)

The voice of the Red-necked Grebe is best known for its penetrating, harsh-sounding territorial Song and display-call (Song) or Whinny-braying (“uööh-Gebrüll” of Wobus 1964).

General Description of the Song and Display-call by Different Authors

Naumann (1838) described the highly peculiar and eerie Song of the Red-necked Grebe as sounding like a combination of the screaming squeal of a terrified young pig and the whinnying of a young foal.

Silloway (1902) visited Swan Lake in Montana in “the oological season of 1902” and reported: “Frequently in the night there was wafted across the open water an outburst of cries from the uneasy colonists of the swamp, the voice of *C. holboellii* mingled with the louder cackle of the loon, to which the former is not greatly unlike. It is a coarse, prolonged nasal *quonk*, the nasal quality being most pronounced, the intonation being very suggestive of the braying of a donkey. Indeed, the natives call this grebe the “jack diver,” and anyone familiar with the nasal volume of tone produced by *C. holboellii* will readily admit the appropriateness of the popular name.”

Bent (1919) reported that the “love song” of Red-necked Grebes in Manitoba consists of “weird cries” and stated that the performance begins with a series of diver(loon)-like wailing cries, loud and piercing at first, and then running off into a series of short, plaintive, vibrating wails, sometimes ending in a more staccato, chattering trill.

Burt (*cited in* Bent 1919) described notes of an adult North American bird, which was captured on the ice on February 14, 1913 as “loud trumpetings, suggesting the cries of the loon and resembling the sound made by what is known as a Gabriel’s horn on an automobile”. Apparently these notes were similar to portions of the Song.

Grinnell (*cited in* Bannerman 1959), “startled by a series of most lugubrious cries” of a pair of *P. g. holboellii* in the delta of an Alaskan river, noted that one of the birds started with a long wail and then the other chimed in with a similar note, both winding up with a series of

quavering cries, very much like the repeated whinnies of a horse.

Cramp *et al.* (1977) described the Song of *P. g. grisegena* as a remarkable, loud, diver-like sound: a roaring, wailing, howling, or hooting “uööh...”, with considerable individual variation.

Brazil (2009) commented that the voice of East Asiatic birds on the territory is a combination of gull-like wailing howls, loud harsh squeals, and Little Grebe-like continuous neighing “kerekerekere...” and that the pairs give a deep mournful “uwaa uwaa”.

Detailed Description and Variability of the Song and Display-call

The Song and display-call is by far the most common vocalization of the Red-necked Grebe. It is uttered by one bird or by a pair in duet. Wobus (1964) and Cramp *et al.* (1977) noted that surprisingly loud sequences of up to 60 consecutive notes are delivered during singing encounters between the birds in different territories, but that the phrases during water-courtship displays are usually shorter: 4-10 in spring and 1-4 in summer, rising in intensity and pitch. Thus, the intensity of the Song varies greatly: in the most extreme form, the members of a pair giving vocalization approach one another to swim side by side. Upon joining, the amplitude of the notes builds, and both birds simultaneously give a chittery, honking call, with the head raised and the feathers of the crests and hind-neck erected, tail cocked, and breasts raised high above the water. The individual notes of the whinny merge into a resonant honk, or the honks break into whinnies, giving the joint display its bray like quality. The amount of honking and chattering in the Song duet is highly variable, often lasting 5-10 seconds (Stout and Nuechterlein 1999).

Social Context and Presumed Functions of the Song and Display-call

(see 15.3.5 and 15.3.6 for more details) The Song (Whinny-braying) appears to serve the general purpose of territorial advertisement as well as accompanying the displays of the water-courtship. The Song duet may be used as display of pair unity.

The harsh-sounding duet is given spontaneously or in response to neighbouring territorial pairs, especially by pairs at territorial boundaries, particularly when some other pairs approach. In breeding areas with many Red-necked Grebes Whinny-braying has a very stimulating

effect. The Song of one pair may be followed by a wave of surprisingly loud calling wafting across the pond.

The conspicuous Defensive-upright display, usually seen as the birds of a pair join each other on the territory, is nearly always associated with the Song and display-call. In response to the Song by intruding pairs, the mates on the territory usually first join together to give the Song in Defensive-upright display, then approach the intruders as a unit (see 15.3.5 for more details).

In the Penguin-dance, both birds give the Song and display-call. Low Head-waggles and possibly the Weed-dance are also accompanied by the Song.

During the Discovery Ceremony of courting pairs, the approaching bird gives a call as it emerges slowly from the water in the Ghostly-penguin posture and turns to approach the partner. This call is identified by Cramp *et al.* (1977) as Song and display-call. However, no sonogram is available to confirm whether this call is the same as the Song or is a specialized call for this display as in other *Podiceps* species. The call may help to orient the bird giving the Cat-display during the ceremony, causing it to pivot in the Cat-display posture and face in the direction of the calling bird (Stout and Nuechterlein 1999).

After the pair-bond is well established, the Discovery Ceremony is replaced by pair meeting (Greeting Ceremony of Stout and Nuechterlein 1999). It is often stimulated by hearing neighbouring pairs. The mates approach each other in hunched posture, then rising out of the water and giving a Song duet as they swim side by side with the head and crests erect (Stout and Nuechterlein 1999).

When a pair is separated, solo bouts of the Song and display-call are used to attract the mate: the calls usually induce the mate to approach and call, thus suggesting a function in individual recognition. The call is given repeatedly when the mate is absent for extended periods. Playbacks of the call induce the mates of a pair on the territory to reunite immediately, and then the birds approach the speaker and call. Incubating birds call individually in response to playbacks, causing the mates to return to the nest area (Stout and Nuechterlein 1999).

Stout and Nuechterlein (1999) note that repeated bouts similar to the whinny like portion of the Song and display-call may be used by lone birds, both males and fe-

males, as Advertising-call preliminary to the Discovery Ceremony. They wonder whether this solo form of the call is the same as the Quacking-call of Cramp *et al.* (1977) (see 6.1.2 and 6.1.3).

Phenology of the Song and Display-call

The Song may be heard all year round, but the grebes are generally quiet during autumn migration and winter. The calling increases in late winter and spring with the onset of courtship behaviour and peaks in April and May.

Daily Pattern of the Song and Display-call

The birds call throughout day and night, but they are most vocal in the early morning and evening. Nocturnal calling is especially intense on moonlit nights.

Places of the Vocalizing of the Song and Display-call

The Song is often heard on open water, particularly during courtship. The duets are more frequent along marshy borders or in the vegetation of the breeding ponds as pairs disperse to the territories.

Role of the Sexes in the Song and Display-call

The relative roles of the sexes are not rigid but vary widely from one bout to the next; either sex initiates a duet, and the notes of the mates overlap irregularly (Stout and Nuechterlein 1999). In duets, the call of one bird (almost certainly the female) is noticeably weaker than the other's. The calls of the presumed male are screaming or squealing in character, strongly nasal, pitched distinctly higher and audible at greater distance, those of the presumed female are shorter, tremulous, and even more whinnying, neighing, or braying in character (Cramp *et al.* 1977).

The Loudness of the Song and Display-call

It is difficult to explain the extreme loudness of the Song and display-call of the Red-necked Grebe. It is possible that the "handicap principle" of Zahavi (1975, 1977, *cited in* Krebs and Davies 2003) provides an explanation. It is important for birds to know the "quality" or condition of a potential partner or opponent (however, there are signalling systems in which there is no fixed link between the signals used and any underlying aspects of the signaller's condition). Zahavi suggested that a signal could provide honest information about the "quality" of the signaller, even in the face of a conflict of interest, provided that it is costly to produce. Giving a very loud Song and display-call must be costly to the signaller, costing the grebe among other things energy. An individual with less strength could not afford to produce much noise.

Red-necked Grebes of greater biological fitness signal this status through handicapping behaviour that effectively lowers this quality. Birds with a loud voice advertise their value to potential mates and rivals. Honesty may then be stable, because only superior individuals stand to gain a net benefit from the display. A "deceitful" mutant that opted to use the costly loud Song even though it was of low quality would suffer a loss of fitness, because the high cost involved would outweigh the benefits to be gained from attracting mates and deterring more rivals. Birds with a louder Song show their good health and probably tend to be preferred by birds of the opposite sex during mate choice. It is possible that they also frighten rivals with greater success. As a result, they tend to gain more rapid access to a higher quality mate and territory during the breeding season. Consequently, it is likely that natural selection produced a very loud Song in the Red-necked Grebe.

Development of the Song and Display-call

Hatch-year young are not known to give the Song on the breeding grounds.

6.1.2 Quacking-call

The Quacking-call ("Quaken" of Wobus 1964) is a quacking "wack..." or "ack...", like the Decrescendo-call of the female Mallard *Anas platyrhynchos*. It normally consists of 4-10, but occasionally up to 100 notes. It is variable, often loud and emphatic, uttered in short or long sequences, slowly or fast, but sometimes quieter. It is often combined with the Song and display-call and usually expressed in spring before the egg-laying period. If not combined with the Song, the Quacking-call is typically given by a lone bird. The call is used at times as Advertising-call but often replaced by the Song and display-call (see 6.1.3). It is also uttered as Anxiety-call; in this case it has been described as a duck-like "quek-quek" (Wobus 1964, Cramp *et al.* 1977, Fjeldså 2004).

6.1.3 Advertising-call

The Advertising of the Red-necked Grebe appears to be less specialized and frequent than in other *Podiceps* species (Cramp *et al.* 1977). The variability of the Advertising-call, facilitating individual recognition, possibly increases the difficulty to identify the call.

Red-necked Grebes use (the whinny-like portion of) the Song and display-call and the rather unspecialized

Quacking-call as Advertising-call (Cramp *et al.* 1977, Stout and Nuechterlein 1999).

Storer (*cited in* Cramp *et al.* 1977) noted that in *P. g. holboellii* a loud, nasal “a a n”, somewhat similar to the comparable call of the Slavonian Grebe *P. auritus* (see below), is (also) used as Advertising-call; it is uttered by either the male or the female, or both, prior to the Discovery Ceremony and also in combination with duet calls and, possibly, other notes. Perhaps, the nominate race does not use this loud, nasal call as Advertising-call. It is important to know whether the Advertising calls of *P. g. holboellii* differ in some aspects from those of the nominate subspecies because Advertising appears to be the first step in pair-formation (Storer 1969), and Nuechterlein (1981a) demonstrated that a difference in the number of notes in the Advertising-call provided a key for reproductive isolation between the Western Grebe *Aechmophorus occidentalis* and Clark’s Grebe *A. clarkii*.

In contrast to the Red-necked Grebe, the other *Podiceps* species have characteristic Advertising-calls. The Great Crested Grebe *P. cristatus* has a loud, far-carrying resonant Croaking (or Crowing), singly or slowly repeated, and followed by a much quieter moaning, and the Slavonian Grebe *P. auritus* utters a loud and nasal “aaanrrh” or “jaorrrh”, usually descending in pitch and ending in a rattle or harsh trill (Storer 1969, Cramp *et al.* 1977, Fjeldså 2004).

6.1.4 Clucking-call

The Clucking-call (“Gackern” of Wobus 1964) is a fast, soft “ga...” in series of up to 10, usually 4-5 notes. A harsher version is rendered as “keck...”; also as “crik” and “teck” (Sage 1973). The sound is given by both members of the pair during the pair-formation and later near the platform or nest during the platform-courtship and mating phases. It sometimes alternates with the Quacking-call and is probably homologous to the Platform-call of *Podiceps auritus*. In general, the Clucking-call expresses a slight, usually sexual excitement (Wobus 1964).

A bird captured in Ohio, February, 1904 uttered a sound described by Sim (1904) as “wit-‘tah”: “not loud but rather high, the first part being higher than the second. It was usually given when the bird had just taken wing exercise, or had waddled across the room. It was often given, too, when the bird’s back was stroked.” It is possible that this “wit-‘tah” is given in the same social context as the Clucking-call.

6.1.5 Hissing-call and Other Threat-calls

The Hissing-call (“Zischen” of Wobus 1964) is a hissing, lightly snoring, throaty sound. The bird utters this harsh, intense and snake-like call in distress and directs it at potential egg predators and predators on young, such as Coot *Fulica atra*, American Coot *Fulica americana*, Great Blue Heron *Ardea herodias*, and occasionally humans. The incubating bird of a pair that Sage (1973) studied in southern Alaska allowed him to approach to within two metres. At this distance the bird erected its head tufts and hissed like a snake. The bird directs the Hissing-call with open bill at potential nest predators that are not dangerous to the adult, when retreat might result in egg loss (Stout and Nuechterlein 1999).

A bird in an encounter with a Coot near the nest gave a long, drawn-out, triple “airrrr...-airrrr...-airrrr.” like the Snarling of the Great Crested Grebe (Cramp *et al.* 1977).

In general, the threat-calls are not well documented. Sim (1904) gave a description of the call of a captured *holboellii* (see 6.1.4) when it was frightened: “When frightened into a desire to inspire fear the grebe opened his mouth very wide (by moving both halves) and gave a rather loud scream which became grating, like the crow’s song, towards the end. It somewhat resembled a whinner (*sic*) though, of course, was not so loud.”

Shelley (1930) described the sound of a bird found on a railroad in New Hampshire, December 10, 1929: “When approached, it made a series of swift lunges of the sharp beak accompanied by discordant, raucous notes: *ca-a-ar*, *c-a-a-ar*, *ca-a-ar*, quite prolonged. Its neck could be stretched to so great a distance that a lunge of the bird would strike an approaching hand two feet distant. Yet when a hand was manoeuvred to touch the back, the bird allowed its feathers to be stroked gently, nervously twitching the head and uttering a soft continuance of whining notes: *qu-a-a-r-r-r-k-k*, beginning deep in the throat and attaining greater volume as the bill was opened preparatory to striking.”

White (1931) kept a Red-necked Grebe, found in the snow in a field in Warner, New Hampshire, January 27, 1930: “An appearance of threatening rage accompanied a series of loud somewhat nasal syllables: “oo, a, a, a, a, a, a,” the opening note of lower pitch. This was a sort of whiney.”

6.1.6 Alarm-call

The Alarm-call is a short, sharp and irregularly spaced tick (“äck”, “tjäck”, “tjöp”, “teck”, etc. Wobus 1964) given by pairs when approached by humans, other mammals, over flying raptors and other large birds, particularly if the chicks are present.

The Red-necked Grebe gives both Hissing- and Alarm-calls in response to danger, but usually in different contexts. It directs the Hissing-call at potential nest predators that are not dangerous to the adult and gives the Alarm-call at irregular intervals while retreating from predators that are dangerous to the chicks or the adults. The Alarm-calls cause the mate and chicks to become alert. Swimming chicks dive, and back-brooded chicks hide beneath the feathers of the adult (Stout and Nuechterlein 1999).

6.1.7 Purring-call

The Purring-call and the Rattling-call are associated with platform behaviour (see 15.3.8).

The soft, raspy Purring-call (“Knätschen” of Wobus 1964) is a drawn-out, largely unarticulated “(kn)ääääääää...”. Purring-calls are soft pair-contact calls most commonly heard near the copulation or nest platform, but intense bouts also are heard on the water, where copulation is not possible. A similar call is given during the initial stages of nest-building and during rearing from the copulation platform. Either sex may give Purring-calls while inviting from the platform, which appears to stimulate the partner to approach and eventually to mount (Stout and Nuechterlein 1999).

6.1.8 Rattling-call

The loud Rattling-call (“Rattern” of Wobus 1964) is a deep “u” sound turning immediately into a rapid series of higher “r” sounds, e.g. “uerrrrrrrrrrrrrr”. It is repeated 3-6 times and given by the male during mounting. During reverse mounting, both the female and the male give overlapping Rattling-calls, with the female louder (Stout and Nuechterlein 1999).

It is unclear whether the female sometimes calls softly during copulations, but the bill is usually closed.

6.1.9 Grunting-call

Stout and Nuechterlein (1999) give a description of the Grunting-call. It is a soft, rapidly repeated call, given by a

parent bringing food to the young. The call bouts consist of 5-15 similar notes. The call induces the chicks hidden beneath the back-feathers of the mate to poke their heads out and peep while begging for food. The parent arriving with food gives repeated bouts until the chicks learn to respond, as is the case in the Black-necked *Podiceps nigricollis* and Western Grebes *Aechmophorus occidentalis* (Buitron and Nuechterlein 1993).

6.2 Calls of the Young

6.2.1 Hatching-call

The Hatching-call (“Schlüpfaut” of Wobus 1964) is a short, sharp “jip” (or “iejp” or “pieh”) (Wobus 1964). It is first given, at intervals of 1-2 seconds, for up to 2 days before and during hatching. It is homologous to the “Squeak” of *Podiceps cristatus* (Cramp *et al.* 1977). This peeping is possibly an attempt to prevent the adult birds from deserting the nest before all young have hatched (see 16.4.9).

6.2.2 Begging and Contact-call

The Begging and contact-call (“Wiebern” of Wobus 1964) is a persisting “bibibibibibi” (Wobus 1964) or “zipp zipp...” (Bergmann *et al.* 2008), similar in structure and rhythm to the song of the Chiffchaff *Phylloscopus collybita*. On seeing an adult coming with food the chicks utter a louder version of this call, described by Bergmann *et al.* (2008) as a rapidly alternating “ti ti tü ti tü...”. Chicks from just under one week old to more than eight weeks give the Begging and contact-call very frequently.

When the young are 6-7 weeks old, but still dependent, they not only use the Begging and contact-call, but also begin to utter a soft “ga” which may later develop into a soft “gagaga” with only a slight “jip” component (Wobus 1964, Cramp *et al.* 1977) (see 16.5.11).

7. External Measurements and Weights of the Nominate Subspecies and *Podiceps grisegena holboellii*

The comparison of external dimensions of the Red-necked Grebe’s body is often crucial in making taxonomic distinctions. Not only do the two subspecies of *Podiceps grisegena* differ in size, but also variation within these subspecies exists (see also 8.1). In addition, within a population significant differences in measurements occur between the sexes.

7.1 Documentation

Measurements quoted in standard reference works are generally of museum skins which, because of shrinkage, will be lower than those obtained from live birds in the field. Fjeldså's (1980) investigations suggest greater post mortem changes in grebe skins than previously expected; wings as well as toes decrease by about 3%. There is a marked change in bill dimensions of grebes, with a fully 4% decrease in length (except in very fine-billed examples), and a considerable reduction in thickness of some (damaged) bills. This shrinkage may not be applicable to other birds, the amount of change probably depending on bill anatomy. The tarsus measurement in grebes, which does not span joints, changes very little.

Many published data, including a number quoted in this chapter, are inadequate because the methods by which they were taken are not (sufficiently) described and the statistical necessity of giving sample size and standard deviation is overlooked.

Measurements of body weight may be unreliable because of considerable seasonal fluctuations. In some circumstances the data may be misleading due to undernourishment. The authors usually do not mention the method by which the body weight data were taken. Thus, it is not known if there was a correction for variable amounts of water in the plumage and for the quantity of food in the stomach and oesophagus.

7.2 Measured Features of Grebes

Innumerable features of grebes can be measured but the five described below are in most common use.

7.2.1 Body Length

This is the length of the stretched grebe from the distal tip of the bill to the end of the body (grebes only have a tiny tail). The measurement is difficult to take consistently and is therefore of no great taxonomic or ecological use.

7.2.2 Wing Length

The wing-length is a fair indicator of the size of an individual within a species. In grebes, the remiges are strongly curved, and different methods of measurements are used. Wing-length is taken on the naturally folded wing from the carpal joint to the tip of the longest primary using a ruler with an end-stop. If the curvature of the wing is not

corrected in any way, a "minimum chord" is obtained. One of the two curvatures can be eliminated by pressing at the greater coverts to flatten the wing on to the ruler to give a "flattened chord". Most of both curvatures can be removed by flattening the wing as above and then straightening the primaries along the ruler with a firm stroking action to give a "maximum chord" wing-length (Bibby 1985).

7.2.3 Bill Length

The external characters of the bills of different species and subspecies of grebes vary in accordance with feeding behaviour. Small individual differences in bill dimensions may influence the diet of birds. Bill length reveals much about the feeding ecology of grebes and is important to study character displacement and character release.

Bill-length can be measured from the distal tip of the bill to the start of the feathering, to the base of the skull or to the nares or the gape, so it is vital to note the method used in any published data. At the Zoological Museum in Amsterdam Piersma (1988*b*) measured a sample of 38 Red-necked Grebes from the Netherlands and discovered that the culmen length was positively correlated with both bill height ($r = 0.30$, $p = 0.035$) and bill width ($r = 0.38$, $p = 0.009$). The culmen length is therefore a measure of overall bill size.

7.2.4 Tarsus (*Tarsometatarsus*, *Metatarsus*) Length

The length of the metatarsus of grebes is generally measured from the posterior side of the ankle joint to the distal end of the metatarsus, with the foot flexed at right angles to the tarsus.

7.2.5 Body Weight (*Body Mass*)

Body weight or mass could be used to describe the size of a grebe. However, the measurements may be unreliable (see 7.1).

7.3 Differences in Measurements Between the Sexes

Kloskowski *et al.* (2006) listed the morphometric measurements of 76 adult breeding Red-necked Grebes from eastern Poland, 39 males and 37 females, sexed by DNA. As measurements of some dimensions can be affected by post mortem changes, the authors used only living birds and six freshly dead individuals, found at the nest.

The standard measurements include the wing length (flattened wing measured from the wrist to the tip of the longest primary), bill length ("exposed culmen" from the distal tip to the tip of the forehead feathering at the proximal base of the bill), long bill length (gape length from the distal tip of the bill to the corner of the mouth), tarsus length (from the middle of the mid-tarsal joint to the distal end of the tarsometatarsus) and body weight. As the length of the tarsus ($n = 47$) did not differ significantly between the sexes ($t = 1.867$, $df = 45$, $p = 0.068$), this character was dropped from further analysis.

All measurements were taken to the nearest 0.1 mm with Vernier callipers, except wing length that was measured to the nearest 1 mm with a flat ruler. Body masses were taken to the nearest 1 g.

The body measurements and weights of breeding Red-necked Grebes from eastern Poland are shown as mean \pm SE (range; n) and \overline{CV} (NB the authors use SE, not SD). All t values for comparison of sexes were significant ($p < 0.001$):

Dimension	Male
Wing length	177.1 \pm 1.0 (163-188; 39) <u>3.5</u>
Bill length	40.8 \pm 0.4 (36.7-44.6; 39) <u>5.4</u>
Long bill	53.8 \pm 0.4 (47.5-57.5; 39) <u>4.3</u>
Body mass	820.3 \pm 12.3 (635-970; 37) <u>9.1</u>
Female	
Wing length	171.1 \pm 1.0 (159-182; 37) <u>3.5</u>
Bill length	38.2 \pm 0.5 (33.8-48.3; 37) <u>7.4</u>
Long bill	49.9 \pm 0.5 (42.3-55.7; 37) <u>5.9</u>
Body mass	739.2 \pm 11.0 (620-847; 31) <u>8.7</u>

The authors concluded that males are significantly larger than females. Owing to considerable overlap in measurements, however, the sexes cannot be accurately separated by biometrics at the population scale. Of the characters measured, long bill length (gape length from the distal tip of the bill to the corner of the mouth) was the best single predictor of sex: 79% of the individuals were correctly identified based on this parameter alone. Adding wing length to the model only slightly increased its discriminatory power. However, neither single bill length measurements nor combinations of morphometric characteristics provided a complete separation of the sexes. Thus, although males averaged larger than females, the zone of overlap was too large for effective application of discriminant functions; the overall classification success of neither model exceeded 80%.

In spite of the fact that in this study the sample of Red-necked Grebe pairs with both mates caught was small, within-pair comparisons appear to increase the accuracy of sex assignment by measurements of bill and body mass. Within 17 pairs, where both pair members were caught, in only two pairs did the female have a longer bill than the male; similarly, in only two (other) pairs was the female heavier than the male. However, only three pairs were captured on the same occasion and in some pairs the mates were caught in different years. When within a pair, the bird with the larger long bill length or body mass was assumed to be male, the accuracy level increased to 88.2%.

7.4 Differences in Measurements Between the Two Subspecies (and Sexes) (see also 8.1)

Many authors published linear measurements and weights of Red-necked Grebes. Because males average larger than females (see above) and the subspecies differ in size, most authors record measurements of both sexes, so a male-male and female-female comparison between the races is possible. The measurement data and conclusions of a number of ornithologists are treated here (in chronological order of publication).

7.4.1 Palmer (1962)

Palmer (1962) gives the wing and bill measurements of breeding-season Red-necked Grebes *P. g. holboellii* of North America and East Siberia and compares them with data of *P. g. grisegena* from Witherby *et al.* (1941). The data (in mm) are shown as mean (range; n):

Dimension	<i>P. g. holboellii</i>	<i>P. g. grisegena</i>
<u>Wing length</u>		
Male	195.6 (185-212; 20)	? (160-180; 12)*
Female	189.3 (182-198; 14)	? (155-176; ?)
<u>Bill length</u>		
Male	50.2 (48.5-56; 20)	? (35-45; 12)
Female	46.7 (45-50; 14)	? (35-40; ?)

* One bird 190 (Witherby *et al.* 1941)

Palmer (1962) gives the weights of North American birds: four males from Alaska, July, averaged 1,113 g and ranged from 1,002-1,270 g, and a female weighed 945 g; a male from Washington, January, weighed 743 g.

The birds of North America and East Asia are larger than those of West Asia and Europe. From the ends of this Holarctic chain, Salomonsen (1935, *cited in* Palmer 1962) compared small series, and the measurements differed to the extent of no overlap except in the length of the middle toe.

7.4.2 Bauer and Glutz von Blotzheim (1966)

These authors cite ranges of measurements (mm) of German birds (bill length from the forehead feathering) and juxtapose them with measurements of *P. g. grisegena* from Witherby *et al.* (1943) and Dement'ev and Gladkov (1951):

	Male	Female
<u>Wing length</u>		
Germany (K Bauer and G Niethammer)	168-176 (<i>n</i> = 4)	159-174 (<i>n</i> = 8)
Russia (Dement'ev and Gladkov 1951)	162-172* (<i>n</i> = 20)	160-170 (<i>n</i> = 10)
Central Europe (?) (Witherby <i>et al.</i> 1943)	160-180** (<i>n</i> = 12)	155-176

Bill length

Germany (K Bauer and G Niethammer)	35-45	35-40
Central Europe (?) (Witherby <i>et al.</i> 1943)	35-45 (<i>n</i> = 12)	35-40

* 162-173 mm (Dement'ev and Gladkov 1969)

** One bird 190 (Witherby *et al.* 1943)

7.4.3 Cramp *et al.* (1977)

Cramp *et al.* (1977) list the measurements of museum skins of the nominate *P. g. grisegena* and compare these with measurements of *P. g. holboellii* from Vaurie (1965), Palmer (1962) and various other sources.

The wing was measured by pressing it against a ruler and stretching it fully; the wing length is the distance from the carpal joint to the tip of the longest primary. The bill length was defined as the chord of the culmen from the implantation of the feathers to the tip of the upper mandible. The tarsus length was measured from the middle point of the joint between the tibia and the tarsus behind to the middle point of the joint between the tarsus and middle toe in front of the leg. The middle toe was measured from this point to the tip of the middle nail.

The linear measurements (mm) of Red-necked Grebes from Cramp *et al.* (1977) are shown as mean \pm SD (range; *n*):

P. g. grisegena *P. g. holboellii*

Wing length

Male 175 \pm 8.09 (164-193; 21) 197 \pm ? (183-212; 20)

Female 169 \pm 9.79 (153-182; 23) 190 \pm ? (173-204; 20)

Wing length of recognizable juveniles

Male 169 \pm 5.00 (160-177; 11)

Female 162 \pm 8.24 (153-177; 13)

Bill length

Male 40.0 \pm 2.47 (34-44; 25) 50.2 \pm ? (47-56; 20)

Female 37.1 \pm 2.25 (33-42; 30) 46.7 \pm ? (45-55; 14)

Tarsus length

Male 55.9 \pm 3.36 (51-63; 17)

Female 53.8 \pm 2.48 (49-60; 26)

Middle toe length

Male 65.2 \pm 2.75 (62-68; 4)

Female 62.9 \pm 2.51 (59-67; 11)

Cramp *et al.* (1977) concluded that the sex differences are significant, except for the length of the middle toe. The wings of recognizable juveniles average shorter, but there are no differences in the length of the bill and the tarsus.

P. g. holboellii is much larger than the nominate subspecies; particularly the bill is much longer.

The authors give the weights of Red-necked Grebes. They cite Bauer and Glutz von Blotzheim (1966):

German breeding birds: four males 806, 823, 900 and 925 g; three females 692, 823 and 873 g; one juvenile male 582 g and a juvenile female 620 g.

Cramp *et al.* (1977) examined a number of beached birds from the Netherlands: a non-breeding male had a weight of 742 g and the mean weight of 10 non-breeding females was 476 g (range 316-764 g); a juvenile male weighed 378 g.

The authors state that *P. g. holboellii* is heavier, range 743-1,270 g (Palmer 1962).

7.4.4 *Bocheński (1994) and Storer (1996)*

Bocheński (1994) examined the skeletons of 59 specimens of *P. g. grisegena* and 48 of *P. g. holboellii*. He discovered that *P. g. holboellii* shows statistically significant sexual dimorphism in almost all the measurements taken (60 out of 73). The male is always bigger than the female. The nominate subspecies *P. g. grisegena* seemed to have relatively few size differences between the sexes; it displayed sexual dimorphism only in 19 measurements. The differences in sexual dimorphism between both subspecies appeared very distinct. This was one of the reasons for Bocheński (1994) considering both forms as separate species (*Podiceps grisegena* and *Podiceps holboellii*).

Storer (1996) reviewed the work of Bocheński (1994). He stated that sexual dimorphism, particularly in bill measurements, is probably universal in grebes (see 7.3). Storer (1996) never failed to find it in study skins of forms for which sufficient material from the breeding grounds was available. In the field, one can often distinguish the sexes of the members of a pair when the birds are together. He lists the bill measurements of males and females of three populations of *P. g. grisegena* for which there is adequate material.

The culmen measurements (mm) of European and western Siberian populations of *P. g. grisegena* from Storer (1996) were measured by J Fjeldså from specimens in various European collections:

Arkhangelsk (= Archangel) and Kola (n = 9)

5 males,
range 40.2-44.2: 40.2; 41.5; 41.6; 43.2; 44.2

4 females,
range 38.1-40.3: 38.1; 40.1; 40.1; 40.3

Kazakhstan and the Ob lowlands of western Siberia (n = 9)

4 males,
range 40.2-43.5: 40.2; 41.6; 41.6; 43.5

5 females,
range 35.1-37.2: 35.1; 35.8; 36.1; 36.2; 37.2

Denmark (n = 31)

15 males,
range 38.0-43.2: 38.0; 38.0; 39.0; 39.2; 39.5; 40.0;
40.2; 40.2; 40.2; 40.3; 40.6; 41.5;
42.0; 42.1; 43.2

16 females,
range 31.5-38.6: 31.5; 33.3; 35.0; 35.9; 35.9; 36.0;
36.1; 36.4; 36.8; 36.8; 36.8; 37.1;
37.2; 38.2; 38.5; 38.6

Storer (1996) inferred that these raw data alone are sufficient to demonstrate clearly sexual dimorphism in three populations of the nominate subspecies. He negated Bocheński's (1994) principal reason for separating the Old and New World races of the Red-necked Grebe into two species. Storer (1996) noted, that the failure to find (clear) sexual dimorphism illustrates some of the problems in using material from old collections, much of which was found in winter, away from the breeding grounds, and was too deteriorated to prepare as study skins. This results in samples of mixed origins and many unsexed or wrongly sexed individuals.

7.4.5 *Stout and Nuechterlein (1999)*

These authors list the linear measurements and mass data of North American Red-necked Grebes and compare these with European birds from R W Storer (linear measurements, original data) and Piersma (1988b) (mass data from Lake IJsselmeer, The Netherlands). The wing length is the "arc" wing length and the bill length was measured from the nostril.

The linear measurements (mm) and mass (g) of North American *P. g. holboellii* and European *P. g. grisegena* of Stout and Nuechterlein (1999) are shown as mean ± SD (range; n):

	<i>P. g. holboellii</i>	<i>P. g. grisegena</i>
<u>Wing length</u>		
Male	197.5 ± 6.9 (186-210; 38)	171.3 ± 7.9 (162-185; 19)
Female	191.5 ± 5.5 (183-201; 24)	167.4 ± 7.7 (156-183; 18)
<u>Bill length (from nostril)</u>		
Male	36.6 ± 3.1 (30.8-43.6; 32)	28.2 ± 2.1 (25.4-32.6; 19)
Female	34.5 ± 3.4 (29.0-44.2; 22)	27.2 ± 1.6 (24.7-30.4; 17)
<u>Bill depth</u>		
Male	13.3 ± 1.0 (10.8-14.8; 28)	11.6 ± 1.2 (10.0-15.0; 14)
Female	12.4 ± 0.8 (11.1-14.7; 21)	10.4 ± 0.8 (9.1-11.8; 14)
<u>Tarsus length</u>		
Male	63.6 ± 3.5 (56.5-72.4; 35)	54.3 ± 2.7 (49.0-57.2; 16)
Female	60.7 ± 2.9 (55.4-65.3; 22)	53.4 ± 2.5 (48.5-57.5; 13)
<u>Body mass</u>		
Male	1,330.9 ± 192.9 (1,082-1,616; 15)	873.5 ± 124 (n = 11)
Female	1,052.4 ± 241.7 (640-1,270; 5)	785.4 ± 97 (n = 8)

Stout and Nuechterlein (1999) come to the conclusion that males average larger than females, but that the sexes are not always distinguishable by size. The authors write that the European and West Asian birds are substantially smaller than the North American and East Asian Red-necked Grebes.

7.4.6 Fjeldså (2004)

In his monograph on grebes Fjeldså (2004) catalogues the measurements and weights of Red-necked Grebes. Measurements given in this book refer to museum specimens, as usual in the taxonomic literature. Fjeldså (2004) explains that most museum measurements are subject to post mortem shrinkage (see 7.1). The measurements were pooled from his own data and literature, where possible.

Fjeldså (2004) gives the ranges of the wing length, the bill length and the tarsus length of the nominate subspecies *P. g. grisegena* and of *P. g. holboellii*. He treated East Asian (East Siberian) specimens separated from the other (North American) birds of the subspecies *P. g. holboellii*.

The wing length was measured by folding and flattening the wing against the ruler, but the author points out that because of the strongly curved remiges of grebes, some publications use the wing chord instead. The bill length was defined as the length of the exposed culmen to the feather edge.

The ranges of the linear measurements of *P. g. grisegena*, *P. g. holboellii* and the East Siberian Red-necked Grebes from Fjeldså (2004) are in millimetres and the ranges of the weights in grams (in brackets *n*):

	<i>P. g. grisegena</i>	<i>P. g. holboellii</i>	Siberian birds
<u>Wing length</u>			
Male	160-192 (49)	186-210 (38)	172-212 (15)
Female	153-186 (44)	183-201 (24)	170-190 (12)
<u>Bill length</u>			
Male	35-50 (49)	46-57 (38)	49-56 (15)
Female	32-44 (44)	44-52 (24)	41-51 (12)
<u>Tarsus length</u>			
Male	49-61 (49)	56.5-72.4 (38)	60-62 (15)
Female	48.5-60 (44)	55.4-65.3 (24)	57-60 (12)
<u>Body mass</u>			
Male	570-1,000 (49)	1,082-1,616 (38)	1,100-1,200 (15)
Female	550-1,000 (44)	640-1,270 (24)	560-1,000 (12)

Fjeldså (2004) remarks that the birds from the East Asian populations have slightly smaller bill dimensions than the North American birds but are also referred to as *holboellii* (see 7.5.2).

7.4.7 Concluding Remarks

All authors agree that the subspecies *P. g. holboellii* is substantially larger and heavier than the nominate race *grisegena*. The average lengths of the wing and tarsometatarsus of European birds are *c.* 87% of those of American birds (see 8.1 for more details).

The most striking difference is the size of the bill. The average bill length of European birds is *c.* 79% of the length of North American birds. Measurements suggest that *holboellii* has a larger bill compared with its skull than the nominate subspecies: the average bill length of *P. g. holboellii* is *c.* 59% of the total length of the cranium and in *P. g. grisegena* it is *c.* 55% (see 8.1 for more details).

7.5 Geographic Variation in Measurements Within the Subspecies (see also 8.1)

The geographic variation among populations within each subspecies may be so large that some authors distinguished new subspecies. Their work is treated here in chronological order of publication.

7.5.1 Hortling (1929)

Hortling listed the ranges of wing and bill lengths (mm) of Finnish birds (in brackets *n*) and contrasted them with those of Danish, Swedish and Central European Red-necked Grebes (from various authors):

	Male	Female
<u>Wing length</u>		
Finland	175-180 (6)	174-178 (4)
	180-190 (3)	167 (1)
Denmark	170-173	159
Sweden		166-184
Central Europe		165-183
“Central Europe” (Witherby 1919-24)	160-180*	155-176
<u>Bill length</u>		
Finland	38-46.5 (9)	33-38 (5)
Denmark	35-39	37
Sweden		39-41
Central Europe		24-41.5
“Central Europe” (Witherby 1919-24)	35-45	35-40

* One bird 190 (Witherby 1919-24)

As a result of these data and egg measurements Hortling (1929) deduced that Finnish (and northern) birds are larger than Danish and Central European birds and probably belong to another subspecies. He proposed the name *Podiceps grise(i)gena schiøleri* Hortling (terra typica Finland). Although this race was later synonymized, geographic variation really exists. Moving from south-western Scandinavia to near the northern distribution limit of the species, the bill increases in length by as much as 11% and becomes slenderer, its shape approaching that of the Great Crested Grebe (Fjeldså 1982a) (see 8.1 for more details).

The ranges of bill length (exposed culmen to the feather edge, mm; in brackets *n*) of Fjeldså (1982a, 1983, 2004) confirm the special status of the northern birds:

<i>P. g. griseigena</i> (without the northern birds)	32-47 (81)
<i>P. g. griseigena</i> , birds from North Finland, Kola, Arkhangelsk, Dvina	40-50 (12)
<i>P. g. holboellii</i> , Siberian birds	41-56 (27)
<i>P. g. holboellii</i> , North American birds	44-57 (62)

It is understandable that some specimens of the “*schiøleri*” type have erroneously been referred to *holboellii* in the literature.

7.5.2 Lönnberg (1936)

Lönnberg (1936) gives the linear measurements (mm) of two males and three females from Kamchatka (acquired by Sten Bergman):

Wing length

Male	185, 189
Female	177, 178, 180

Bill length

Male	51, (the second male 51?)
Female	40, 46, (the third female 48?)

Tarsus length

Male	60, 62
Female	58, 59, 60

Lönnberg (1936) compares the Kamchatka birds with *holboellii* and conjectures that the Kamchatka birds belong to a separate subspecies which he named after Sten Bergman *Podiceps grise(i)gena bergmani* Lönnberg. Although the East Asian populations tend to have slightly smaller dimensions than the North American birds (see 7.4.6), *P. g. bergmani* has not been recognized and Kam-

chatka and other East Asian populations are referred to as *holboellii*.

7.5.3 Dolgushin (1960)

Dolgushin (1960) gives the wing lengths of two populations from Kazakhstan, and Dement’ev and Gladkov (1969) of birds from Lake Balkhash:

North Kazakhstan and the basin of the Syrdarya River	147-183 mm
Balkhash and Alakol’ Lakes basin	170-210 mm
Lake Balkhash, according to Dement’ev and Gladkov (1969)	176-182 mm

Dement’ev and Gladkov (1969) record that Red-necked Grebes from Lake Balkhash are somewhat smaller than East Siberian birds, but larger than the western Red-necked Grebes. Dolgushin (1960) notes that in Kazakhstan two subspecies of the Red-necked Grebe breed: the nominate in North Kazakhstan and the basin of the Syrdarya, and the rather long-winged subspecies *Podiceps grise(i)gena balchaschensis* Korelov in the South-east part of the country, in the Balkhash-Alakol’ basin. However, all the specimens from the latter area examined by Fjeldså (1982a) are within the *griseigena* range and hardly qualify for taxonomic recognition. Until now the exact status of these birds is uncertain.

7.6 Comparison of Measurements of Red-necked, Great Crested and Slavonian Grebes

7.6.1 Measurements of Red-necked and Great Crested Grebes

Cramp *et al.* (1977) catalogue the wing length (the distance from the carpal joint to the tip of the longest primary, measured by pressing the wing against a ruler and stretching it fully), the bill length (the chord of the culmen from the implantation of the feathers to the tip of the upper mandible) and the tarsus length (measured from the middle point of the joint between the tibia and tarsus behind to the middle point of the joint between the tarsus and the middle toe in front of the leg) of *Podiceps griseigena griseigena* and *Podiceps cristatus cristatus* (museum specimens).

The linear measurements (mm) of *P. g. griseigena* and *P. c. cristatus* from Cramp *et al.* (1977) are shown as mean \pm SD (range; *n*):

	<i>P. g. grisegena</i>	<i>P. cristatus cristatus</i>
<u>Wing length</u>		
Male	175 ± 8.09 (164-193; 21)	195 ± 4.2 (175-209; 28)
Female	169 ± 9.79 (153-182; 23)	184 ± 5.6 (168-199; 19)
<u>Bill length</u>		
Male	40.0 ± 2.47 (34-44; 25)	51.8 ± 1.9 (41-55; 22)
Female	37.1 ± 2.25 (33-42; 30)	46.1 ± 1.9 (38-50; 23)
<u>Tarsus length</u>		
Male	55.9 ± 3.36 (51-63; 17)	63.6 ± 2.6 (59-71; 23)
Female	53.8 ± 2.48 (49-60; 26)	61.6 ± 2.4 (57-65; 23)

It is clear that the Great Crested Grebe is larger than the nominate subspecies of the Red-necked Grebe.

Fjeldså (2004) lists the measurements and weights (body mass) of Red-necked Grebes and Great Crested Grebes from museums. He gives ranges of the wing length (the wing folded and flattened against the ruler), the bill length (exposed culmen to the feather edge) and the tarsus length of *P. g. grisegena*, *P. g. holboellii* and *Podiceps c. cristatus*.

The ranges of the linear measurements of *P. g. grisegena*, *P. g. holboellii* and *P. c. cristatus* from Fjeldså (2004) are in millimetres and the ranges of the weights in grams (in brackets *n*):

	<i>P. g. grisegena</i>	<i>P. g. holboellii</i>	<i>P. c. cristatus</i>
<u>Wing length</u>			
Male	160-192 (49)	186-210 (38)	175-209 (204)
Female	153-186 (44)	183-201 (24)	168-199 (199)
<u>Bill length</u>			
Male	35-50 (49)	46-57 (38)	42-58.8 (204)
Female	32-44 (44)	44-52 (24)	39-51 (199)
<u>Tarsus length</u>			
Male	49-61 (49)	56.5-72.4 (38)	59-71 (23)*
Female	48.5-60 (44)	55.4-65.3 (24)	57-65 (199)
<u>Body mass</u>			
Male	570-1,000 (49)	1,082-1,616 (38)	596-1,490 (204)
Female	550-1,000 (44)	640-1,270 (24)	568-1,380 (199)

* From Cramp et al. (1977). Erroneously, Fjeldså (2004) reported 59-55.

P. g. grisegena is smaller than *P. c. cristatus*; but *P. g. holboellii* is about as large and long-billed as the latter. The geographic variation in the Red-necked Grebe (not only

between the subspecies but also within the subspecies) is probably caused by selection due to the presence or absence of Great Crested Grebes *Podiceps cristatus* (see 9.1.5 and 14.5 for more details). The differences between the subspecies might be interpreted as a character release in North America in response to allopatry of Great Crested Grebes. Alternatively, it might be postulated that the Red-necked Grebe was American in origin and was adapted to a situation with no large congener. Spreading to the western Palearctic, the Red-necked Grebe showed character displacement in response to sympatry of Great Crested Grebes, except in its northern breeding area (North Finland, Kola, Arkhangelsk and the Dvina basin), where the Great Crested Grebe is rare or absent (Fjeldså 1983) (see 7.5.1).

7.6.2 Measurements of Red-necked and Slavonian Grebes

Samples of Red-necked and Slavonian Grebes *Podiceps auritus* that had drowned in gill nets in Lake IJsselmeer (The Netherlands) while foraging in winter were analysed for body mass and linear dimensions by Piersma (1988b). Although his main purpose was to study the nutrient reserve levels and diet of grebes, he gives accurate linear measures of the birds which are helpful to compare measurements of both species.

The measurements taken were: wing length (straightened chord), exposed culmen length, tarsus length (length of the metatarsus, from the posterior side of the ankle joint to the distal end of the metatarsus, with the foot flexed at right angles to the tarsus), body length (length of the stretched bird from the bill tip to the end of the body) and body mass.

To correct the fresh body mass for variable amounts of water in the plumage, Piersma (1988b) multiplied the fresh body mass by 0.978 in “moist” birds, 0.931 in “wet” ones and 0.913 in “very wet” ones, these values being derived from experiments. He furthermore subtracted the fresh mass of fish in the oesophagus and also the average fresh mass of the stomach content (which is on average 12 g in Red-necked Grebes and 8 g in Slavonian Grebes).

The linear measurements (mm) and mass (g) of freshly drowned Red-necked and Slavonian Grebes from Lake IJsselmeer, The Netherlands, collected during the non-breeding season, are shown as mean ± SD and, in brackets, *n* (Piersma 1988b):

Dimension	<i>Podiceps g. grisegena</i>	<i>Podiceps auritus</i>
<u>Wing length</u>		
Male	178.5 ± 8.0 (11)	145.8 ± 3.2 (6)
Female	170.3 ± 4.0 (7)	132 (1)
<u>Bill length</u>		
Male	44.1 ± 3.1 (10)	25.0 ± 2.2 (6)
Female	37.8 ± 1.9 (8)	21 (1)
<u>Tarsus length</u>		
Male	55.5 ± 3.4 (9)	44.8 ± 2.5 (6)
Female	51.7 ± 2.4 (6)	42 (1)
<u>Body length</u>		
Male	443 ± 19 (10)	340 ± 10 (5)
Female	415 ± 14 (8)	300 (1)
<u>Body mass</u>		
Male	873.5 ± 124 (11)	502.3 ± 54 (6)
Female	785.4 ± 97 (8)	393 (1)

Clearly, Slavonian Grebes are much smaller than Red-necked Grebes. The bill of Red-necked Grebes is almost twice as large as the bill of Slavonian Grebes.

8. Systematics and Origins

8.1 Geographical Variation in the Red-necked Grebe; Description of the Subspecies

Two very well marked subspecies in the Red-necked Grebe are recognized. The nominate *Podiceps grisegena grisegena* (Boddaert) breeds in Europe and West Asia, and *Podiceps grisegena holboellii* Reinhardt ("Holboell's Grebe") breeds in North America and East Asia (Storer 1979). Since the Red-necked Grebe is absent in Central Siberia, the distribution areas of the two forms do not overlap.

The two subspecies differ in body size, bill size and colour (for photographs of *P. g. holboellii*, see Fig. 17, 18, 19 and 20). *P. g. holboellii* is substantially larger and heavier than the nominate race *grisegena* (see also chapter 7). Storer (1992) stated that the lengths of the humerus and tarsometatarsus (tarsus) of a small skeleton of *P. g. grisegena* from Europe are less than 75 percent of those of a large *P. g. holboellii* from North America. The average lengths of the wing and tarsometatarsus of European birds are c. 87% of those of American birds (calculated from various sources).

The most striking difference is the size of the bill. The average bill length of European birds is c. 79% of those of North American birds (calculated from Cramp *et al.* 1977, who defined the bill length as the length of the chord of the culmen from the implantation of the feathers to the tip of the upper mandible, and Bocheński 1994, who measured the distance from the tip of the upper mandible to the processus frontalis of the os nasale, and Stout and Nuechterlein 1999, who used the length from the nostril). The average bill length of *P. g. holboellii* (defined as the distance from the tip of the upper mandible to the processus frontalis of the os nasale) is c. 59% of the total length of the cranium (defined as the distance from the tip of the upper mandible to the protuberantia occipitalis) and in *P. g. grisegena* it is c. 55% (calculated from Bocheński 1994). These measurements suggest that *holboellii* has a larger bill compared with its skull than the nominate subspecies.

In the breeding birds of the race *holboellii* the yellow colour of the bill extends more distally on the lower mandible. The birds are rather pale, showing a lighter back, cheeks and neck (Fjeldså 1982a, Storer 1996, Fjeldså 2004). Among the breeding plumage examples of *P. g. holboellii* from Kolyma, Anadyr, Primorskiy Kray (Primorye Territory), Sakhalin, Kamchatka, Alaska, and Greenland and Iceland (stragglers), the fore-necks were tawny, the breast cinnamon, not burnt sienna (deep reddish-brown) and ferruginous (reddish brown or rust-coloured) as in the nominate race. The dorsal feathers of *holboellii* had much more pronounced light feather edges (Fjeldså 1973b).

Bocheński (1994) examined the skeletons of 59 specimens of *P. g. grisegena* and 48 of *P. g. holboellii* and concluded that the latter (in contrast to *P. g. grisegena*) shows a great sexual dimorphism in the size of all skeletal elements. The subspecies also show absolute size differences (which may reach the level of no overlap), differ in the proportions of their bodies and in their colour, and occupy completely separate distribution areas (and, consequently, probably do not interbreed). Bocheński (1994) considered them as separate species (*Podiceps grisegena* and *Podiceps holboellii*). However, it is probable that Bocheński's sample included examples of the main breeding range of the nominate subspecies, as well as of extreme northern populations so that geographic variation masked sexual dimorphism. Storer (1996) demonstrated based on culmen measurements, a clear sexual



Fig. 19: Juvenile Red-necked Grebe *P. g. holboellii*. Photo: A Konter (Canada)

Fig. 19: Juveniler Rothalstaucher P. g. holboellii.



Fig. 20: Juvenile Red-necked Grebe *P. g. holboellii*, throat-touching. Photo: A Konter (Canada)

Fig. 20: Juveniler Rothalstaucher P. g. holboellii, "Kehle-berührend" (throat-touching).

dimorphism in three populations from Europe and West Siberia for which there is adequate material [9 birds – males and females - from Kazakhstan and the Ob lowlands of western Siberia, 31 from Denmark and 9 from Arkhangelsk (Archangel) and Kola]. Storer's study negated Bocheński's principal reason for separating the Old and New World races of the Red-necked Grebe into two species (see also 7.4.4). However, Mlíkovský (2010a) remarks that further research may confirm a split as *holboellii* is larger and much longer-billed than the nominotypical *griseigena*. Perhaps it is important to stress that the exact definitions of the terms "species" and "subspecies" are still controversial. This explains why there is no consensus of opinion about the precise taxonomic rankings of the different populations of Red-necked Grebes.

Geographic variation exists among populations within each subspecies. Moving from south-western Scandinavia to near the northern distribution limit of the species (inland areas from Kuopio to Finnish Lapland, Kola, Arkhangelsk, Dvina), the mean wing length increases by 1.5% and the tarsus by 2.5%. The bill increases in length by as much as 11% and becomes slenderer, its shape approaching that of the Great Crested Grebe (Fjeldså 1982a). Hortling (1929) proposed the name *Podiceps grise(i)gena schiøleri* Hortling (terra typica Finland) for the rather large, stocky and quite long-billed Finnish and northern birds. However, this race has not been recognized. Some specimens of the "*schiøleri*" type have erroneously been referred to *holboellii* in the literature (see also 7.5.1).

Birds from the Balkhash-Alakol' area (South-East Kazakhstan) are described as rather long-winged, and this population was considered as a separate subspecies *Podiceps grise(i)gena balchaschensis* Korelov (Dolgushin 1960). However, all specimens from this area examined by Fjeldså (1982a) are within the *griseigena* range, and hardly qualify for taxonomic recognition. The exact status is uncertain, and it is possible, but unlikely, that the isolated populations in South-East Kazakhstan and Kyrgyzstan (Oz. Sonkel) may represent outposts of *holboellii*. Other possibilities are that they either belong to the nominate subspecies *griseigena* or that they constitute intermediate populations (Kuročkin 1985, O'Donnel and Fjeldså 1997, Fjeldså 2004, Gavrillov and Gavrillov 2005) (see also 7.5.3).

Red-necked Grebes from East Asian populations have slightly smaller bill, tarsus and wing dimensions than the North American birds. Lönnberg (1936) described birds from Kamchatka as a separate race *Podiceps grise(i)gena bergmani* Lönnberg. Thomasson (1956) and some other authors considered all the East Asian Red-necked Grebes as belonging to *bergmani*. The subspecies has not been accepted and the birds from East Asian populations are referred to as *holboellii*. However, the fact remains that Nearctic birds are somewhat larger and longer-billed than East Asian individuals, which may suggest that the two forms occupy separated breeding and wintering areas, so there is probably no interbreeding (East Asian individuals may winter mainly along East Asian coasts and Nearctic birds mainly along Pacific and Atlantic coasts of North America, Stout and Nuechterlein 1999). If separable at a taxonomic (subspecific?) level, the name *bergmani* would be available for the East Asian form (Mlíkovský 2010a) (see also 7.4.6 and 7.5.2).

The geographical variation in the Red-necked Grebe might be interpreted as a character release in response to allopatry of Great Crested Grebes, or as a character displacement in response to sympatry of this species (Fjeldså 1982a, 1983) (see 9.1.5 and 14.5 for more details).

8.2 Taxonomic Position of the Red-necked Grebe in the Grebe Family

8.2.1 The Genera of Grebes

The grebes (Podicipedidae) are the only family of the order Podicipediformes. The family is fairly homogeneous, and its internal taxonomy is based on anatomical, morphological and ethological characteristics (Llimona and Del Hoyo 1992). Because grebes possess complex, stereotyped behaviour which is unusually well adapted for analysis, ethological studies are important in the determination of the taxonomic position (Storer 1960).

Fjeldså (2004) recognizes seven genera (with 22 species):

1. *Rollandia* ("golden grebes", 2 species)
2. *Tachybaptus* ("dabchicks", 5 species)
3. *Podilymbus* ("piedbills", 2 species)
4. *Poliiocephalus* ("white-haired grebes", 2 species)
5. *Podiceps* (Great Grebe, 1 species)
6. *Podiceps* ("plumed grebes", 8 species)
7. *Aechmophorus* ("swan grebes", 2 species)

Studies in the 1960s led to the recognition of two main lineages in the grebe family (tribes or clades). The first group *Tachybaptus-Podilymbus* (“Podilymbini”) is characterized by the lack of nuptial plumes and the chicks have rufous down in one or more patches on the crown. Members of this group have a well-developed *Musculus flexor perforatus digiti II* in the shank with a separate bony canal through the hypotarsus for its tendon of insertion. This muscle flexes the second toe and presumably provides flexibility in the use of the foot (the canal is consistently absent in *Tachybaptus dominicus* of the New World, a condition which probably resulted from an independent loss of the muscle). *Tachybaptus* and *Podilymbus* show simple displays (Storer 1963a, 1967, 2000a, Fjeldså 2004) (for a photograph of a Little Grebe *Tachybaptus ruficollis*, see Fig. 21).

The species of the second group *Podiceps-Aechmophorus* (“Podicipedini”) have nuptial plumes, and downy young with a bare crown patch. They show increased specializations for diving, involving the loss of the above-mentioned hypotarsal canal. The clade shows a weaker ability to stand upright, culminating in *Aechmophorus* and *Podiceps gallardoi*, and is well known for its spectacular and complex courtship rituals (Storer 1967, Fjeldså 2004).

More recently, a phylogenetic analysis of morphological data of grebes supported a basal divergence between a group (clade) uniting the “dabchicks” (*Tachybaptus* and *Poliiocephalus*) and a group uniting *Podilymbus*, *Rollandia*, *Podiceps* and *Aechmophorus* (Ksepka *et al.* 2013). Thus, Ksepka *et al.* (2013) did not recognize the group “Podilymbini” (*Tachybaptus* and *Podilymbus*) of Storer (1963a) and classified *Tachybaptus* and *Podilymbus* into two separate groups. In their vision, the genus *Podilymbus* belongs to the clade of *Aechmophorus* and *Podiceps*. In this monograph, the classification of Storer (1963a, 1967, 2000a) and Fjeldså (2004) is accepted.

The genus *Rollandia* (restricted to South America) shares some traits with the *Tachybaptus-Podilymbus* group and could be basal to all other living grebes, diverging before the grebes split up into the two clades (Fjeldså 1985, 2004). That *Rollandia* is the genus probably nearest to the ancestral stock has been confirmed by cladistic analysis. It and the genus *Poliiocephalus* (formed of two species, endemic to Australia and New Zealand) share similar courtship ceremonies which, according to detailed analysis, are potential precursors of more elaborate behaviour patterns of other grebes. The overall similarity of these ceremonies, which are unlike those of other



Fig. 21: Little Grebe in breeding plumage. Photo: H Niesen (Netherlands)

Fig. 21: Zwergetaucher im Brutkleid.

grebes, and their occurrence in two “primitive” grebes, *Rollandia* and *Poliocephalus*, which are confined to the Southern Hemisphere, is consistent with a southern origin of grebes (Storer 2002).

Fjeldså (2004) stated that *Poliocephalus* shows similar platform behaviour as *Podiceps* and *Podicephorus*, but the courtship displays are simple, appearing in-between those of *Rollandia* and *Podicephorus*.

The genus *Podicephorus* is monotypic and is erected for the Great Grebe by Bocheński (1994). Until the end of the 20th century most authors placed *major* in *Podiceps* (*Podiceps major*), but many acknowledged that the species did not belong in this genus. The Great Grebe resembles the Red-necked Grebe in plumage colours and some authors united both species in the genus *Pedetaithya* J J Kaup, 1829. Simmons (1962) proposed to place the Red-necked Grebe together with the Great Grebe in one superspecies. His species group *Pedetaithya* (which is situated within the genus *Podiceps*) only comprises this superspecies *Podiceps major-griseigena*. However, *major* differs from the Red-necked Grebe and the other *Podiceps* species in many behavioural, morphological and anatomical characters, and the relationship is a rather distant one. Great Grebes are intermediate between the “primitive” genera and *Podiceps* in the character of the hypotarsal canal for the tendon of the *Musculus flexor perforatus digiti II* (this canal is small or absent in *major*) (Storer 2000a).

Unlike the *Podiceps* species, Great Grebes have no Discovery Ceremony (perhaps their Nodding and Turning Ceremony corresponds with the Discovery Ceremony) and no Cat-display. They do not perform a Penguin-dance and a Weed-dance (Storer 1963a, b, Greenquist 1982). Clearly, the Great Grebe is not closely related to any genus hitherto known and erecting a new genus is well justified. The generic name *Podicephorus* is not appropriate (mixing Greek and Latin), but Storer (1996) and Fjeldså (2004) considered it valid.

8.2.2 The Genera *Aechmophorus* and *Podiceps*

A number of similarities, for example the existence of nuptial plumes and the absence of the extra canal in the hypotarsus, show that there is a close phylogenetic relationship between *Aechmophorus* and *Podiceps*. *Aechmophorus* shares with *Podiceps* Habit-preening, a Weed Ceremony and Parallel-barging (Fjeldså 1982b, Storer

and Nuechterlein 1992) and not surprisingly the swan grebes were classified as *Podiceps* (*P. occidentalis* and *P. clarkii* Lawrence, 1858) in earlier days. However, a number of differences justify the division into two genera.

The two species of *Aechmophorus* are larger than the *Podiceps* species, having a longer and slender bill and a very long neck. Their slender bodies have a quite close-fitting plumage of rather short feathers compared with other grebes. *Aechmophorus* is also defined from relatively long primaries and a black-and-white plumage at all seasons (Fjeldså 2004).

Although the downy young of both genera have a bare crown patch, the highly characteristic, striped pattern of *Podiceps* chicks is nearly obliterated in *Aechmophorus*. The sides of the head of small *Aechmophorus* chicks have only a suggestion of striping, but this pattern is faint, almost like damask and best seen in fluid-preserved specimens (Storer 1967, Storer and Nuechterlein 1992). The near obliteration is unique among grebes and supports the conclusion that *Aechmophorus* is best considered a valid genus.

The swan grebes with their very long and sinuous neck are unique among grebes in possessing striking chevron-shaped processes on the posterior cervical vertebrae. These are associated with a mechanism that permits them to thrust forward the head like a spear (Storer 2000a).

Apart from the structure of the cervical vertebrae, there are more differences in skeletal morphology between *Aechmophorus* and the other genera:

1. *Aechmophorus* possesses an elongated crest projecting backwards beyond the os parietale. There is a distinct bend between the crest and the os occipitale. In the other genera there is no such crest (*Podicephorus major* shows an “uncharacteristic” state) (Bocheński 1994).
2. In the cranium of grebes there is a narrow groove (ending with an opening in its upper part) on each side of the foramen occipitale magnum (large opening in the skull through which the spinal cord passes). In *Aechmophorus* the openings are approximately at the height of the upper part of the foramen, in *Podiceps* and the other genera they are usually approximately half-way up (or lower) (Bocheński 1994).

3. In *Aechmophorus* the edge of the os occipitale is rectangular. On its upper side, above the foramen occipitale magnum, there is a small peak. The other genera never show this pattern, with the exception of *Podiceps major*. In *Podiceps g. grisegena*, *P. g. holboellii* and *P. cristatus* the edge of the os occipitale normally forms a very wide arch (Bocheński 1994).
4. The *Podiceps* species differ from *Aechmophorus* in having a distinct drop from the intercotylar depression to the hypotarsus (there is a gradual gradient in *Aechmophorus*), and in having a deep muscle scar on the internal side of the hypotarsus (Murray 1967).
5. *Aechmophorus* has a relatively long metatarsus (Sharpe 1898, cited in Fjeldså 2004).

The most remarkable ceremony of the *Podiceps* species is the Discovery Ceremony, which constitutes the initial ceremony of most pair-bonding. The Discovery Ceremony is a common, derived feature of *Podiceps* – a sequence remarkable enough to be a relevant part of a generic diagnosis. *Aechmophorus* does not show this ceremony and also lacks a Cat-display, an important element of it (Fjeldså 1982b, Storer and Nuechterlein 1992). Although Silvery *Podiceps occipitalis* and Junín Flightless Grebes *Podiceps taczanowskii* resemble swan grebes in many behavioural respects (particularly the significance of Parallel-rushing by several birds in aggressive disputes and courtship), the majority of the similarities may be superficial and are most probably due to parallel ethological adaptations for colony-breeding (Nuechterlein, cited in Fjeldså 1982b).

8.2.3 The Genus *Podiceps*

Podiceps is the most diversified genus, with eight species, and these are normally divided into two main subgroups. The first (the crested subgroup) is composed of the Red-necked, Great Crested (see Fig. 22 and 23) and the Slavonian (Horned) Grebes (see Fig. 24), three species that are often sympatric. The second (the eared subgroup) consists of five closely related species. The Black-necked Grebe (Eared Grebe) *Podiceps nigricollis* (see Fig. 25), the probably extinct Colombian Grebe *Podiceps andinus*, often considered only a subspecies of the former, and the Silvery Grebe (Silver Grebe) *Podiceps occipitalis* form a superspecies, which usually includes the Junín Flightless Grebe (Puna Grebe) *Podiceps taczanowskii*. However, this species is sympatric on Lake

Junín, in Peru, with the Silvery Grebe's race *juninensis*, which has also been claimed as a distinct species, on the grounds of morphological and ethological differences with the nominate form. The fifth species of the subgroup is the Hooded Grebe *Podiceps gallardoi*, rather surprisingly discovered in 1974 and only known from Patagonia. It is very close to the other species of the eared subgroup and has been reported to have hybridized with the Silvery Grebe (Llimona and Del Hoyo 1992).

The crested species are well defined from plumage characters, notably of the downy young, and the Red-necked Grebe is grouped with Great Crested and Slavonian Grebes in part because of these characters (Stout and Nuechterlein 1999). The crown pattern of the downy young of the crested species is characterized by a central white stripe or spot behind the bare crown spot. This lies between or anterior to the ends of the white neck stripes which form the borders of the dark mid-dorsal stripe. The next lateral white stripes on the neck run forward, diverging as they reach the crown and then converging to join on the forehead. The central white patch on the crown is narrowest in *grisegena* and broadest in *cristatus*. In addition to lacking this patch, young of *nigricollis* and *occipitalis* differ from those of the species of the crested group in having two white stripes on each side of the crown (Storer 1967; see drawings in Storer 1967, p. 474, and in Harrison and Castell 2002, p. 38). The striped Hooded Grebe chick most closely resembles that of the Silvery Grebe (Nuechterlein and Johnson 1980/1981).

Unlike the eared *Podiceps* species, the Red-necked, Great Crested and Slavonian Grebes show stereotyped and complex Weed Ceremonies with Weed-dances (associated with parallel Weed-rushes in Slavonian Grebes) (Cramp *et al.* 1977, Fjeldså 1982b, Stout and Nuechterlein 1999). The birds, holding weed, approach in threat postures. During the Weed-dance they use similar postures as in the aggressive Tall penguin-dance. The Weed-trick displays of the eared group are quite different. The weed presentation in these species is quite simple and normally separate from dancing or barging displays, and is apparently related to nest-building behaviour, closely associated with sexual motivation (Fjeldså 1982b, 2004).

Another difference between the two subgroups is that the crested species are pugnacious and territorial, show sustained postures in Forward-threat (Forward-display) and perform ritualized threat dives (Token-dives)



Fig. 22: Great Crested Grebe in breeding plumage, Cat-display. Photo: H Niesen (Netherlands)

Fig. 22: Haubentaucher im Brutkleid, Katzenstellung.

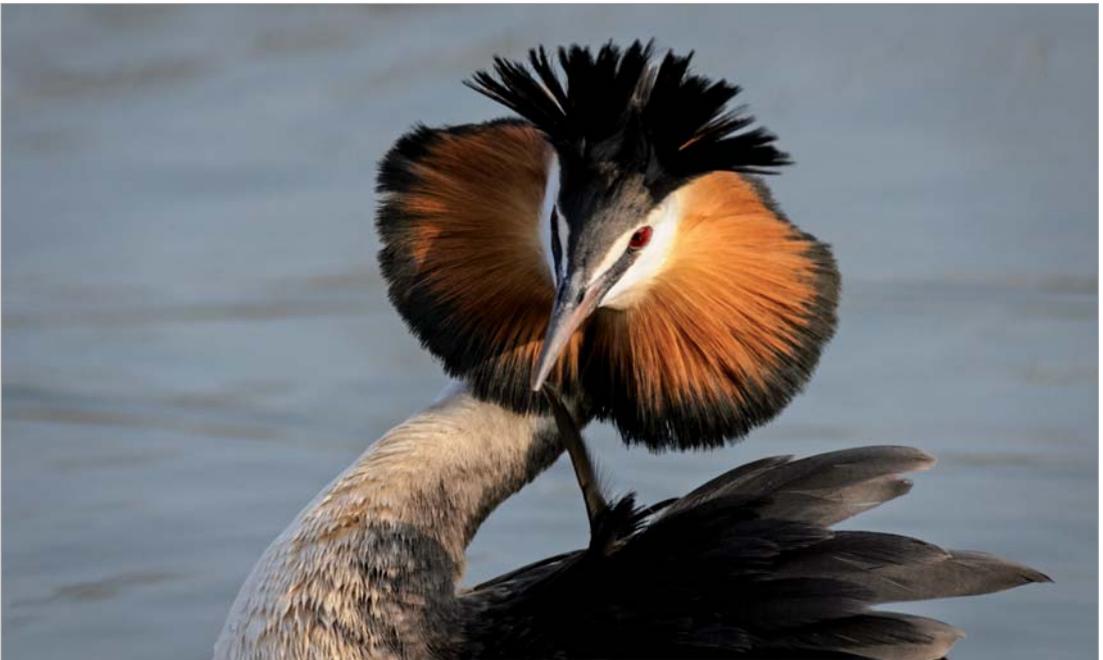


Fig. 23: Great Crested Grebe in breeding plumage, Habit-preening. Photo: N Paklina (Netherlands)

Fig. 23: Haubentaucher im Brutkleid, Scheinputzen.



Fig. 24: Slavonian (Horned) Grebe *Podiceps auritus cornutus* in breeding plumage. Photo: A Konter (Canada)

Fig. 24: Ohrentaucher *Podiceps auritus cornutus* im Brutkleid.



Fig. 25: Black-necked Grebe in breeding plumage, with downy young. Photo: H Niesen (Netherlands)

Fig. 25: Schwarzhalsstaucher im Brutkleid, mit Dunenjungen.

(Cramp *et al.* 1977, Fjeldså 1982b, Vlug 1983, 2002a). The eared species are gregarious and breed in colonies. They deviate from the Red-necked Grebe and the two other crested species by a simplification of the agonistic behaviour, which probably was conditioned by the colony-breeding: the birds suppress the Hunched-threat and the stationary Forward-threat, and they never perform Token-dives (Fjeldså 1982b).

We may conclude that there is evidence that the members of the crested subgroup are closely related. Comparative cytogenetics suggests that within this subgroup Red-necked Grebes are more closely related to Slavonian (Horned) than to Great Crested Grebes: there is no difference in the number or morphology of chromosomes of *Podiceps grisegena* and *auritus*; the diploid number of chromosomes in both species is 80, but *P. cristatus* has a diploid number of 78 and has a centric rearrangement in chromosome 12 (Shields 1982).

8.3 Relationships of Grebes and Divers

Historically Gaviiformes (divers or loons) and Podicipediformes have been regarded as closely related, due to their similarity to each other. Both are foot-propelled diving birds and have the feet set far back on their streamlined and short-tailed or almost tail-less bodies. The bony elements of their feet are strongly flattened (Fjeldså 2004, Wiki 2004).

Mayr and Clarke (2003), Fjeldså (2004) and Wiki (2004) (*cf.* Cracraft 1982) mention further similarities between grebes and divers:

Head, Skull and Bill:

1. The shape of the skull is similar
2. The schizognathous palate is very similarly modified
3. A zygomatic process is present
4. The pointed bills are holorhinous

Trunk:

5. The sternum lacks a robust spina externa rostri
6. The pelvis is elongate, compressed mediolaterally with a very long post-acetabular part
7. 17-18 vertebrae are ankylosed in the synsacrum

8. The corpus of the pygostyle is perforated caudoventrally

Wing:

9. The humerus has a long and low deltoid crest

Toes and Legs:

10. The femur is short, stout and distinctly curved
11. The hypotarsus possesses medial and lateral cristae which surround the flexor tendon canal
12. The *Musculus gastrocnemius* possesses two heads
13. The *Musculus fibularis longus* does not branch to the *Musculus flexor perforatus digiti III*
14. The tendon of *Musculus flexor digitorum longus* is enclosed within an osseous canal

Despite these similarities many characters of divers and grebes vary considerably. Gardner (1925) found that the tongue of divers differs from that of grebes, although they have similar food habits. Stolpe (1932, 1935) examined osteological and myological characters and catalogued extensive differences between the two taxa (Stolpe 1935, p. 124) which combined with fundamental lack of homology between the key elements of the diving apparatus, persuaded Stolpe against a close relationship between them. He concluded that divers and grebes were an exemplar of convergent evolution, with similar morphologies dictated by shared environmental stimuli grafted onto disparate phenotypes. Stolpe's research reached broad consensus in the ornithological community (Wiki 2004).

Storer (1960) investigated the evolution in diving birds and confirmed the fundamental lack of homology between the varying analogous modifications for a diving niche in both grebes and divers. As Stolpe (1935), he concluded that divers and grebes are outstanding examples of convergent evolution. Three of the major morphological differences indicative of the convergent evolution of the foot-propelled diving birds are in the cnemial crest (a long bony extension of the tibiotarsus and/or patella to which the powerful extensor muscles of the leg are attached), the pelvic musculature, and the structure of the foot (Storer 1960). In their analysis of genetic distance data, Sibley and Ahlquist (1990) reached the conclusion that the divers are not closely related to the grebes and that the grebes have no close living relatives. They assumed that the grebe lineage branched early from the common ancestor of the other groups in

the Ciconiides and seemed to be the sister group of the Phaethontida (tropicbirds), Sulida (e.g. boobies and gannets), and Ciconiida (e.g. herons, flamingos, storks, penguins, petrels and albatrosses).

Gadow (1893, pp. 122-4), Stolpe (1935), Hudson (1937), Storer (1960), Cramp *et al.* (1977), Storer (1982), Johnsgard (1987), Sibley and Ahlquist (1990), Fjeldså (2004) and Wiki (2004) cite a number of differences between the two taxa:

Plumages:

1. The dorsal apterium is limited to the neck in divers, to the back in grebes
2. There are two generations of natal down in divers, in grebes only one
3. The chicks are uniformly dark brown in divers; grebe chicks are normally distinctly striped
4. There are 11 primaries in divers (10 functional), 12 in grebes (11 functional)
5. Divers have at least 23 secondaries, grebes 17-22
6. There are 16-20 normal tail-feathers in divers; in grebes the rectrices are vestigial

Head, Skull and Bill:

7. The tongue of divers possesses a large patch of spinous processes at the base; in grebes there is a single caudal row of such processes
8. Divers have large supraorbital glands; these are small in grebes
9. The hind process of the lower mandible is long in divers; this process is short or absent in grebes

Trunk and Neck:

10. There are 14-15 cervical vertebrae in divers, 17-21 in grebes
11. Divers have paired carotids; grebes have a single left carotid
12. The sternotracheal musculature is symmetrical in divers, asymmetrical in grebes
13. The dorsal (thoracic) vertebrae are free in divers, fused in grebes
14. Divers have a long sternum (twice as long as wide) and the posterior border is notched; grebes have a broad and short sternum, notched at each side, plus a triangular middle notch
15. Divers have a remarkably short preacetabular

pelvic length; in grebes the preacetabular pelvic length is substantially longer

16. The pelvic muscle formula in divers (*Gavia immer*) is ABCDXAmV, in grebes (*Podiceps nigricollis*) BCX

Wing:

17. Divers have a long and narrow carpometacarpus; the carpometacarpus in grebes is short and narrow

Toes and Legs:

18. Divers have a very long cnemial crest (cnemial process) on the tibiotarsus and no patella; in grebes a large, pyramidal patella and the tibiotarsus together form the crest
19. The hypotarsus in divers is ridged, terminating in a triangular, open area; the hypotarsus in grebes is complex, with canals and grooves
20. The anterior toes are webbed in divers; in grebes are all the toes uniquely lobate (lobed)

Pneumatization of the Skeleton:

21. Divers have a very dense skeleton with almost a total lack of pneumatization; the skeleton of grebes is virtually nonpneumatic, but the long appendicular bones and some parts of the skull are pneumatized

Not only morphological, but also molecular data have usually failed to support the holophyly of a proposed diver/grebe clade (e.g. Hackett *et al.* 2008). Yet cladistic analyses continue to unite these groups based upon characters which are known to be convergent, on grounds of parsimony (Wiki 2004). Cracraft (1982) believed that his cladistic analysis of the skeletons of Gaviidae and Podicipedidae supports the hypothesis that they (together with the Hesperornithiformes) form a monophyletic group, which he named "Gaviomorphae". Mayr and Clarke (2003) offered an analysis of neornithine phylogeny. Their primary analysis resulted in support for a sister group relationship between the two taxa. They remarked, however, that exclusion of the Gaviidae and reanalysis of the data set, recovered the sister group relationship between flamingos Phoenicopteridae and grebes proposed from molecular sequence data.

8.4 Relationships of Grebes and Hesperornithiformes

In most skeletal features grebes parallel the Hesperornithiformes, which are among the best known of the

Cretaceous birds. Hesperornithiformes had teeth and were flightless, heavy-boned, fish-eating, foot-propelled diving birds. They rotated the toes in a fashion like grebes and therefore apparently had lobate webbing (Feduccia 1999, Tudge 2002). Many authors regarded them as early grebes or divers and believed that grebes originated in the Cretaceous. Consequently, grebes were perceived as being primitive. Gadow (1893), who laid the foundation for modern classification, placed the grebes and divers near the beginning of his classification list of birds, near the primitive and extinct aquatic birds with teeth. The avian systematists of the following century based their classification on that of Gadow, and so grebes (and divers) were perceived as being primitive and placed near the beginning of most published sequences of birds.

However, the bulk of evidence supports the theory that there is no phylogenetic relation between grebes and Hesperornithiformes. In *Hesperornis* and its relatives, the cnemial crest is formed by the enormous patella alone; in grebes it is compounded by a fusion of the patella and the tibiotarsus. This, among other things, demonstrates that the Hesperornithiformes are merely convergent with, rather than related to, grebes (Storer 1960, Feduccia 1999).

8.5 Relationships of Grebes and Flamingos

A hypothesis on flamingo relationships was set up by Van Tuinen *et al.* (2001), who analysed mitochondrial and nuclear DNA sequences as well as DNA-DNA hybridization data and found strong support for sister group relationship between flamingos Phoenicopteridae and grebes. A monophyly of the taxon Phoenicopteridae + Podicipedidae has not been proposed before, probably because each of these two groups is so exceptionally specialized for a particular lifestyle. Flamingos are long-legged filter-feeders whereas grebes are morphologically quite divergent foot-propelled diving birds (Mayr 2004). Not only molecular but also morphological and oological analyses strongly support sister group relationship between the two taxa. Both groups have similarly built, long, sinuous necks and very short bodies, and they resemble each other also in many skeletal details.

Mayr (2004) carried out a cladistic analysis of a character matrix of 70 morphological characters for 17 ingroup taxa. The following characters were optimized as synapomorphies of the taxon Phoenicopteridae + Podicipedidae:

Skeleton:

1. At least the fourth to the seventh cervical vertebrae are strongly elongated, and the processus spinosus is forming a marked ridge. The shape of the cervical vertebrae of flamingos is very characteristic and strongly resembles that of grebes (see number 13 of the synapomorphies)
2. Both taxa have at least 23 praesacral vertebrae (all vertebrae cranial to synsacrum). In flamingos, there are 23 praesacral vertebrae; in grebes the number varies from 23 (e.g. *Tachybaptus ruficollis*) to 26 (e.g. *Podiceps grisegena*) (in most other birds there are between 18 and 21 praesacral vertebrae)
3. At least four thoracic vertebrae are fused to a notarium. In flamingos, four vertebrae are fused; in grebes the number usually varies between four and five
4. The humerus has a marked oval depression at the insertion site of *Musculus scapulohumeralis cranialis*. This character was regarded by some authors to be a unique feature of flamingos, but it is also present in grebes
5. The distal end of the ulna has a marked depressio radialis
6. The phalanx proximalis digiti majoris is very elongated and narrow craniocaudally (ratio length to craniocaudal width more than 4.5)
7. The distal rim of the condylus medialis of the tibiotarsus is distinctly notched

Musculature:

8. *Musculus iliotibialis lateralis, pars acetabularis* is absent
9. *Musculus caudofemoralis, pars caudalis* is absent

Plumage:

10. The wing has 11 (functional) primaries

Eggs:

11. The eggs are covered with a chalky layer of amorphous calcium phosphate

Two additional morphological synapomorphies of flamingos and grebes were described by Manegold (2006):

12. The presence of nail-like unguis phalanges
13. Prominent caudolateral projections on the ventral side of the cervical vertebrae (processes ventrolaterales)

Virtually none of the morphological characters presented above has been recognized as potential synapomorphies of a flamingo-grebe clade before the work of Mayr (2004), although the derived similarities shared by flamingos and grebes are difficult to explain by convergence, given the very different living habits of both taxa (but see below for comments from Storer 2006). The name *Mirandornithes* was coined by Sangster (2005) for the flamingo-grebe clade.

Interesting in this context is that all known species of the family Amabiliidae (a taxon of the parasitic tapeworms or cestodes) are grebe specialists, except for the monotypic nominate genus, which is confined to flamingos (Storer 2000b). Cestodes have a high degree of host specificity and the presence of a taxon which is found exclusively in grebes and flamingos is further evidence for their close relationship (Mayr 2004).

Storer (2006) doubts the grebe-flamingo connection. He sees two basic problems with Mayr's (2004) paper. The first involves the author's failure to use the mass of basic natural-history information relevant to the subject. Storer (2006) alleged that Mayr (2004) failed to appreciate that crossing-over is a common way for a parasite to move from one definitive host to another. Similarly, according to Storer (2006), Mayr's (2004) inability to explain how the structure of the feet could change from webbed in flamingos to the far more complex structure of grebes' feet, or vice versa, indicates that any such connection must have occurred before either line took to the water, which is unlikely in Storer's (2006) opinion. Storer (2006) claimed that the second problem with Mayr's (2004) paper is his not considering whether convergence might be involved in some characters, such as the notarium. Storer (2006) concludes that these points weaken the argument for any sister-group relationship between grebes and flamingos. However, Mayr (2007) refuted the criticism well.

Not only Storer (2006), but also Livezey (2011) criticizes the grebe-flamingo connection. Livezey (2011) performed a combined-evidence analysis of 2,954 morphological characters combined with 2,944 nucleotide sequences for the RAG-1 nuclear gene. This analysis supported two shortest trees, a strict consensus of which was largely resolved. In both trees, *Phoenicopterus* was the sister group of *Ciconia*, and *Gavia* the sister group of *Podiceps*. However, many other molecular and morphological analyses

support the sister group relationship between flamingos and grebes (e.g. Chubb 2004, Cracraft *et al.* 2004, Ericson *et al.* 2006, Hackett *et al.* 2008, Mayr 2008).

There is a Tertiary fossil sister group of the flamingos, the swimming or perhaps diving Palaelodidae that may have been grebe-like in appearance and behaviour. The foot bones of *Palaelodus* (Palaelodidae) show many similarities with those of grebes and other foot-propelled diving birds, e.g. the tarsometatarsus is mediolaterally compressed, the hypotarsus is complex and some flexor tendons are enclosed in bony canals. Mayr (2004) wrote that the shared similarities in the foot structure of grebes and palaelodids are best interpreted as plesiomorphic resemblances which were already present in the last common ancestor of Podicipedidae, Palaelodidae and Phoenicopteridae. It thus seems that an aquatic way of living is primitive for the clade grebes + palaelodids + flamingos, and not evolved independently in stem group representatives of Podicipedidae and Palaelodidae, particularly as extant flamingos still occasionally feed while swimming (Mayr 2004).

At first sight, a monophyly of the taxon Phoenicopteridae and Podicipedidae seems strange. However, considering their ecological requirements, it is indeed not that difficult to imagine a common origin. Fjeldså (2013) wrote that one needs simply to forget the traditional view that grebes dive to catch fish. Most grebe species, in fact, feed mainly on small invertebrates, chiefly crustaceans and insect larvae, not much bigger than the plankton organisms consumed by flamingos. As already stated, it is noteworthy that grebes and flamingos share a family of parasitic tapeworms Amabiliidae that exploit various aquatic bugs Hemiptera, dragonflies Anisoptera and damselflies Zygoptera as intermediate hosts (see also 8.6). Both groups prefer shallow wetlands with extraordinary concentration of arthropods, as are usually found in isolated or ephemeral wetlands without fish populations, which otherwise tend to control the food webs of wetlands. Some grebe species spend part of the year in saline lakes, often together with flamingos, but the two groups have clearly diverged at some point in time, the flamingos specializing on duck-like filter-feeding in the shallow parts of the salt pans, while the grebes specialized to become superb divers (Fjeldså 2013). The above mentioned palaelodids, being rather unspecialized swimmers, may have given rise to grebes and flamingos.

Relationships of Mirandornithes (flamingo-grebe clade) with other birds are yet unresolved. Combined analysis of mitochondrial and nuclear DNA sequences placed Mirandornithes in an unresolved polytomy with numerous non-passerine groups. Several theories on the placement of Mirandornithes exist. The results of a phylogenomic study of Hackett *et al.* (2008) suggested that the flamingo-grebe clade is a sister taxon to the Columbiformes (pigeons and doves), Mesitornithiformes (mesites), Pteroclidiformes (sandgrouses), and Phaethontidae (tropicbirds) clades. After the publication of Hackett *et al.* (2008) a number of authors accepted a relationship between the Mirandornithes and Columbimorphae (pigeon-sandgrouse-mesite) clades and brought them together in the Columbea. However, other studies often contradict the results of the work of Hackett *et al.* (2008).

There are arguments for a relationship between the (flamingo-) grebe clade and gruiform birds (rails, cranes and bustards) (see 8.6). Morgan-Richards *et al.* (2008) do not share this view. They give a description of the evolutionary relationships of modern birds based on complete mitochondrial genomes and conclude that the flamingo-grebe clade may well form a sister clade to the Charadriiformes (shorebirds); their site-stripping technique showed this relationship to be stable, from which they infer a common evolutionary history.

Livezey and Zusi (2007) formulate a higher-order phylogeny of modern birds based on comparative anatomy and concluded that the Charadriiformes are the sister-group to the Ralliformes (rails and finfoots). Therefore, the theory that grebes arose from marsh inhabiting rail-like ancestors (see 8.6) is not necessarily in contradiction to the findings of Morgan-Richards *et al.* (2008).

8.6 The Origins of Grebes

It is currently believed that the members of the genus *Rollandia* are closest to the ancestral stock of the grebe-family (see 8.2.1). Two lines from it exist, one leading to the large-footed and wide-bodied grebes, which feed largely on sessile or slow-moving organisms; and the other, leading to the more stream-lined, smaller-footed and fast-swimming pursuit divers. The former leads through the Old World members of *Tachybaptus* to *Podilymbus*, whereas the latter leads through *Poliiocephalus* and *Podiceps* to *Podiceps* and *Aechmophorus* (Storer 2000a). *Rollandia* shares some traits with the *Tachybap-*

tus-Podilymbus group and, speaking generally, species of these genera inhabit small open sheets of water in marshes and swamps. This would suggest that ancestral grebes were associated with dense vegetation cover, where they fed on a large variety of arthropods. Specializations for chasing fish on open lakes represent more recent developments (Fjelds  2004).

It is possible that gruiform birds (rails, cranes and bustards) have a basal position in the large water bird assemblage, and the early members of this assemblage may have been small, rail-like birds (Sibley and Ahlquist 1990, Fjelds  2004). Because grebes show some similarities to gruiform birds in their neck musculature and skull (Feduccia 1999) and the ancestral grebe-flamingo clade supposedly lived in marshes (see 8.5), it is very well probable that grebes arose from marsh inhabiting rail-like ancestors (Fjelds  2004, Storer 2004). In becoming adapted for an aquatic existence, the grebes developed not webbed feet, but stiff lobes firmly attached to the toe-bones. The spaces between the toes would have permitted stems of stiff vegetation (which might have damaged the webs) to stand between the toes as the birds moved through the marshes (Storer 2004). The serrated rear edge of the tarsus of grebes could possibly help cutting stalks of lax waterweeds (Fjelds  2004).

Mature nymphs of dragonflies climbing out of the water to metamorphose on stems of aquatic vegetation might have been among the first aquatic invertebrates to attract evolving grebes to forage in the water. Studies on helminths (parasitic worms) offer some support for this view. As already mentioned (see 8.5), cestodes (tapeworms) are the most abundant intestinal parasite of grebes. With one exception each, two related families of tapeworms, the Amabiliidae with seven genera and 30 species and the Dioecocestidae with a single genus and seven species specialize on grebes as their definitive hosts and all but two of the known intermediate hosts of these parasitic worms are the nymphs of dragonflies or the closely related damselflies (Storer 2000b, 2004).

It is difficult to determine the time of origin of the grebes. Early birds diversified throughout the Jurassic and Cretaceous, becoming capable fliers with supercharged growth rates, but were decimated at the end-Cretaceous extinction. True modern birds – members of the crown group Neornithes – are a mostly post-Cretaceous radiation, although there is some fossil evidence

for Cretaceous species. After the mass extinction, the Neornithes explosively diversified, culminating in more than 10,000 species distributed worldwide today (Brusatte *et al.* 2015). Based on tentative calibrations of the molecular clock (provided by Moum *et al.* 1994), Fjelds  (2004) stated that grebes possibly diverged from their nearest now living relatives about 44.7 million years ago in the middle Eocene, but Ericson *et al.* (2006) assumed that grebes separated from their sister group, the flamingos, in the Oligocene. Torres *et al.* (2014), using mitochondrial (mtDNA) and nuclear (nDNA) markers, calibrated the divergence of flamingos and grebes at 32.6 million years ago (early Oligocene) based on *Adelalopus hoogbutseliensis*, a stem phoenicopteriform from the earliest Oligocene of Belgium. They calibrated the divergence of extant grebes at 8.7 million years ago (late Miocene) based on *Thiornis sociata*, a grebe from the late Miocene of Spain.

America (maybe the Southern Cone of South America) seems to be the likeliest place of the origin of grebes because it has the greatest number of genera and species, including all the most “primitive” genera, except *Poliocephalus* of Australia and New Zealand. However, South America, Antarctica and Australia were once one plate, which rifted in two not until about 44 million years ago. Australia and Antarctica became separate continents, but South America and Antarctica retained their Gondwanan connection. The region of Patagonia and its exceptionally wide continental shelf were attached to the Antarctic Peninsula. The link between South America and Antarctica became tenuous and was eventually severed completely, crustal separation leaving deep water between them by 36 million years ago. The continent of Antarctica after this break was now isolated, surrounded by an ever-broadening, cool, circumpolar ocean with unrestricted circulation around the continent. Antarctica lost the modifying influence of warm-surfaced neighbouring continents and became thermally isolated (Redfern 2002). Thus, one has to consider that at the time of the origins of grebes the land masses that once made up the southern continent Gondwanaland were still close together and that Antarctica may have had pleasant (temperate) summers (Flower and Kennett 1994). However, we must take into account that long and dark winters would force the Antarctic grebes to move out to the coasts in winter. Marine wintering would have facilitated dispersal to New Zealand and Australia (ancestors of *Poliocephalus*) (Fjelds  2004). Storer (2002) wrote it as fol-

lows: “At the time estimated (...) for the separation of grebes from their relatives, South America, Antarctica, and Australia were connected as the continent, Gondwanaland. Up until the mid-Miocene, the climate of Antarctica was sufficiently warm to support populations of grebes. So, in spite of the tenuous evidence, I think it quite likely that the grebes arose either on Antarctica or South America, but probably not Australia, because of its much smaller grebe fauna....”

It is worth noting that the phylogeny of the dabchick/pied-bill group of grebes is consistent with the view that this lineage colonized the Old World via Antarctica and land areas on the periphery of the Indian Ocean (Fjelds  2004).

A southern origin of grebes would also explain why grebes apparently sprung into existence in essentially their modern form, when judged from the northern hemisphere fossils (Olson 1989, *cited in* Fjelds  2004).

8.7 Origins of the Red-necked Grebe

Podiceps is the largest and most recently diverged genus within Podicipedidae. Ogawa *et al.* (2015), using genetic data from mitochondrial markers, estimated that the last common ancestor of the Red-necked Grebe and the Slavonian (Horned) Grebe existed around 3.38 million years ago (Pliocene). We must assume that the divergence of the Red-necked Grebe and the Great Crested Grebe occurred at the same time or somewhat later (*cf.* Fjelds  2004, p. 142) or earlier (*cf.* Shields 1982). The place of origin of *Podiceps grisegena* is unknown. At least two scenarios are possible. Did the species arise as a large form in North America, adapted to a situation with no large *Podiceps cristatus*, and expanded its range into the western Palearctic where the residents subsequently became smaller through competition with the large congener (character displacement)? Or did it arise as a small species in Europe, expanded its range eastward to North America where it became larger in the absence of *Podiceps cristatus* (character release)? (Fjelds  1983, Storer 1992).

8.8 Fossil Evidence

The known fossil record of grebes is poor, going back only to the middle Oligocene of Kazakhstan *c.* 30 million years ago from where a few unstudied bones are known (Storer 2004). The earliest fossils confidently referred to

grebes appear in the early Miocene, about 25 million years ago, but the similarity between ancient and modern species prevents our gaining much insight into evolutionary relations (Feduccia 1999).

Sveč (1984) described the earliest definite fossil grebe, *Miobaptus walteri*, from the early Miocene (Ottomanian) of the Czech Republic. He concluded that this fossil species was a fully-formed grebe, morphologically and consequently perhaps also ecologically similar to the recent Little Grebe *Tachybaptus ruficollis*.

Thiornis sociata from late Miocene (Vallesian) deposits in Spain was originally described as a gallinule, family Rallidae (Gruiformes), but Olson (1995) clearly showed that *Thiornis* was a grebe. It is a nearly complete skeleton lacking the skull and upper cervical vertebrae but including impressions of the tail and the tips of several primary feathers. Olson (1995) proposed to place it in the genus *Podiceps* as *Podiceps sociatus*, but Storer (2000a) wrote, that if this species belongs in any recent genus it is best placed in *Tachybaptus* and not in *Podiceps*. The skeleton Olson (1995) and Storer (2000a) analysed needs to be re-examined carefully for phylogenetic assessment.

No other satisfactorily preserved and adequately described grebe species from the Miocene are known. The material of *Podiceps oligocaenus*, perhaps from the early Miocene of Oregon, is only very poorly preserved. The locality and therefore the date of this fossil are in question, and so it is impossible to draw reliable conclusions from this material (Sveč 1984, Fjeldsø 2004).

It seems reasonable to conclude from the few fossils remains that the early grebes may have been relatively small and broad-bodied. So *Tachybaptus*, *Poliiocephalus* or *Rollandia* may be more appropriate for analysing affinities of grebes than the large and streamlined fish-pursuing species such as Great Crested and Western Grebes.

By the Pliocene (about 5.1–2 million years ago) all the fossil grebes are inseparable from living genera (Feduccia 1999). A number of fossils referred to as *Tachybaptus*, *Podilymbus*, *Podiceps* and *Aechmophorus* are known from Pliocene deposits (Wetmore 1937, Murray 1967, Olson 1994), for example *Podiceps subparvus* and *Podiceps arndti* from California. The last one is from the Upper Pliocene San Diego Formation and possibly very close

to *Podiceps grisegena*, differing in several characters of the leg bones (Storer 1992).

The fossil species of grebes, particularly those of the genus *Podiceps*, are in great need of revision. A detailed analysis of the increasing amount of fossil material available and of the abundant recent material might well lead to a greater understanding of the evolutionary history of *Podiceps grisegena* and other recent members of the genus (Storer 1992).

9. Habitat and Interspecific Competition

9.1 Breeding Habitat

The Red-necked Grebe nests mainly in boreal but also in temperate and steppe climatic zones. Its range extends considerably farther to the north (to 71° N in Eurasia) than the Great Crested Grebe, and it even breeds in freshwater pools in the zones of the taiga and shrub tundra (Voous 1960, VlUG 2002a). In North America, it breeds in the northern prairies, western parklands, and forests, north to near the northern limit of trees (70° N) (Stout and Nuechterlein 1999).

The breeding-habitat of *Podiceps grisegena* overlaps with that of the Slavonian Grebe. However, in the western Palearctic *grisegena* is markedly more continental than *auritus*. The species flourishes here best away from oceanic fringing lands and arctic-alpine terrain (Cramp *et al.* 1977).

The Red-necked Grebe breeds predominantly on water bodies in lowlands and on great plains, e.g. in the lowlands around the Baltic Sea, in the Danube delta, in deltas in the Ukraine, and in the steppes of Central Asia. However, sometimes it nests on lakes in mountains or mountainous regions. In eastern areas of Turkey it utilizes small, marshy wetlands to at least 2,250 metres above sea level (m.a.s.l.) for nesting (Kirwan *et al.* 2008). The species nests up to 1,902 m.a.s.l. in Armenia (Lake Sevan) and to 3,016 m.a.s.l. in Kyrgyzstan (40–50 pairs on Lake Sonkel'). In Kazakhstan *grisegena* breeds on Lake Kulsay in the Kungey Alatau Mountains, and in East Asia on mountain lakes of East Kamchatka (Kuročkin 1985). In North America, too, the birds inhabit mostly lowlands and are uncommonly found at higher elevations on lakes in mountainous regions (Stout and Nuechterlein 1999). Their nests have been located from 150 to 1,370 m elevation in

British Columbia; most were reported here between 760 and 910 m (Campbell *et al.* 1990).

9.1.1 Breeding Habitat of the Nominate Subspecies (*Europe and West Asia*)

In Europe, the major breeding locations are inland water bodies, typically fairly shallow (often up to 1.5 m deep), having at least some littoral plants such as reed *Phragmites* or bulrush (cattail) *Typha*, and an abundant growth of submerged vegetation, in which larger invertebrates and small vertebrates flourish (Vlug 1997, 2000, 2002a). Compared with the Great Crested Grebe, the Red-necked Grebe usually inhabits smaller, shallower, and less eutrophic water bodies with a large amount of macrophytes (emergent, underwater and floating plants). In contrast to *Podiceps cristatus*, *P. griseogenus* does not prefer water bodies with considerable open areas (Thomasson 1956, Cramp *et al.* 1977, Lammi 1983, Vlug 1993). With increasing eutrophication, Red-necked Grebes abandon their breeding waters, but the Great Crested Grebe benefits, to a large extent, from hypertrophication. A strong dominance of Red-necked Grebes in a wetland means that the ecosystem has huge populations of aquatic invertebrates and small vertebrates; a dominance of Great Crested Grebes indicates extremely large populations of cyprinid fish (Fjeldså 2004, Kloskowski *et al.* 2010, Vlug 2011).

The smallest recorded breeding site of Red-necked Grebes measured 20 x 20 m and thus had a water area of 400 m² (0.04 ha) (Uckermark, Brandenburg, Dittberner 1996). Though many breeding sites are small, it is not the size that is of overriding importance in habitat selection, but the amount of food and availability of nesting places. Larger shallow lakes with much vegetation also contain Red-necked Grebe prey and suitable nesting sites, and are frequently occupied by the species (Vlug 2000, 2002a). Lake Felchow, Brandenburg, provides an example. On this shallow lake of 160 ha 40 pairs were breeding in 1968 (Dittberner 1996). Another example is Lake Tåkern, a large (46 km² = 4,600 ha), shallow lake, with a maximum depth of 1.5 m and a mean depth of 1 m; in the early 1980s 130 pairs were recorded on this Swedish lake (Svensson *et al.* 1999). In South Finland and Estonia Red-necked Grebes seem to prefer shallow lakes of roughly 20-200 ha (Fjeldså 1973a).

In Central Europe, the Red-necked Grebe is found primarily on extensively farmed fish-ponds and other small

water bodies such as peat-ditches (“Torfstiche”), fens (low-level moors, “Niedermoore”), artificial (man-made) ponds, village ponds, ponds in soil mining areas (“Bodenabbaugebiete”), gravel pit lakes, marl pit ponds, sewage (clarification) ponds (“Klärteiche”), sewage farms (“Rieselfelder”), pools left over from brown coal open cast mining (“Tagebaurestseen”), flooded meadows, fields and polders, natural ponds, field ponds (pothole lakes, “Feldsölle”), ponds in forested areas, temporary water bodies, small channels and stretches of open water in marshes, oxbow lakes, temporary flood water bodies and wetlands near rivers, and lagoons (Tischler 1941, Menzel 1965, Krägenow 1977, Schmidt 1983, Vlug 1993, 2002a, Tomiałojć and Stawarczyk 2003, Dittberner and Dittberner 2006, Zimmermann 2006, Górecki and Stajszczyk 2007, Hessische Gesellschaft für Ornithologie und Naturschutz 2010, Gedeon *et al.* 2014, Krüger *et al.* 2014, Vökler 2014; J Wübbenhorst).

Schleswig-Holstein and Hamburg

In Schleswig-Holstein and Hamburg, Germany, an average of 75% of the breeding population nested on 194 man-made fish-ponds, 3% on 15 other man-made water bodies, 15% on 23 lagoons, 5% on 34 natural ponds, and 3% on 21 lakes (for photographs of breeding sites in Schleswig-Holstein, see Fig. 26, 27, 28, 29, 30, 31, 32 and 33). An average of 33% of the breeding pairs in Schleswig-Holstein used water bodies between 0.05 and 5.0 ha, 17% between 5.1 and 10 ha, 48% between 10.1 and 50 ha, and only 2% occupied water bodies larger than 50.1 ha (Vlug 1993). *Podiceps griseogenus* mostly avoids deep lakes. However, the importance of such lakes in Schleswig-Holstein as breeding sites is growing slightly (especially Selenter See, 2,239 ha, 0-2 breeding pairs 1969-88, 21 breeding pairs 1996, and c. 30 breeding pairs 2008) (Vlug 2000, 2011). On these deep lakes Great Crested and Red-necked Grebes sometimes co-occur in larger numbers. The latter prefer shallow bays with luxuriant vegetation, seldom stray far from the shore and forage primarily within their shallow territorial waters. Great Crested Grebes, on the other hand, usually forage pelagically in deeper waters.

Mecklenburg-Vorpommern (Mecklenburg-Western Pomerania), Brandenburg, and Poland

In Mecklenburg-Vorpommern, Germany, 44 of 80 occupied breeding waters were ponds between 0.5 and 10 ha. The remaining breeding waters were 6 lakes > 50 ha, 15 lakes < 50 ha, 11 marshes and temporary water bod-



Fig. 26: Messin, a fish pond in Schleswig-Holstein near Testorf (6,3 ha, 2017: 3-4 breeding pairs of Red-necked Grebe). Photo: G and R K Berndt (4.7. 2012)

Fig. 26: Messin, ein Fischteich in Schleswig-Holstein bei Testorf (6,3 ha, 2017: 3-4 Brutpaare des Rothalstauchers).



Fig. 27: Rastorfer Gutsteich, an old millpond in Schleswig-Holstein near Rastorf (2 ha, 2016: 1 breeding pair of Red-necked Grebe). Photo: G and R K Berndt (8.5. 2015)

Fig. 27: Rastorfer Gutsteich, ein ehemaliger Mühlenteich (Weiher) in Schleswig-Holstein bei Rastorf (2 ha, 2016: 1 Brutpaar des Rothalstauchers).



Fig. 28: Bekmissen, a flooded marshy area near Schönwalde in Schleswig-Holstein (2017: 1 breeding pair of Red-necked Grebe). Photo: G and R K Berndt (11.5. 2017)

Fig. 28: Bekmissen, ein angestautes Sumpfgebiet (Weiher) bei Schönwalde in Schleswig-Holstein (2017: 1 Brutpaar des Rothalstauchers).



Fig. 29: Struckteich, a flooded marshy area near Zarpen in Schleswig-Holstein (14 ha, 2000: 54 breeding pairs of Red-necked Grebe; 2017: no breeding pairs). Photo: G and R K Berndt (8.7. 2000)

Fig. 29: Struckteich, ein angestautes Sumpfgebiet (Weiher) bei Zarpen in Schleswig-Holstein (14 ha, 2000: 54 Brutpaare des Rothalstauchers, 2017: keine Brutpaare).



Fig. 30: A flooded area near Flemhude, Schleswig-Holstein (13 ha, 2017: 11 breeding pairs of Red-necked Grebe).

Photo: G and R K Berndt (2.5. 2012)

Fig. 30: Ein angestautes Gebiet (Weither) bei Flemhude in Schleswig-Holstein (13 ha, 2017: 11 Brutpaare des Rothalstauchers).



Fig. 31: Old gravel pit near Langwedel, Schleswig-Holstein (2017: 3 breeding pairs of Red-necked Grebe).

Photo: G and R K Berndt (9.6. 2014)

Fig. 31: Alter Kiesgrubensee bei Langwedel, Schleswig-Holstein (2017: 3 Brutpaare des Rothalstauchers).



Fig. 32: A pond created by excavation near Westermarkelsdorf, island of Fehmarn, Schleswig-Holstein (aerial view; the larger body of water on the right of the photograph) (3 ha, 2017: 40 breeding pairs of Red-necked Grebe). Photo: S Lunk (May 2015)

Fig. 32: Baggerteich bei Westermarkelsdorf, Fehmarn, Schleswig-Holstein (Luftaufnahme; das größere Gewässer rechts auf dem Bild) (3 ha, 2017: 40 Brutpaare des Rothalstauchers).



Fig. 33: A lagoon near Hohenfelde, Schleswig-Holstein (1.5 ha, 2017: 10 breeding pairs of Red-necked Grebe). Photo: G and R K Berndt (30.5. 2011)

Fig. 33: Ein Strandsee bei Hohenfelde, Schleswig-Holstein (1,5 ha, 2017: 10 Brutpaare des Rothalstauchers).

ies, and 4 lagoons (Krägenow 1977). In Uckermark, Brandenburg, 12 of 102 inhabited water bodies were < 1 ha, 35 between 1 and 9 ha, 49 between 10 and 99 ha and 6 > 100 ha (Dittberner and Dittberner 2006). In Poland the species is found mainly on fish-ponds and small field ponds (even < 1 ha), but also on oxbow lakes, flooded meadows, gravel pit lakes, small lakes, large shallow lakes and shallow parts of large eutrophic lakes (Tischler 1941, Tomiałojć and Stawarczyk 2003, Górecki and Stajszczyk 2007). Censuses between 1983 and 1985 in Śląsk (Silesia) revealed 600-800 breeding pairs; 96% of the 94 breeding sites were fish-ponds (Dyrzc 1991).

Fennoscandia and the Baltic States

In Fennoscandia and the Baltic States, the Red-necked Grebe nests on smaller and shallower luxuriantly vegetated lakes, on peat-bog pools, ponds, artificial water bodies, small areas of open water in extensive reed swamps, and in shallow bays of large lakes (Vlug 1997, Grell 1998, Norevik 2014). Veromann (1994) stated that the species in Estonia prefers medium-sized and smaller lakes of the karst region in the northern part of the country where the water level fluctuates strongly. These lakes are often eutrophic, being rich in submerged and emergent vegetation, but they can also be almost dystrophic. In Lithuania up to 50% of the total breeding population in the country (between 1996 and 1999) nested on 17 large fish-pond systems (Švažas *et al.* 2000). In Denmark, *grisegeta* mainly occurs in smaller eutrophic lakes, pools created by peat digging, forest lakes, marshes and peat-bogs (Preuss 1969, Olsen 1992, Grell 1998). In Sweden, South Finland, and Estonia, the shallow breeding lakes are often larger (in South Finland and Estonia mainly between 20 and 200 ha) and more eutrophic than those occupied by Slavonian Grebes and are frequently found in open farmland (Fjeldså 1973a, 1977a). In Finland, the species breeds also in the bays of Lake Saimaa (4,400 km²) and a few pairs nest on the Finnish seacoast (Lammi 1983).

An estimated 10% (c. 40 pairs) of the population of Norrland (northern Sweden) in the period from 1975 to 1980 were breeding on the brackish coastal waters of the Gulf of Bothnia, especially on the skerry coast of Piteå and Luleå (Grenmyr 1984, Svensson *et al.* 1999). The percentage of pairs nesting in the coastal areas in Norrland is increasing. Norevik (2014) stated that c. 40% of the population in northern Sweden in 2011 were found along the Baltic Coast and that almost all the other pairs

were breeding in natural inland waters, none were found in artificial water bodies. The situation was different in Götaland (southern Sweden), where none of the birds were recorded in coastal habitats and c. 80% were nesting in artificial water bodies (Norevik 2014).

In the southern parts of the Murmansk Region, the Red-necked Grebe nests on shallow waters (mean depth 1.2 – 3.0 m) from 3.1 to 6.8 ha (*n* = 5 breeding waters) with an abundance of vegetation, especially Yellow Water-lily *Nuphar lutea*, Broad-leaved Pondweed *Potamogeton natans*, Reddish Pondweed *Potamogeton alpinus*, Least Bur-reed *Sparganium minimum* and Slender Sedge *Carex lasiocarpa* (Bakkal *et al.* 2002).

East Europe, European Russia, Turkey and West and Central Asia

In East Europe, European Russia, Turkey and West and Central Asia, the species frequents ponds, small marshy wetlands, larger wetlands, marshy lakes, forest and steppe lakes, and oxbows. This kind of breeding habitat is fairly limited, and so the Red-necked Grebe has a patchy distribution (Johansen 1959, Gordienko 1980, Koshelev 1981, Vlug 1997, 2002a, Kirwan *et al.* 2008).

In South and West Ukraine, it breeds in fresh stagnant waters with a lot of plants and many invertebrates or small fish. Here it reaches high densities on fish-ponds and in deltas (Koshelev *et al.* 1998, Kuchinskaya 2001).

In Kazakhstan and other areas in Central Asia *Podiceps grisegeta* usually inhabits fairly small and shallow water bodies in (forest, lowland and upland) steppes, semi-deserts and deserts (Wassink and Oreel 2007, Ayé *et al.* 2012).

9.1.2 Breeding Habitat of Podiceps grisegeta holboellii (North America and East Asia)

The subspecies *P. g. holboellii* in North America and East Asia breeds mainly on relatively small, shallow, freshwater lakes, often with many plants, on well-vegetated ponds and marshes, and on shallow, sheltered marsh areas and secluded bays of larger lakes, usually with at least some emergent and submergent flora. It is also found on bogs, quiet river channels, alkaline lakes, large irrigation ditches, and borrow pits (Dement'ev and Gladkov 1951/1969, Palmer 1962, Campbell *et al.* 1990, Stout and Nuechterlein 1999, Shimba 2007, Brazil 2009).

The Red-necked Grebe in Eastern Asia nests on richly vegetated marshes and lakes (Dement'ev and Gladkov 1951/1969). During the summer it frequents shallow lakes and marshes in Hokkaido, Japan, breeding where these are reed- or sedge-fringed (Brazil 1991). On the island of Sakhalin it nests on shallow and small fresh water bodies and saline lagoons with a wealth of emergent and submerged vegetation (Eremin *et al.* 1986, Nechaev 1991).

Its breeding grounds in North America are sloughs, ponds, marshy lakes, and deep marshes with many channels and pond-like openings (Job 1936, Pough 1951, Terres 1980). Munro (1941) remarked that studies of "Holboell's Grebe" nesting habitat indicate that preference is shown for shallow lakes usually not less than ten acres (c. 4 ha) in extent, and fairly shallow marsh areas on larger lakes. Palmer (1962) wrote that the summer habitat of the North American Red-necked Grebe consists of quiet inland waters, other than small ponds, having some (often many) emergent plants; it inhabits water bodies on prairies and in woodland. Its breeding range extends out on the tundra. Johnsgard (1987) asserted that in both North America and Europe the species evidently favours water areas surrounded by well-grown forest over those in prairie areas.

In Alaska and Canada the breeding birds are found on shallow freshwater lakes, marshes and slow moving rivers, usually, but not necessarily, with margins or islands of emergent plant life such as *Scirpus* or *Phragmites* (Armstrong 1983, Godfrey 1986).

Yukon Territory

In Yukon Territory the Red-necked Grebe builds its nests in marshy areas of large and small forested lakes and ponds (Sinclair *et al.* 2003).

Northwest Territories

Fournier and Hines (1998) stated that in North America, Red-necked Grebes have been reported to prefer shallow lakes, usually not less than 2-4 ha in extent, for nesting. They investigated a population near Yellowknife, Northwest Territories, and felt that their data supported this observation in that a greater percentage of the ponds available in size categories ≥ 2.1 ha were occupied when compared to smaller size categories, i.e., these ponds appeared to be preferred. However, approximately 41% of all ponds utilized on their study area were less than 2 ha in size and only 35% exceeded 4 ha in size (Fournier and Hines 1998).

British Columbia

In British Columbia the species breeds on sheltered, usually shallow, freshwater lakes (91%; $n = 823$) with emergent and submergent vegetation, in both open and forested regions. Sloughs, alkaline lakes, slow river channels, large open irrigation ditches, bogs, and ponds are used occasionally for nesting (Campbell *et al.* 1990).

Alberta

In Alberta Red-necked Grebes are found on small, shallow lakes greater than 2 ha in size, or in shallow, protected areas and bays of larger lakes. Suitable lakes usually have an extensive emergent and submergent plant life. While the birds are most often found on permanent water bodies, small semi-permanent lakes and potholes may also attract a nesting pair (Semenchuk 1992).

Kevan (1970) investigated a breeding population of Red-necked Grebes on Astotin Lake in Elk Island National Park, Alberta, in 1968 and 1969. She found 89 pairs in 1969. Astotin Lake is a kettle lake with an area of 5.616 km² (561.6 ha), and an average depth of 3.04 metres. Because of its shallowness, and high productivity, the lake is very eutrophic. It has a sinuous shoreline some 19.5 km long, providing numerous protected bays. These bays support rank growths of emergent vegetation. It is in these bays that nesting Red-necked Grebes are most numerous. There are seventeen islands, providing more shoreline and emergent vegetation. Towards the centre of the lake is a large *Phragmites communis* (= *australis*) bed called Reed Island. The lake has large areas with submergent vegetation. The Brook Stickleback *Culaea inconstans* is the only fish in the lake. It is quite numerous, providing food for grebes, herons, gulls, coots, terns, divers (loons) and mergansers.

Riske (1976) studied the grebes in the Pine Lake area in central Alberta. During 1970-76 a maximum of 60 Red-necked Grebe pairs were recorded on Pine Lake, a generally shallow lake with a maximum depth of 10.7 m and a surface area of 402 ha. The author also investigated the species at a total of 17 separate potholes. Eleven of thirteen of the *holboellii*-inhabited potholes and small lakes ranged in size from 2-12 ha. Only two out of a total of 44 occupancies over a three-year period were observed on potholes of less than 2.0 ha in extent. Twelve of thirteen of the occupied water bodies were permanent. Six of the occupied potholes were surrounded by pasture

and seven were surrounded by cropland. About 77 per cent of the utilized potholes (10) had shorelines that were characterized by having less than one-third of the periphery lined by emergent vegetation but over one-third ringed by trees (Riske 1976).

Saskatchewan

The Red-necked Grebe is fairly common on lake-margin marshes of central Saskatchewan and the Cypress Hills. The species' abundance decreases markedly on the sterile lakes of the Precambrian Shield. It nests on the comparatively fresh waters of the Cypress Hills, Last Mountain Lake, Wascana Lake and Condie Reservoir, but is generally only a rare transient on the predominantly saline lakes of the prairies (Smith 1996).

Manitoba

Bent (1919) described vividly the habitat of the Red-necked (Holboell's) Grebe on the marshes of Lake Winnipegosis, Manitoba: "The extensive, deep-water marshes about the southern end of Lake Winnipegosis, intersected by numerous sluggish streams or dotted with many small, shallow ponds, all of which are full of fish or other forms of aquatic life, furnish ideal breeding grounds for this (Red-necked Grebe, JJV) and other water fowl. The banks of the Waterhen River, which flows northward from Lake Winnipegosis into Waterhen Lake, are broadly lined with many miles of tall golden canes swarming with bird life of various kinds; countless yellow-beaded blackbirds are busy with their nesting in the densest canes or clinging to the tops of the swaying stalks and pouring out their ceaseless chatter; Franklin's gulls or black terns are flying overhead with gentle notes of protest; various species of ducks are swimming in the creeks and pond holes; and the graceful western grebes glide in and out among the canes where their nests are hidden. Here the shy Holboell's grebe breeds in abundance, probably more abundantly than anywhere else throughout its extensive range; though it is so seldom seen that one does not realize how common it is until a systematic search is made for nests. Waterhen River and the lake into which it flows are said to have been so named on account of the abundance there of this species, although the name "waterhen," or "poule d'eau," is applied to any of the grebes or coots."

De Smet (1983) studied the Red-necked Grebe in Turtle Mountain Provincial Park, southern Manitoba, during 1980 and 1981. In the Turtle Mountains, single pairs of

Red-necked Grebes nested in lakes ranging from 1.8 to 25.9 ha in size (see 11.3.3 for more details).

Ontario

Sandilands (2005) asserted that the Red-necked Grebe in southern Ontario appears to be confined to very large water bodies, and Peck and James (1983) stated that the species nests in Ontario in marshy areas of freshwater lakes. But Harris (2007) remarked that, although the species in Ontario usually occurs in shallow lakes and bays larger than 2 ha, smaller ponds are used if other water bodies are nearby.

Wheeler (2001) found a large breeding population of Red-necked Grebes on Whitefish Lake (3,015 ha) in the district of Thunder Bay in 1993 (59 pairs) and 1994 (39 pairs). The population was strongly associated with uncultivated Wild Rice *Zizania palustris* stands in shallow bays of the lake.

Wisconsin

In Wisconsin, which is outside the species' core breeding area, most wetlands used for nesting are shallow prairie pothole types with a fairly good cover of emergent vegetation that was usually Hardstem Bulrush *Scirpus (Schoenoplectus) acutus* or cattail (bulrush) *Typha*. Sedge marshes also are used for nesting (Brooks 2006, Mueller 2007) (see 11.3.3 for more details).

Minnesota

Sometimes the breeding lakes are nearly devoid of emergent vegetation, and, at least in Minnesota, the species is often found on fairly large lakes that also support breeding Common Loons *Gavia immer* (Johnsgard 1987). It prefers water bodies where it can nest on places protected from wind and wave action (Campbell *et al.* 1990, Stout and Nuechterlein 1999). A population of 80-100 breeding pairs was found on Lake Osakis, a large (2,537 ha), windblown lake in Central Minnesota. About 80% of the lake is between 1 and 10 m in depth. The birds nested in emergent vegetation, primarily Lesser Bulrush (Narrowleaf Cattail) *Typha angustifolia*, but also Hardstem Bulrush *Scirpus (Schoenoplectus) acutus* and Common Reed *Phragmites australis (communis)* (Nuechterlein *et al.* 2003).

North Dakota

In North Dakota, the species nests on freshwater or slightly brackish permanent water areas that usually are at least 10 acres (4 hectares) in area. It also occurs on

shallow river impoundments. Submerged plants, such as pondweeds, are usually present (Johnsgard 1979, 1987).

9.1.3 Differences Between the Breeding Habitats of the Two Subspecies

It is suggested that, generally, the water bodies occupied by *P. g. grisegena* tend to be smaller, shallower, more eutrophic and with more emergent plants than those used by *P. g. holboellii* (Stout and Nuechterlein 1999). However, this needs further study as the habitat of nominate *grisegena* overlaps much with *holboellii*. *P. g. holboellii* near Yellowknife, Northwest Territories, Canada, inhabits ponds as small as 0.1 ha; the mean size of ponds used for breeding here is 3.7 ha, range 0.1–18.2 ha ($n = 110$ breeding ponds) (Fournier and Hines 1998) (cf. Munro 1941, Riske 1976 and De Smet 1983 in 9.1.2) and the nominate *grisegena* is often found on fairly large lakes, for example in Central, North, and North-East Poland, Estonia, and South Finland (Vlug 2000).

It is also suggested that *holboellii* is an ecological counterpart of the piscivorous Great Crested Grebe (Fjeldså 1983). However, like the nominate form it can live perfectly well on fishless waters (Bent 1919, Stout and Nuechterlein 1999, Paszkowski *et al.* 2004, McParland *et al.* 2010).

9.1.4 New Artificial and New Natural Shallow Waters as Breeding Habitat

New artificial or new natural shallow waters are often colonized quickly after flooding by large numbers of Red-necked Grebes (e. g. 54 pairs in 2000 on Struckteich, 14 ha, Schleswig-Holstein; 35 pairs in 2005 on Dodauer See, Lake Dodau, 17 ha, Schleswig-Holstein; 53–55 pairs in 2006 on Stuerscher See, Lake Stuer, Mecklenburg-Vorpommern) (Vlug 2000, Schonert 2001, Zimmermann 2006, Müller 2010, Vlug 2011).

The development of population numbers on these new water bodies clearly shows how changes in the availability of food and nesting place influence habitat selection. After flooding the terrestrial plants die off and form a rich litter which constitutes a substrate for detritus feeding macroinvertebrates, e.g. water boatmen Corixidae, larvae of plumed gnats Chironomidae, Water Slaters *Asellus aquaticus* and pond snails Lymnaeidae. Nutrients become available to unicellular algae and these microorganisms are consumed by large numbers of small crus-

teans such as water fleas Copepoda. Ten-spined Sticklebacks *Pungitius pungitius* use the small copepods as food. Many amphibians, diving and scavenger beetles occupy the new ponds. All these macrozoans (larger invertebrates and small vertebrates) are important food organisms for Red-necked Grebes and many species of ducks. During the first years Red-necked Grebes and other aquatic birds have few competitors for this rich food source. It is also important that in the first years after flooding many marsh plants are abundant, e.g. Reed Canarygrass *Typhoides (Phalaris) arundinacea*, Water Meadow Grass (Reed Sweet Grass) *Glyceria aquatica (maxima)*, bulrush *Typha* and Common Reed *Phragmites australis*. They provide Red-necked Grebes with nesting places, and many macrozoans live between their underwater stems (Vlug 2011).

The Red-necked Grebe populations increase sharply after flooding, but after a number of years a large decline usually occurs (Vlug 2000, Schonert 2001, Zimmermann 2006, Müller 2010, Vlug 2011). An example is the population of Struckteich, Schleswig-Holstein (see Fig. 29). In 1998, a few months after flooding, 25 pairs bred on this lake. The maximum number, 54 breeding pairs, was recorded in 2000. From then on the numbers declined: 2001 35 pairs, 2002 26, 2003 7, and 2004 3. A number of factors are responsible for this decline. The detritus-based biomass of macroinvertebrates is substantially reduced when the plant litter from the first period has broken down. There is also a gradual increase in the number of invertebrate predators and of large fish which compete with Red-necked Grebes for food. However, it must be stressed that also without fish the decline of Red-necked Grebes and other waterbirds takes place (cf. Andersson and Danell 1982). A number of years after flooding a thick layer of mud often builds up, and the water turbidity increases. The result is that the submerged vegetation, in which macrozoans thrive, disappears. In many new ponds the emergent marsh plants also vanish after a few years, especially when there are large rising water levels (Vlug 2011).

Fish-ponds in Central Europe have one important characteristic in common with new, artificially-created shallow waters, namely the rapid colonization by organisms after flooding. Fish-ponds have an outlet for water and are normally drained in autumn and flooded in spring. In the draining process, a part of the mud is washed away, and during the winter dry period, mineralization

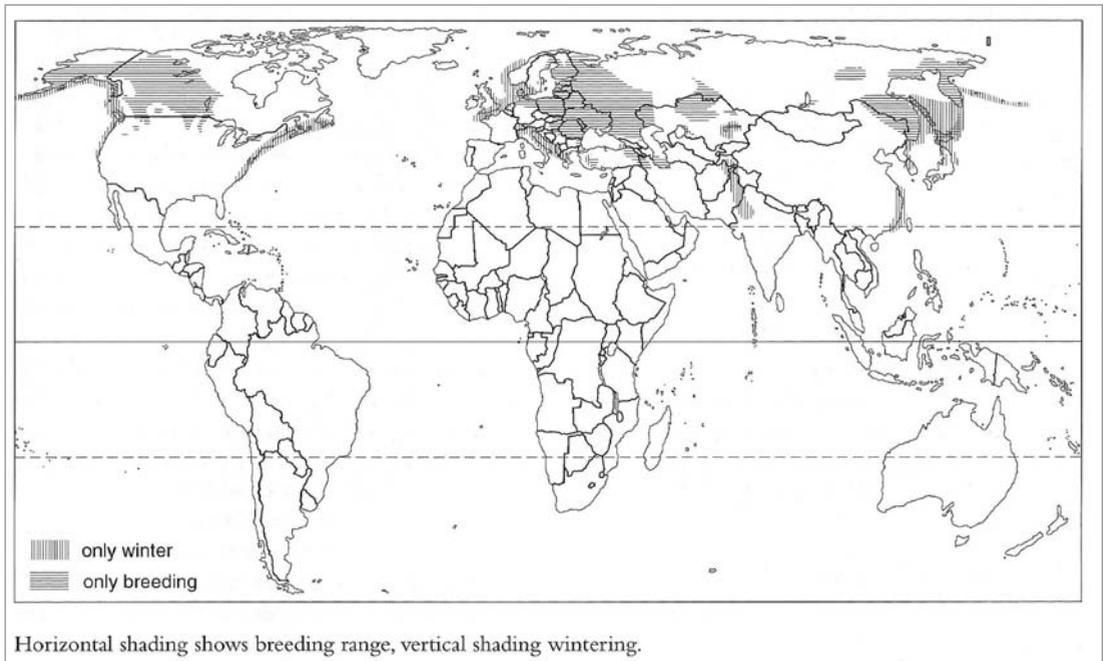


Fig. 34: Breeding and winter distribution of the Red-necked Grebe. From: J Fjeldså (2004), *The Grebes Podicipedidae*, Oxford University Press, page 183, reproduced with kind permission of the author.

Fig. 34: Brut- und Winterverbreitung des Rothalstauchers (only winter = nur im Winter, only breeding = nur Brutvorkommen).

and drying up of the pond-bottom create favourable conditions for rooting submerged macrophytes in the following hydrophase. In spring relatively clean rainwater or water from brooks fills the pond. After re-flooding, the fish-ponds can be quickly colonized by many macroinvertebrates, amphibians, Ten-spined Sticklebacks, Red-necked Grebes and other aquatic birds. In ponds where no draining and re-flooding occurs, a thick layer of mud often builds up, the submerged vegetation disappears and Red-necked Grebes and many other waterbirds often desert the fish-ponds (Vlug 1993, 2000).

9.1.5 Breeding Habitat Selection and Interspecific Competition

Interspecific competition is the interaction which occurs when two or more individuals of different species use a resource in short supply (Campbell and Lack 1985). The competition between species is an important agent in natural selection (Birkhead *et al.* 2014). It is a process that could limit the distribution and abundance of particular bird species. It is one of the paradigms of ecology that, where resources (nest sites or food, for example) are limiting, species with identical needs cannot persist

together indefinitely in the same area. Invariably one will be better adapted or more efficient and will out-compete and replace the other completely. Hence, different species of birds normally differ from one another in distribution, habitat or feeding ecology, or in more than one of these respects (Lack 1971, Newton 2013). Birds living in the same area have distinct ecological niches. Such niche divergence could imply that interspecific competition has been important in their evolution, leading to the species differences that we see today, because any individuals that overlapped in needs too much with other species in the past could have been eliminated by selection (Newton 2013).

The nominate form *grisegena* has a breeding range, habitat and feeding choices that overlap with three other *Podiceps* species. These species are regarded as competitors (Onno 1966, Fjeldså 1973a, Spletzer 1974, Fjeldså 1977a).

Competition Between Red-necked and Great Crested Grebes

Observations of interspecific agonistic behaviour in breeding waters create the impression that Great Crested

Grebes drive away Red-necked Grebes from large, deep lakes to small, shallow waters, for which *grisegena* seems to be morphologically unfit (Spletzer 1974). Spletzer (1974) discovered that in water bodies where Red-necked Grebes outnumber Great Crested Grebes, fights between them are frequently to the disadvantage of the larger species, as the Red-necked Grebes normally win here. However, Great Crested Grebes are at an advantage in larger and deeper lakes with high fish densities (Spletzer 1974, Fjelds  2004). Fjelds  (2004) stated: "Although a large number of wetlands could provide suitable conditions for both, they are still usually inhabited only by one. In some lakes the two species nest in separate years only, and the breeding usually fails for one or both species if both manage to settle in the same year."

However, interspecific agonistic encounters are not necessarily translated into a constrained breeding habitat selection. It is true that Great Crested Grebes very occasionally usurp the territory of Red-necked Grebes, and it is possible that interspecific competition for breeding places may limit the number of Red-necked Grebes in some wetlands suited to both species. However, general habitat choice of *grisegena* is hardly affected by competition with Great Crested Grebes. It is more likely that *grisegena* is, with regard to feeding selection and leg and jaw morphology, better adapted than *cristatus* to a life in shallow waters with an abundance of vegetation. Both species are sufficiently separated ecologically to be able to limit competition to a large extent (Vlug 1993, 2000).

Investigations of population fluctuations of Red-necked and Great Crested Grebes in 37 waters inhabited by both species in Schleswig-Holstein, Germany, do not usually show a significant statistical negative correlation. Thus an increase in numbers of *cristatus* in a lake or pond does not normally cause a decrease in the numbers of *grisegena* or vice versa (Vlug 1993). However, there is sometimes a negative correlation caused by a change in habitat that benefits one species and harms the other. An example is Dodauer See, Lake Dodau, in Schleswig-Holstein. In 2003 the biomass of fish in this pond was low and that of aquatic invertebrates high; 24 breeding pairs of Red-necked Grebes were recorded that year and no Great Crested Grebes. After the biomass of fish became larger and that of macroinvertebrates smaller, *Podiceps cristatus* occupied the pond (7 pairs in 2014) and the population of *P. grisegena* vanished (no breeding pairs in 2014) (Vlug 2011; J J Vlug).

Vlug (1993) investigated 94 breeding sites of Red-necked Grebes in Schleswig-Holstein between 1985 and 1990 (94 breeding sites during 6 years = 564 cases). Great Crested Grebes lived in total in 29% of these 564 cases on Red-necked Grebe breeding sites. However, they were very rarely observed on small breeding sites of *grisegena* between 0.05 and 2.9 ha (only in 0.4% of 234 cases). With increasing size of the *grisegena* sites (from 3 ha to 44 ha), they were to be found in ever greater numbers (50% of 330 cases). If Great Crested Grebes lived on these *grisegena* waters, they did so as a rule at the same time as Red-necked Grebes (in 94% of 166 cases) and rarely alone. So it is unlikely, that *cristatus* has, to any great extent, driven away *grisegena* from one habitat (large, deep lakes) to another (alleged pessimal) habitat (small, shallow waters) (Vlug 1993).

Character Displacement and Character Release

According to Fjelds  (1982a, 1983), geographic variation in the diet and consequently in the habitat choice of the Red-necked Grebe is probably caused by selection due to the presence or absence of Great Crested Grebes, that is by character displacement or character (competitive) release. Character displacement refers to the phenomenon where differences (form and function of the bill and jaw muscles) among both grebe species are accentuated in regions where they co-occur but are minimized or lost where their distributions do not overlap. Character (competitive) release, defined as the expansion of an ecological niche in the absence of a competitor, is essentially the mirror image of character displacement. As already stated above, Red-necked and Great Crested Grebes are nowadays sufficiently separated ecologically to be able to limit competition to a large extent, probably by natural selection resulting in character displacement or release (see 14.5 for more details).

Competition Between Red-necked and Slavonian (Horned) Grebes

Both Red-necked and Slavonian Grebes differ in habitat requirements from the Great Crested Grebe, but the habitat choice of *grisegena* closely resembles that of *auritus*, at least in the Baltic area (South Finland and Estonia). However, there are still differences. The Red-necked Grebe is found mainly on larger water bodies and prefers the most highly eutrophic localities with a wealth of vegetation (Fjelds  1973a). Onno (1958, cited in Fjelds  1973a) found Red-necked Grebes in Estonia almost entirely on shallow, eutrophic lakes with an ex-

tremely luxuriant plant life. Slavonian Grebes also bred on these lakes and on shallow pools, rich in vegetation and nutrients, but were found mainly in more humus-influenced localities in uncultivated regions.

Red-necked and Slavonian Grebes are probably severe competitors (Hall and Lundström 2010). Fjeldså (1973a) asserted, that they may well occur together on the species list of one locality, but this is either because they may live well isolated by vegetation cover in larger swamps, or else because they breed in the same pond only in separate years. Fjeldså (1977a) wrote, that the relations between the Red-necked Grebe and the Slavonian Grebe are, if that is possible, even more hostile than among the other grebe species. Bent (1919) reported: "Mr. Allan Brooks (1903) says that in British Columbia, where both species are abundant, the Holboell's grebe "wages incessant war upon" the horned grebe, "the large birds diving and coming up beneath the smaller ones time and again to the terror of the poor little fellows, who often desert their nests in consequence." It must be a formidable foe with such a sharp and powerful beak." In some districts with mainly smaller lakes the term "mutual exclusive distribution" is perhaps a better description than "ecological segregation" (Fjeldså 1973a) (*cf.* the role of competition in Slavonian and Pied-billed Grebes on those wetlands that are high quality, but too small to contain multiple grebe pairs, Osnas 2003). According to Fjeldså (1973a), the Slavonian Grebe has virtually disappeared from a number of localities as a result of an increase in numbers of the Red-necked Grebe. Interspecific territorialism does occur and naturally the smaller *auritus* is physically subordinate, and rarely maintains itself, being left with only smaller suitable waters that lack a dense plant life (Fjeldså 1973a, Cramp *et al.* 1977).

All in all, it seems plausible that in some areas with mainly smaller water bodies, Red-necked Grebes may expel Slavonian Grebes from the larger, fertile lakes with dense vegetation in open farmland to the smallest marshes, often in less fertile wooded regions (Fjeldså 1973a, 1977a). It is likely that *grisegena* and *auritus* are less separated ecologically than *grisegena* and *cristatus*. However, it is still not clear to what extent the competition of Red-necked and Slavonian Grebes affects the habitat choice of the latter.

Competition Between Red-necked and Black-necked Grebes

It is sometimes assumed that *grisegena* displaces the Black-necked Grebe from breeding sites suited to both (Scholl 1974, Spletzer 1974, Koop 1998). However, this needs further study. Probably, the two species differ sufficiently from one another in habitat occupation strategies, association with gull colonies, and feeding choice to reduce competition to an acceptable level (Vlug 2000). Sometimes, *Podiceps nigricollis* and *P. grisegena* are found in considerable numbers in the same place (Dittberner and Dittberner 1970, Prinzing 1979, Koop 1998, Dittberner and Dittberner 2006).

Competition Between Red-necked Grebes and Fish

The selection of breeding sites by Red-necked Grebes can be affected by competition with (Common) Carp *Cyprinus carpio* and other Cyprinidae. These fish, especially the old, large specimens, compete directly for food, but can also impede indirectly the development of prey for Red-necked Grebes (macroinvertebrates and small vertebrates such as tadpoles).

Diet composition studies show that invertebrates preferred by Red-necked Grebes and other waterfowl are often also preferred by common, and usually abundant fish species such as Carp *Cyprinus carpio*, Crucian Carp *Carassius carassius*, Roach *Rutilus rutilus*, Common Bream *Abramis brama*, Tench *Tinca tinca* and Perch *Perca fluviatilis* (Eriksson 1979, Steffens 1980, Eadie and Keast 1982, Giles *et al.* 1990, Vlug 1993, Wagner 1997, Vlug 2011). Dietary analysis of 36 fish stomachs in Lake Tåkern showed that the dominant prey consumed by Tench was water boatman *Corixa*. Other food items of importance were mayflies Ephemeroptera, caddisflies Trichoptera, molluscs Mollusca and plumed gnats Chironomidae. Perch and Roach showed preferences for Ephemeroptera, Trichoptera, and *Corixa* (Wagner and Hansson 1998). Actually, there is a large feeding overlap between breeding Red-necked Grebes and the fish community, indicating that it should be advantageous for Red-necked Grebes to choose breeding habitats with low fish abundance. Fish-removal from lakes increases food for Red-necked Grebes and other waterfowl (Eriksson 1979, Andersson 1982, Giles 1994, Wagner 1997).

In experimental cages, one-year-old Carp totally eliminated young larvae of amphibians palatable to fish (Kloskowski 2011). This suggests food competition be-

tween Red-necked Grebes and fish (amphibians sometimes made up the majority of the biomass of food delivered to grebe chicks). However, Kloskowski (2011) investigated the guts of Carp and found that their diet overlapped little with that of *grisegena*. No remains of vertebrates or adult insects were found in fish of any age. Microcrustaceans and benthic true-flies Diptera consistently predominated in the alimentary tracts of Carp of all sizes, whereas these prey animals were absent from grebe diets. Invertebrate taxa present in grebe stomachs were poorly represented in the diet of Carp. Food competition between fish and grebes appeared unimportant. But amphibian larvae, as soft-bodied prey, are likely to be underestimated in the alimentary tracts of fish, and, as already mentioned above, Carp proved to be a catastrophic agent of mortality of tadpoles in experimental cages. Although Kloskowski (2011) found little overlap of diet (in gut contents) of Carp with that of *grisegena*, his own study and many other studies showed that large fish impair in many ways the abundance of aquatic invertebrates eaten by Red-necked Grebes.

As already stated above, fish can also impede indirectly the development of prey of Red-necked Grebes. Bioturbation associated with bottom-feeding habits of Carp and Common Bream *Abramis brama* may cause internal eutrophication. This eutrophication is increased by the faeces production of fish. In ponds with many Carp and Common Bream, the excessive richness of nutrients stimulates the growth of phytoplankton and the water loses its transparency. The increase of water turbidity impairs the growth of submerged plants, in which macroinvertebrates, tadpoles and small fish occur abundantly. Water fleas *Daphnia* are filter feeders, ingesting mainly unicellular algae and various sorts of organic detritus, and can restore water transparency. However, Carp and other cyprinids eat huge numbers of water fleas, especially *Daphnia magna*, a very effective filter feeder (Vlug 1993). Eutrophication also stimulates the growth of epiphytic algae which cover the submerged vegetation, an extra threat to these underwater plants. The grazing activity of freshwater snails Mollusca on the epiphytic community can be very efficient, but these snails are eaten by fish. An additional threat to the submerged plants is that they are food for some cyprinids such as Rudd *Scardinius erythrophthalmus*. With the disappearance of the submerged flora, the prey of *grisegena* may decrease considerably and even almost disappear (Vlug 1993).

There is still another class of explanations for the impact of large Carp on resources of grebes. All amphibian species except the inedible Common Toad *Bufo bufo* tend to avoid ponds with large fish (Resetarits *et al.* 2004, Binckley and Resetarits 2008). Adult amphibians have a substantial escape capacity and are typically too large to be vulnerable to attacks by Carp. Thus, their low densities at ponds with larger Carp cannot be ascribed to direct predation. Perhaps a combination of avoidance behaviour by adult amphibians and consumption by fish may explain the low numbers of larvae rather than direct eating by fish alone. Similar avoidance-based mechanisms may explain the distribution patterns of some aquatic insects, as indicated by low densities of highly mobile imago forms of water-beetles (diving beetles Dytiscidae and scavenger beetles Hydrophilidae) in ponds with large Carps compared to carp-free and carp-fry ponds (Binckley and Resetarits 2005, 2008, Kloskowski 2011).

Kloskowski *et al.* (2010) discovered that the abundance of aquatic macroinvertebrates and larval amphibians in fish-ponds in South-East Poland was decreasing with increasing Carp age/size. Also the population density and breeding success of Red-necked Grebes in these ponds were strongly negatively affected by an increasing age/size of Carp (see below).

Investigated breeding sites of Red-necked Grebes in Scania, southern Sweden, were either devoid of fish or had only Ten-spined Sticklebacks *Pungitius pungitius*. The biomass (dry weight) of larger invertebrates and small vertebrates in these breeding sites was 16 times greater than at investigated non-breeding sites. Beetles comprised 30% by dry weight of the total macrozoan (larger invertebrate and small vertebrate) community at the breeding sites, whereas they were completely absent at the non-breeding sites. As for the sticklebacks, they do not compete with Red-necked Grebes as they eat zooplankton and small invertebrates, and they are themselves suitable prey for the Red-necked Grebe (Wagner 1997).

In many areas, high densities of cyprinids had a marked negative impact on the number of Red-necked, Black-necked and Slavonian Grebes:

The Red-necked Grebe was locally a common breeder in the Czech Republic at the end of the 19th century. During the first half of the 20th century it became rare, and in the 1990s only one regular breeding site was recorded, and the maximum number of pairs was 5 (Cepák and

Musil 1997, Kren 2000, VlUG 2002a). The breeding population of Black-necked Grebes in the Czech Republic also declined (1985-89 up to 5,000 pairs, 1996-2000 up to 600 pairs) (Cepák and Musil 2000). One important cause of the decline in numbers of both species may have been the negative effect of increasing fish stocks in fish-ponds. These water bodies are the most common wetland type in the Czech Republic; the fish production here (mostly Carp *Cyprinus carpio*) was about 50 kg/ha until the end of the 19th century, increasing to more than 1,000 kg/ha from 1950 to 1980 (Cepák, Musil and Voldánová 1999, Cepák, Musil and Pykal 2005, Musil 2006).

The diet composition of the Slavonian Grebe overlaps with that of *grisegena*, and an assumed main cause of the decline of Slavonian Grebes in Sweden (46% between 1972 and 1996) was food competition with cyprinid fish; as the eutrophication from agriculture increased, the cyprinid populations expanded (Douhan 1998, Stedman 2000) (however, cf. Fjeldså 1973a).

Fjeldså (2004) stated that Podicipedidae are sometimes described as “opportunists”, because of their tendency to colonize newly flooded or excavated areas and sewage farms. He noted that it may be more to the point to say that most Podicipedidae (except specialist piscivores) specialize in habitats where they avoid competing for food with fish. This is the case in wetlands that are recently formed and isolated from the main waterways.

When interpreting the habitat choice of Red-necked Grebes, and their local and regional population trends, much more attention should be given to the role of fish populations, in addition to the external factors leading to eutrophication of the breeding waters.

Wagner (1997) concluded that wetlands without fish have to be protected from the introduction of fish to avoid extinction of the Red-necked Grebe. However, competition with cyprinid and other fish does not seem to be always as strong as he suggests. Red-necked Grebes in North America often nests on lakes with fish. Here they occupy a higher trophic position than grebes from lakes without fish. On lakes with fish *holboellii* eats a mixed diet of fish and a wide range of macroinvertebrates; on Armstrong Lake in Alberta, it consumes small-bodied fish (Brook Stickleback *Culaea inconstans* and Fathead Minnow *Pimephales promelas*), along with many aquatic and terrestrial invertebrates (dragon- and damselflies Odonata and beetles Coleoptera such as diving

beetles Dytiscidae). On fishless lakes, aquatic insects, crustaceans Crustacea, and leeches Hirudinea provide the primary food (Stout and Nuechterlein 1999, Paszkowski *et al.* 2004, McParland *et al.* 2010).

McParland and Paszkowski (2006) wrote that a number of studies suggest that not only large fish, but also small-bodied fish that colonize eutrophic, hypoxia-prone wetlands such as prairie potholes can reduce aquatic invertebrates. They added Brook Stickleback and Fathead Minnow to a fishless wetland in central Alberta, Canada. Fish reduced the biomass of gastropod (snail) prey of Blue-winged Teal *Anas discors*, and teals increased their foraging effort when fish were added. When the fish failed to overwinter due to a deficiency in the amount of oxygen, gastropod biomass increased. Red-necked Grebes did not exhibit any changes in foraging effort as a result of the fish addition or the subsequent fish extirpation. Red-necked Grebes appear to treat small-bodied fish and invertebrates as equivalent prey.

On European fish-ponds and natural lakes full of fish, Red-necked Grebe may have high population densities. Wagner and Hansson (1998) studied the Red-necked Grebe on Lake Tåkern, a large (46 km²) and shallow lake (maximum depth of 1.5 m) in Sweden (130 pairs were recorded here in the early 1980s, Svensson *et al.* 1999). Their study area in the littoral zone of the lake was divided into two habitats, the “lagoon” and the “reed” habitats. The lagoon habitat was a large opening (approximately 4 ha in size) in the reed habitat. The reed habitat consisted of a mosaic of many small openings surrounded by Common Reed *Phragmites australis*. Despite the fact that the lagoon habitat may be characterized as a potential breeding site, no Red-necked Grebes bred here. Instead, the grebes selected the more densely vegetated reed habitat as nesting place. Wagner and Hansson (1998) discovered that in this habitat the macroinvertebrate biomass (dry weight) was 5-10 times higher than in the lagoon habitat. There was a high biomass of backswimmers *Notonecta*, water boatmen *Corixa* and diving beetles *Dytiscus* in the reed habitat, but not many fish (only one fish was caught here). In the lagoon habitat, however, many fish were caught, especially Rudd *Scardinius erythrophthalmus* (the majority larger than 250 mm), Perch and Tench. The results indicate that there is a habitat separation between the breeding Red-necked Grebes and fishes in this and (most probably) other lakes.

In Central Europe, many Red-necked Grebes are found on fish-ponds. In smaller fish ponds, mainly younger Carp are introduced which do not compete with Red-necked Grebes and may even serve as important food for *grisegena* (Markuze 1965, Vlug 1993, Kloskowski 2004, 2011).

Kloskowski (2011) investigated body-size-dependent interactions between Carp and Red-necked Grebe in fish-ponds in South-East Poland. He found that young-of-the-year (0+) Carp are an essential food source for young grebes. Only adult Red-necked Grebes were able to consume 1-year-old (1+) fish, while 2-year-old (2+) Carp attained a size refuge from grebes. Breeding birds avoided settling on ponds with 2+ Carp. Amphibians made up the majority of the biomass of food delivered to grebe broods on carp-free ponds and were the second most important prey on ponds with 0+ Carp. Also, amphibians featured prominently in the food of young grebes on ponds with 1+ Carp.

Carp pisciculture in the breeding waters of Red-necked Grebe in Schleswig-Holstein is carried out comparatively extensively and the ponds usually have a multifarious structure with an abundance of vegetation (Vlug 1993). With a high fish density, aquatic macroinvertebrates concentrate in littoral habitats or emergent and submerged vegetation, where they are safer from predation by fish, but where they are mostly available to Red-necked Grebes. However, in bodies of water without a multifarious structure and with high numbers of large-bodied cyprinids, these fish can impair population density and breeding success of the Red-necked Grebe (Vlug 2000, Kloskowski 2011). Kloskowski (2011) found that fledging success of *grisegena* in South-East Poland was 2.8 times greater in ponds with young-of-the-year (0+) Carp than in ponds with 1-year-old (1+) Carp; in ponds with 1+ Carp, the chicks received on average 2.6-3 times less prey biomass from their parents, and over 1/3 of the broods suffered a total failure.

Kloskowski (2012) discovered that breeding grebes avoided settling on ponds containing fish too large for them to ingest (2-year-old or 2+ Carp), but exhibited little preference between ponds with medium-sized one-year-old Carp that could be exploited by pre-laying birds, and ponds designated for young-of-the-year Carp, where only invertebrates and amphibians were available as prey in early spring. As mentioned above, the resulting

food shortage in 1+ ponds led to severe egg-to-fledging mortality rates compared to fishless ponds or those containing young-of-the-year fish. In natural habitats, dominance of large fish in spring need not be associated with later absence of small-sized fish, as many temperate species spawn in spring. Kloskowski (2012) calls the mismatch between habitat preferences of grebes and severe brood losses on 1+ ponds an ecological trap.

Kloskowski and Frączek (2017) provided evidence that Red-necked Grebes breeding on 1+ ponds with scarce food resources transferred their flightless young (2-4 weeks old) to other, unconnected ponds. No brood movements from good-quality 0+ ponds (with young-of-the-year Carp) were recorded. Prior to the chick transfer, adult grebes used to fly for food to the pond where they later moved with the young (foraging flights to nearby ponds were also recorded in some sedentary pairs breeding in poor-quality habitat patches, in 6 of 14 pairs). Although a large proportion of breeding grebes in the study area of Kloskowski nested on 1+ ponds acting as ecological traps, brood movements to new ponds accounted for only four (3.3%) out of 120 successful nesting attempts. The infrequency of this strategy may be explained by the lack of suitable territories in close proximity and the high risk of predation or fatal injury.

9.1.6 Breeding Habitat and Eutrophication

In the 17th, 18th and 19th centuries, Red-necked Grebes and other Podicipedidae were generally rather scarce in Europe, which had strongly degraded landscapes with large areas of fallow land and oligotrophic cultural heathlands. In the 18th century, the Red-necked Grebe was very rare in Sweden and Linnaeus (1758) did not know the species. From about the middle of the 19th century *Podiceps grisegena* and other Podicipedidae became increasingly common and extended their northern distribution limits (Thomasson 1956, Merikallio 1958, O'Donnell and Fjeldså 1997, Väisänen *et al.* 1998, Svensson *et al.* 1999, Vlug 2000, Fjeldså 2004, Valkama *et al.* 2011, Ottosson *et al.* 2012). The population of Red-necked Grebes in Sweden increased in the last part of the 20th century. Svensson *et al.* (1999) reported that at least 600 pairs were breeding in the country in the late 1980s, and Ottosson *et al.* (2012) estimated the population at c. 1,100 pairs in the early 21st century. In the 1950s, c. 2,000 *grisegena* pairs were reported in Finland (Merikallio 1958). In the late 1980s/early 1990s, the Finnish population was estimated at 5,000-7,000 pairs (Väisänen *et al.* 1998), and in the period from 2006 to

2010 the estimation was 6,000-8,000 pairs (Valkama *et al.* 2011).

This marked increase in most grebe populations and the extension of their northern distribution limits was once attributed to legal protection and climatic amelioration, but probably an even more important factor was the eutrophication caused by the use of fertilizers and incipient pollution (O'Donnell and Fjelds  1997). As soil management improved 150-200 years ago, the wetlands became richer, with increasing biomasses of macrophytes (emergent, submergent or floating plants) such as Stoneworts *Chara*, Pondweeds *Potamogeton*, and Water Milfoils *Myriophyllum*. At the same time the biomasses of macroinvertebrates expanded. However, in many areas this increasing trend was reversed around the middle of the 20th century, with the development of highly mechanized modern agriculture, as intensive use of nitrate fertilizers leads to hypertrophic conditions in the wetlands. Many lakes go through a series of "trophic cascades", until they reach a new equilibrium – or evil circle – where large populations of cyprinid fish, especially Common Bream *Abramis brama* and Roach *Rutilus rutilus*, "control" the ecosystem (Fjelds  2004) (see 9.1.5). These changes had a marked negative impact on a number of populations of Red-necked, Little, Black-necked and Slavonian Grebes. The piscivorous Great Crested Grebe is the only grebe in Europe that benefits, to a large degree, from hypertrophication – to the extent that it is sometimes referred to as "the pollution bird" (Fjelds  2004).

9.2 Moulting Habitat

The simultaneous (flightless) wing moult of the Red-necked Grebe in Europe usually takes place in tidal waters, and only a small number of birds undergo the post-breeding moult on inland waters, e.g. on fish-ponds in Schleswig-Holstein (Germany) and on lakes in Switzerland (Vlug 1996, Vlug 2000, Maumary *et al.* 2007, Koop 2012). The most important moulting areas are probably in the shallow bays of the Baltic Sea (Vlug 1996). In two marine areas (Om  St lgrunde and Sejer bugten) near the island of Sj lland (Zealand), Denmark, large numbers of Red-necked Grebes were observed in the moulting season, at the end of August/early September. In 1990, an estimated number of 1,500 grebes were moulting here. The birds were observed 2-8 km from the nearest shore in water of a depth of 3-20 m, the majority in 8-15 m deep water. The Red-necked Grebes were never recorded together with fish-eating species occurring in

the same area (divers Gaviidae and Great Crested Grebes). However, a very striking association between *griseogena* and Velvet Scoter *Melanitta fusca* was observed in 1990, as the majority of Red-necked Grebes were recorded in or near moulting flocks of these ducks (Pihl 1995).

In North America, important moult sites have been identified not only in marine waters, but also on large inland lakes (Stout and Nuechterlein 1999). An estimated 1,300 Red-necked Grebes completed their autumn moult around Manitoulin Island, Lake Huron, in 1994. The moulting sites were scattered around the island in large bays and near small islands. Within the moult areas, the grebes usually remained between 100 and 2,000 m from the shoreline. The moult sites around Manitoulin Island had water depths of 3-55 m, were somewhat sheltered (large bays and/or lee sides of islands) and had a varied underwater topography (i.e. deep areas near shallow areas, forming shelves, holes, etc.). The moulting Red-necked Grebes were present in loose flocks of 1-40 birds per flock at each site. In addition to the moulting adults, there were often a few juveniles present at most sites near the island (Stout 1995, Stout and Cooke 2003).

Reeve (*cited in* Gunn 1951) observed a large concentration of (undoubtedly moulting) Red-necked Grebes in the moulting period near Port Britain (in the vicinity of Port Hope), Lake Ontario, Canada: "The greatest number Mr. Reeve has ever observed was on September 6, 1945, when the lake in front of his property was literally black with Red-necked Grebes, their numbers being conservatively estimated at upwards of 3,000. ... During the day, the birds seldom stray from a rectangular area about half a mile or less in length and one quarter of a mile in width, the nearest birds usually being about 300 yards (c. 275 m, JJV) offshore." Gunn (1951) continues: "Just what makes this particular location so attractive to the grebes has been a matter of some speculation. The situation lies in a rather shallow bay, about 1.5 miles long and half a mile deep. The shore is a pebbly beach with no emergent aquatic plants. The depth of the water in the favoured location, about one-third of a mile offshore (c. 500 m, JJV), is about 20 feet (c. 6 m, JJV). To sample the bottom in this area, Mr. Reeve used a weighted net. The haul was found to consist almost entirely of an abundance of aquatic algae of the family Characeae (Muskgrass)." More recent observations do not include such large numbers at this site or at any other location on Lake Ontario in autumn (Stout 1995).

Red-necked Grebes in Boundary Bay, Pacific coast of British Columbia (e.g. 22 September 1998 2,229 birds), were undergoing body moult, and some birds were in wing moult or had incompletely grown remiges (re-growth). They were typically found in shallow portions of the sub tidal zone (<13 m deep at low tide) but also used the intertidal zone on high tides (Stout and Cooke 2003).

9.3 Winter Habitat

9.3.1 Winter Habitat Characteristics

The Red-necked Grebe is strongly maritime in winter and is more attracted to the sea than the Great Crested Grebe (Durinck *et al.* 1994). During the greater part of the year it lives in marine areas, and only for a short period, c. 4 months, can we find it in its breeding waters (Scholl 1974, Vlug 1996). So, we can consider the species as essentially a marine bird. It uses estuarine or coastal waters, often bays, inlets, estuaries and narrows, but is also frequently recorded over shallows located well offshore (Cramp *et al.* 1977, Campbell *et al.* 1990, Brazil 1991, O'Donnell and Fjeldså 1997, Stout and Nuechterlein 1999). It seems to prefer deeper water than the Black-necked Grebe (Brazil 1991). The mean surface water temperatures in North America in the wintering areas of Red-necked Grebes are at or below 12°C on the Pacific Ocean and 10°C on the Atlantic Ocean (Root 1988, *cited in* Stout and Nuechterlein 1999). Sometimes the species forms commensal feeding associations with Velvet Scoters *Melanitta fusca* (Byrkjedal *et al.* 1997).

On the wintering grounds along the coast of Central Norway (where an estimated number of at least 2,000 Red-necked Grebes winter), *grisegeta* prefers somewhat exposed but shallow, coastal waters with a depth of 5-10 m, with islets and skerries, and a mixture of soft and hard, partly vegetated, bottom (Folkestad 1978). In the Baltic Sea, Red-necked Grebes have mainly been observed in offshore areas of 5 to 20 m water depth; most birds (81%, $n = 1,698$ Red-necked Grebes) were observed in waters up to 15 m depth. It seems that they often use areas further away from the coast than the Great Crested Grebe. A large winter concentration has been recorded in shallow parts of the north-western Kattegat with a maximum of 3,600 estimated birds (Durinck *et al.* 1993, 1994, Garthe *et al.* 2003, Sonntag 2009). In Britain, the species winters for preference in sheltered coastal localities (Chandler 1986). Wintering Red-

necked Grebes in the southern North Sea in The Netherlands were only observed close inshore. They occurred concentrated at some locations in the Dutch delta area (Camphuysen and Leopold 1994).

Smaller numbers winter on large, deep inland freshwater lakes in Europe, especially in Switzerland and South Germany (Bezzel 1985, G eroudet 1987, G onner 1999, Winkler 1999, Maumary *et al.* 2007). The inland-wintering Red-necked Grebes prefer water with high visual clarity, such as Starnberger See (Lake Starnberg, Southern Bavaria), Bodensee (Lake Constance) and Lac L eman (Lake Geneva). In late autumn and winter, the Red-necked Grebes in Lake Starnberg, Lake Constance and other inland lakes prefer shallow parts of the lake, harbours and boathouses, where they live mainly on young fish. On 14 December 1986, 42 Red-necked Grebes were recorded in the harbour of Bernried, Lake Starnberg, where huge numbers of small fish gather. From about the end of December onwards, a lot of fish migrate in the direction of the lake centre. Many Red-necked Grebes leave Lake Starnberg in this period, and the remaining birds are inclined to follow the fish. They are often recorded in the concentrations of Great Crested Grebes. Now they frequently capture larger fish at greater depth; this is easier because cyprinids are rather inactive in winter. Red-necked Grebes sometimes pursue fish up to a depth of at least 42 m in Lake Starnberg (on 9 February 1990 a bird was drowned in a fishing net at this depth) (M uller *et al.* 1989, 1990).

9.3.2 Winter Habitat Selection and Interspecific Competition Between Red-necked, Slavonian and Great Crested Grebes

Sonntag (2009) and Sonntag *et al.* (2009) investigated interspecific interactions between Red-necked, Slavonian and Great Crested Grebes wintering in the southern Baltic Sea in the period between 2000 and 2008. In this part of the Baltic Sea about 750 Red-necked Grebes, 1,000 Slavonian Grebes and 8,500 Great Crested Grebes are present during winter (Mendel *et al.* 2008, *cited in* Sonntag 2009). Water depth has a clear effect on the distribution of the three grebes wintering here. A generalized additive model indicated a preferred occurrence of Red-necked Grebes in waters up to 30 m and of Great Crested Grebes up to 26 m depth (although not significant). Slavonian Grebes prefer water depths up to 18 m with optimum values at about 10-12 m. Of all recorded birds, 81% of Red-necked Grebes ($n = 1,698$), 82% of Great Crested Grebes

($n = 9,032$) and 93% of Slavonian Grebes ($n = 2,453$) were seen in waters up to 15 m depth. Although Great Crested and Red-necked Grebes could occur in deeper waters than Slavonian Grebes, only small proportions were actually found in waters more than 20 m deep.

Sonntag (2009) stated that within the areas suitable with regard to water depth, the three grebe species exhibit distinctive distribution patterns. Red-necked Grebes are widespread throughout the study area (the southern Baltic Sea) and are found in coastal as well as in offshore areas. Great Crested Grebes are the most widespread species, but they are restricted to coastal areas and lagoons and only seldom occur in offshore areas. Slavonian Grebes are mainly restricted to the eastern study area, with only low numbers in the western part. They concentrate in the offshore area of the Pommersche Bucht (Pomeranian Bight), but are also found locally along the coast. Thus, Red-necked and Slavonian Grebes are clearly spatially separated from Great Crested Grebes. However, according to Sonntag (2009), *grisegena* and *auritus* are less clearly separated from each other, but seem to exclude each other at least in areas with highest local abundances.

Sonntag (2009) and Sonntag *et al.* (2009) asserted that the overall diet composition of the three species is very similar. They studied the feeding selection by analysing the stomach contents of birds accidentally caught and drowned in set nets in the Pomeranian Bight in the eastern part of the southern Baltic Sea (23 Red-necked, 20 Great Crested and 4 Slavonian Grebes). Fish dominated the diet of the three grebe species and accounted for 85.2% of all prey *items* in Red-necked Grebes, 76.1% in Slavonian Grebes, and 69.1% in Great Crested Grebes. Gobies Gobiidae occurred most frequently and were the dominant species (in *numerical* abundance) in all three grebes, accounting for 97.2% of all fishes consumed in Red-necked Grebes, 95.3% in Slavonian Grebes and 76.9% in Great Crested Grebes.

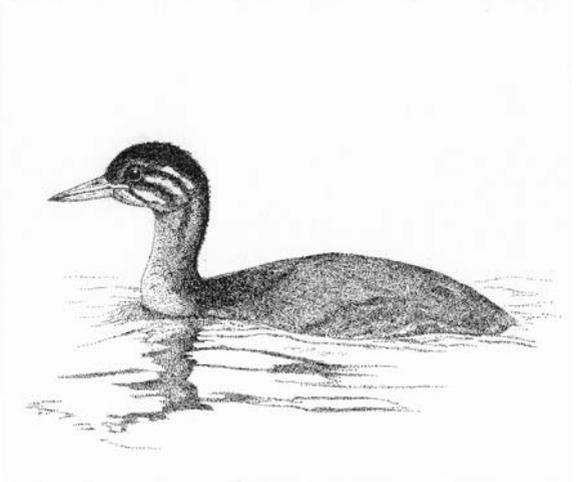
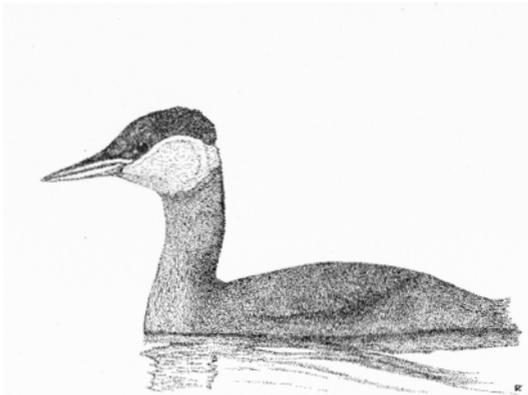
The authors concluded that interspecific competition might affect the distribution patterns of the three species rather than the use of different dietary niches. Red-necked and Slavonian Grebes correspond in the importance of gobies with regard to relative proportions of the number of consumed fish prey *items*, 97.2% and 95.3%, respectively. But gobies also dominated the diet of Red-necked and Slavonian Grebes with respect to total consumed fish *biomass* and accounted for 90.3% and 87.0%,

respectively. Thus, *grisegena* and *auritus* show no indication for a separation through different feeding niches, and it is indeed possible that interspecific competition has a certain effect on their distribution patterns in the Baltic Sea.

However, the relations between Great Crested and Red-necked Grebes are not comparable with those between Red-necked and Slavonian Grebes. The diet of Great Crested Grebes differed from the two other species due to a larger number of Ruffe *Gymnocephalus cernuus* and the occurrence of some large Pike-perch *Sander (Stizostedion) lucioperca*, the latter completely missing in the diet spectrum of the other two grebe species. Although the numerical importance of percid fishes Percidae was low compared to gobies, their much greater length accounted for significant differences in biomass values. In Great Crested Grebes, percids comprised the majority of consumed fish biomass (79.7%) (Sonntag 2009).

A number of authors state, that the morphological differences between Red-necked and Great Crested Grebe (leg and jaw morphology) are relatively large and have an effect on feeding selection (Onno 1966, Fjeldså 1983, VlUG 1993). Great Crested Grebes are more agile divers than Red-necked Grebes and are able to catch larger and quicker fish. In the Baltic Sea, they prefer coastal areas and lagoons, where they not only find small gobies but also suitable larger prey such as percid fishes. Pike-perch and Ruffe are freshwater fish species, but due to the low salinity they also occur in lagoons and nearshore areas strongly influenced by riverine freshwater influx (Hahlbeck 1993, Gerstmeier and Romig 1998, Hahlbeck and Müller 2003, Sonntag 2009). For *grisegena* it is difficult to catch fast moving, nektonic animals such as larger fish. Fish caught by this bird in the Baltic Sea often live at the bottom (gobies, for example). Red-necked Grebes possibly find these fishes by systematically searching the bottom of the sea, exactly in the same way in which they systematically search for the larvae of aquatic insects, molluscs and crustaceans at submerged plants and the bottom of their breeding waters (VlUG 2009).

Although Sonntag (2009) and Sonntag *et al.* (2009) believe that the conditions in the Baltic Sea do not allow for a habitat sharing of *grisegena* and *cristatus* via the utilisation of different dietary niches, it is highly probable that differences in morphology and feeding selection explain their distribution pattern better.



10. Distribution

10.1 Breeding Range

The geographical breeding range of a species can be loosely defined as the area which is regularly occupied by breeding individuals, excluding areas in which the species very rarely nests. It is difficult to determine the breeding range and its limits, especially because “regularly occupied” and “very rarely nesting” are hard to define. Additionally, the species shifts the boundaries of its geographical breeding range continually.

Although the overall geographical breeding distributions of most species at sub-continental to continental scales are especially determined by aspects of the prevailing macroclimate (Huntley *et al.* 2007), factors other than climate also influence the distribution of species, including human land use, suitability of habitat, food, predators, pathogens, overwhelming competitors or excessive persecution. The current ranges of many species may therefore be much smaller than climate alone would permit (Newton 2003, 2013).

Broadly speaking, geographical ranges might be limited by: 1. ecological factors acting *within the existing range* to prevent a population from increasing, and spreading to adjacent areas (no production of colonists needed to occupy new grounds); 2. ecological barriers (such as unsuitable climate or habitat) acting *at the boundaries of the existing range* to prevent spread; and 3. physical barriers, such as oceans or mountain ranges which curtail dispersal, and hence determine the maximum possible extent of a range. The same ecological factors that act to constrain population growth within the existing range might also, by acting more severely, prevent spread outside it (Newton 2003).

Because factors such as macroclimate and habitat (outside or within the existing range) change, the boundaries of the breeding range change too.

As with many other species, the Red-necked Grebe is not limited in distribution by a single factor operating around the entire range boundary, but by different factors operating along different parts of this boundary or by interactions between different limiting factors (*cf.* Newton 2003). *Podiceps grisegena* is a markedly continental breeding bird, flourishing best away from oceanic fringing lands, and the species (almost) never nests in

countries like Norway, Great Britain, Ireland and Iceland. It seems that a maritime climate hampers reproduction. This because during the first days after hatching the chicks are very vulnerable to chilling, and damp, cool and stormy weather is a major source of mortality (Vlug 2002a, 2005). However, this does not explain the absence (or extreme rarity) of the species in countries such as Switzerland, Austria and Italy. Here other unknown factors prevent breeding.

Population fluctuations and brood success of the Red-necked Grebe in Schleswig-Holstein, northern Germany, have been monitored over several decades (see 11.2.1, 11.2.2 and 11.3.1 for more details). This country is between the North and Baltic Seas at the range boundary of the species. Presumably because of the maritime climate, the mean brood success (= percentage of pairs raising at least one young) is low (38% in the period 1969-2014, $n = 14,976$ pairs; the range of regional means in Europe is 17% to 80%) (Vlug 2005; J J Vlug) (see 11.2.2). However, there is one caveat: the data from the different areas and countries are not strictly comparable, since there is no consistent method of measurement. Sometimes, such as in Schleswig-Holstein, all the birds on the breeding waters (breeders and birds that have been totally prevented from breeding) are included in the calculations and sometimes only the birds proven to have bred on the pond or lake.

Many populations at the range boundary are characterized by large population fluctuations, but that is not the case with the Red-necked Grebes in Schleswig-Holstein. The species was already in the 19th century a common breeding bird in the country (Boie 1819, *cited in* Scholl 1974, Naumann 1838, Kjærboilling 1852, *cited in* Scholl 1974), and relatively large numbers were also found in the monitoring period (1969-2014) (see 11.2.1, 11.2.2 and 11.3.1 for more details). In the period from 1985 to 2014 the number of breeding pairs in the country remained fairly constant and fluctuated from *c.* 500 to *c.* 700 pairs. Although the population between 1969 and 1978 was smaller, it was also relatively stable, and the number of breeding pairs fluctuated around 350 (with a roughly estimated range of 330 to 370 pairs) (Vlug 2005; J J Vlug). High densities of breeding pairs in Schleswig-Holstein were recorded, which is atypical for populations at the range boundary: up to 8 pairs on an inland pond of 1 ha = 8.0 breeding pairs/ha, and up to 40 pairs on a pond on the island of Fehmarn of 3 ha = 13.3 breeding

pairs/ha (J J Vlug). Nowhere in the whole breeding range of the species were such high densities ever observed.

It is unlikely that mortality in Schleswig-Holstein exceeds the reproduction and that the persistence of the population is dependent on immigration. The relatively high and stable numbers are probably regulated by territorial behaviour, and the number of new breeders recruited from the non-breeding surplus in any one year possibly depends largely on the number of vacancies created by the loss of previous breeders. It is likely that at least the majority of the population in the country lives within an inner boundary within which reproduction equals or exceeds mortality, but it is possible that the small population along the (extreme) west coast of Schleswig-Holstein (c. 5% of the total population) lives within an outer boundary, enclosing the outer zone along the coast where the reverse occurs, and where persistence is dependent on immigration (cf. Newton 2003).

The breeding distribution of the Red-necked Grebe is discontinuously Holarctic. The species has an almost circumpolar range, but it does not occur in Central Siberia. The size of its total breeding-resident range is very roughly estimated at 50,300,000 km² (BirdLife International 2017) (however, cf. BirdLife International 2015a). It inhabits northern waters and nests especially in boreal but also in temperate and steppe climatic zones, mainly breeding in rather continental areas at 35–65° N (Voous 1960, Fjeldså 2004). The breeding range of *Podiceps grisegena* extends considerably further north than that of the Great Crested Grebe *P. cristatus* (especially in East Asia) and other Holarctic grebes, except for the Slavonian Grebe *P. auritus* (Voous 1960, Kuročkin 1985, O'Donnel and Fjeldså 1997, Sibley 2000, Fjeldså 2004). Within its range, the occurrence of the Red-necked Grebe is sporadic and irregular and limited to suitable water bodies. There is unsatisfactory knowledge of its breeding range in Asia (Vlug 2002a).

Two very well marked subspecies in the Red-necked Grebe are recognized. The nominate *Podiceps grisegena grisegena* (Boddaert) breeds in Europe and West Asia, and *Podiceps grisegena holboellii* Reinhardt ("Holboell's Grebe") breeds in North America and East Asia (Storer 1979). It is possible, but unlikely, that the isolated populations in the south-east of Kazakhstan and Kyrgyzstan (near the breeding range of the nominate race) may represent outposts of *holboellii*. Other possibilities are that

they either belong to the nominate subspecies *grisegena* or that they constitute intermediate populations (Kuročkin 1985, O'Donnel and Fjeldså 1997, Fjeldså 2004, Gavrillov and Gavrillov 2005) (for distribution map, see Fig. 34).

10.1.1 Breeding Range of the Population in Europe-West Asia

Summary

The western border of the breeding range runs from Sweden through Denmark to The Netherlands at c. 6° 25' E. Then the border bends in a south-eastern direction and runs through Germany, Hungary and South-East Europe to Turkey. The northernmost breeding places are at c. 67° N in Sweden, Finland and Kolskiy Poluostrov (the Kola Peninsula). From Arkhangelsk the range boundary apparently descends sharply south, through the districts of Vologda and Kalinin (Tver). Then, it bends in an eastern direction to the Kama basin (Ufa) and Urals, where the species is recorded to c. 56° N. It breeds in West Siberia north to Surgut at c. 61° N. The easternmost breeding place is found in NW China at c. 82° E. The southern limit of the breeding range passes through Kyrgyzstan (Kirghizia), Kazakhstan, Turkmenistan to the north-west of Iran near the Caspian Sea. It breeds in Armenia, Naxçivan (Nakhchivan) and Turkey, which holds the southernmost breeding sites (c. 37°).

Details

The western border of the breeding range runs from Sweden and Denmark to The Netherlands. The westernmost regularly occupied breeding place is found in the last mentioned country, in the province of Drenthe at c. 6° 25' E (Vlug 2002b, Boele *et al.* 2014). Then the border bends in a south-eastern direction and runs through Germany, Hungary and South-East Europe to Turkey (Voous 1960, Vlug 1997, Snow and Perrins 1998, Bijlsma *et al.* 2001, Fjeldså 2004, Gedeon *et al.* 2014).

Partly because of climatic factors, the species seldom nests west of this limit, although in exceptional cases it is found breeding beyond the regular range (Vlug 1997): Norway (Artsdatabanken 2014, *cited in* Norevik 2014), Ireland (Hillis and O'Sullivan 2012, *cited in* Balmer *et al.* 2013), Britain (Anonymous 1989, Spencer *et al.* 1990, Parslow-Otsu and Elliott 1991, Vlug 2002a, Ogilvie *et al.* 2003, Forrester and Andrews 2007, Balmer *et al.* 2013), Belgium (Voet and Maes 1981, Bultinck 1989), France (Gengler 1925, Tostain *et al.* 1981, Sibley 1995, Croset and Thiollay 2007, Dubois *et al.* 2008), Baden-Württem-

berg (Gönner 1999, Vlug 2002a), Bavaria (Zach 1978, Bandorf 1982, Bezzel *et al.* 2005) and Austria (von Oesterreich and Brehm 1879, Zimmermann 1943, Ferguson-Lees 1957, Tratz 1960, Rokitansky 1980, Dvorak *et al.* 1993, Gönner 1999).

The range extends north to the Arctic Circle (66°33'N) and perhaps somewhat further. The northernmost breeding place in Sweden is at *c.* 67° N (near Pajala), or possibly at 68° N (Svensson *et al.* 1999, Vlug 2002a, Ottosson *et al.* 2012). In the north of Finland, an isolated breeding place was found near Lokka at *c.* 68° N (Lammi 1983); however, subsequent breeding there (from 1986 to 1989) was not certain (Väisänen *et al.* 1998). It is possible that the species in this country nested near Palojoensuu at 68° N during the period between 2006 and 2010 (Valkama *et al.* 2011).

On Kolskiy Poluostrov (the Kola Peninsula) the range of the Red-necked Grebe extends to *c.* 67° N (Snow and Perrins 1998, Bakkal *et al.* 2002). The species breeds south of the White Sea, near Arkhangelsk and in the basin of the Northern Dvina River (Fjeldså 1982a, Fjeldså 1983, O'Donnell and Fjeldså 1997, Snow and Perrins 1998). The range boundary apparently then descends sharply south, through the districts of Vologda and Kalinin (Tver) (Kuročkin 1985, however *cf.* Snow and Perrins 1998). Then, it bends in an eastern direction to the Kama basin (Ufa) and Urals, where the species is recorded to *c.* 56° N (Dement'ev and Gladkov 1951/1969, Storer 1979, Ryabitsev 2002). Nowadays, it does not occur in the north-eastern part of European Russia (Volga-Kama area and the Komi Republic) (Kuročkin 1985, Vlug 1997); however, the species is reported to be a scarce breeder in the Pechora delta, 68° N, well north of the main range (Snow and Perrins 1998).

It breeds in West Siberia north to Surgut at *c.* 61° N, and east to *c.* 81° E (Barabinskaya Step' and Kulundinskaya Step') (Dement'ev and Gladkov 1951/1969, Koshelev 1981, Kuročkin 1985). The easternmost breeding place is found in NW Xinjiang (NW Sinkiang) in NW China in the valley of Tekes River (*c.* 43° N, *c.* 82° E) (Meyer de Schauensee 1989).

The southern limit of the breeding range passes through Kyrgyzstan (Kirghizia) (Van der Ven 2002, Ayé *et al.* 2012) and Kazakhstan. There are isolated populations in the Balkhash-Alakol' area in the south-east of Kazakhstan and on Oz. Sonkel in Kyrgyzstan (Fjeldså 2004) (see

10.1). The Red-necked Grebe is a common and widespread breeder in the northern and south-eastern parts of Kazakhstan, but is absent from the Zhambyl, South Kazakhstan and Mangghystau provinces (Gordienko 1980, Kuročkin 1985, Flint *et al.* 1989, Wassink and Oreel 2007, Ayé *et al.* 2012, Wassink 2015). It was breeding in the lower Syrdarya valley and the adjoining region (Spangenberg and Feigin 1936, *cited in* Wassink 2015) but there is no recent evidence of this (Koblik 2012, *cited in* Wassink 2015). The species nests on lakes near the lower Amu Darya in Turkmenistan (Dement'ev and Gladkov 1951/1969, Kuročkin 1985) and in the north-west of Iran near the Caspian Sea (O'Donnell and Fjeldså 1997, Porter *et al.* 2007, Porter and Aspinall 2010). It breeds in Armenia and Naxçivan (Nakhchivan) (Kuročkin 1985, Flint *et al.* 1989, Adamian and Klem 1997, Snow and Perrins 1998) and Turkey, which holds the southernmost breeding sites (Ereğli Marshes, 37°30'N) (Kirwan 1993, Snow and Perrins 1998, Kirwan *et al.* 2008).

In earlier days, the species possibly bred further south. There are old records of many being present on the Ras el Doura lakes in Morocco (Favier, *cited by* Irby 1875, Bannerman 1959). Irby (1875, p. 220) stated: "I have seen specimens of the Red-necked Grebe obtained in Morocco by Favier so young that they must have been bred in the country; and although I was unable to procure a specimen for identification, I am confident I saw several of this species at Ras-Dowra in April."

10.1.2 Breeding Range of the Population in East Asia

Summary

The westernmost nesting region in East Asia is an isolated breeding area consisting of Ozero Baykal (Lake Baikal) (*c.* 108° E) and the area east of this lake. The species breeds in the region of the Lena-Vilyuy basin (*c.* 125° E, and to 66° N). The range extends north to the basin of the Indigirka River (to 71° N) and the Kolyma River estuary (to 69°30'N). It breeds east in Chukotka Autonomous Okrug to *c.* 178° E. The range extends south to *c.* 42° N, and the species breeds on the island of Hokkaido (northern Japan) and in Ussuriland near Vladivostok. Then the border bends in a north-western direction, through NE China to probably *c.* 60° N and *c.* 115° E in eastern Siberia.

Details

The population in East Asia is separated from that in Europe-West Asia because the species is absent from Cen-

tral Siberia (Voous 1960, Kuročkin 1985, Flint *et al.* 1989, O'Donnel and Fjeldså 1997, Fjeldså 2004, Anonymous 2008); only in southernmost Central Siberia the species breeds rarely but regularly on lakes of the Minusinsk depression in the Republic of Khakasiya (Prokofyev 1987, *cited in* Anonymous 2008). Our knowledge is still very incomplete and uncertain. The maps in Dement'ev and Gladkov (1951/1969), Voous (1960), Cramp *et al.* (1977) and Flint *et al.* (1989) give a continuous breeding range in East Asia, but the maps in Kuročkin (1985) and Fjeldså (2004) (see Fig. 34) show a broken distribution. The following is based partly on the work of Kuročkin (1985). However, the statements in his text do not always correspond with his distribution maps.

The westernmost nesting region in East Asia is an isolated breeding area consisting of Ozero Baykal (Lake Baikal) (*c.* 108° E), where the Red-necked Grebe is a rare and local breeder (Mlíkovský 2009), and the area east of this lake, the Buryatiya Republic. In this republic the birds nest in the valley of the Barguzin River, near the upper reaches of the Vitim River and on the Eravnoe Lakes (a group of lakes on the watershed between the Selenga and Vitim Rivers) (Dement'ev and Gladkov 1951/1969, Kuročkin 1985 and Fjeldså 2004).

According to Dement'ev and Gladkov (1951/1969), Voous (1960), Cramp *et al.* (1977) and Flint *et al.* (1989), the westernmost limit of the continuous main breeding range in East Asia is perhaps *c.* 115° E, which requires clarification. However, the species undoubtedly breeds in the region of the Lena-Vilyuy basin (*c.* 125° E, and to 66° N) (Dement'ev and Gladkov 1951/1969, Kuročkin 1985). The range extends north to the Yana River valley (to 68° N), the basin of the Indigirka River (to 71° N) (Kuročkin 1985) and the Kolyma River estuary (to 69°30'N) (Dement'ev and Gladkov 1951/1969, Flint *et al.* 1989).

It breeds east to the middle and lower reaches of the Kanchalan River basin and to the Anadyr basin (*c.* 178° E), in the Koryak Mountains (Koryakskiy Khrebet, Koryakskoye Nagorye) (*c.* 178° E) and on the Parapolskiy Dolina; however, it does not occur on the Chukchi Peninsula (Chukotskiy Poluostrov) (Dement'ev and Gladkov 1951/1969, Voous 1960, Kuročkin 1985, Flint *et al.* 1989). It nests to the north-west coast of the Sea of Okhotsk, on the peninsula of Kamchatka, the Komandorskiy Islands, in the lower reaches of the Amur basin,

on Sakhalin and the Kuril'skiye Ostrova (Kuril Islands) (Kuročkin 1985, Eremin *et al.* 1986, Nechaev 1991).

The range extends south to *c.* 42° N, and the species breeds on the island of Hokkaido (northern Japan) (Voous 1960, Brazil 1991, Fujino *et al.* 2006, Shimba 2007, Brazil 2009) and in Ussuriland (e.g. on Lake Khanka, a freshwater lake located on the border between Primorskiy Krai, Russia and in the province of Heilongjiang, China) (Knystautas and Šibnev 1987, Brazil 2009). Then the border bends in a north-western direction, through Manchuria and the province of Heilongjiang (NE China) (Étchécopar and Hüe 1978, Meyer de Schauensee 1989, MacKinnon and Phillipps 2000, Brazil 2009) to probably *c.* 60° N and *c.* 115° E in eastern Siberia (Dement'ev and Gladkov 1951/1969, Voous 1960, Flint *et al.* 1989).

10.1.3 Breeding Range of the Population in North America

Summary

It is difficult to determine the limits of the North American breeding range because the occurrence of the species is sporadic and limited to suitable water bodies (even in the “main” range), and many breeding places, especially at the eastern and southern limits, are more or less isolated from this “main” range.

The species nests north to *c.* 70° N in Alaska. From Alaska the northern border of the breeding range runs through the north of the Yukon Territory to the north-west of the Northwest Territories. Then the border bends in a south-eastern direction through the Northwest Territories and the north-east of Saskatchewan to Manitoba and Ontario. The eastern border is in the south-west of Québec, perhaps at *c.* 78° W. The southern border runs from Québec through the south-east of Ontario to Wisconsin and Minnesota. Then it runs through North Dakota and the southern parts of Saskatchewan to Alberta and the north-west of Montana. In the north-west of Wyoming is an isolated nesting area. From Montana the border continues its way through northern Idaho to the north-east of the state of Washington. The southernmost (isolated) breeding area is at *c.* 42° N in the south of Oregon. The range extends west to the north-east of the state of Washington, the western part of British Columbia and the south-west of the Yukon Territory. The westernmost breeding place is found on the Seward Peninsula in Alaska at *c.* 166° W.

Details

The following is based mainly on the work of Stout and Nuechterlein (1999). The occurrence of the Red-necked Grebe in North America is sporadic. It breeds on small and shallow lakes in the northern prairies, western parklands, and forests.

In Alaska, the species is found south to the Alaska Peninsula, Kodiak Island, Matanuska-Susitna Valley, Kenai Peninsula and the northern foothills of the Chugach Mountains (Stout and Nuechterlein 1999, Mills and Andres 2004, Randall 2005, Mills 2007). On the Seward Peninsula (c. 65° N), it breeds in the east and southeast, as well as in the interior lowlands and west into the Imuruk basin (to c. 166° W). The birds nest north to near the northern limit of trees. They breed north to the Kobuk and Noatak Rivers, and up to the river drainages to the Brooks Range (Stout and Nuechterlein 1999). A very northerly breeding site was described by Nelson (1953): a pair of Red-necked Grebes was found on 18 July 1949 nesting on an oxbow of the Itkillik River near its junction with the Colville River, 70°10'N, in Arctic Alaska.

The northern border of the breeding range runs from Alaska to the Yukon Territory. In the north of this territory the Red-necked Grebe is regularly seen at Old Crow and Old Crow Flats at c. 68° N (Sinclair *et al.* 2003). In the Northwest Territories, the range extends north to the inner Mackenzie delta, and then the border bends in a south-eastern direction to the Great Bear Lake, and the north-eastern part of the Great Slave Lake. Then, the northern limit of the breeding range passes through the extreme north-eastern part of Saskatchewan (the species breeds near Fond-du-Lac), through Manitoba to Ontario (Godfrey 1986, Stout and Nuechterlein 1999). Red-necked Grebes nest in central (Thompson Junction, Thicket Portage) and south Manitoba (Lake Winnipegosis, Turtle Mountain Provincial Park), but they do not breed in the north-eastern third of the province (Bent 1919, De Smet 1983, Godfrey 1986). In Ontario, the species is not widely distributed. It is most abundant in the western parts of the province, from Thunder Bay to the Red Lake region (James 1985, Stout and Nuechterlein 1999). Small numbers breed locally and irregularly outside of the main range in the far north (Favourable Lake, Big Trout Lake), east (Cochrane region), and south-east parts of Ontario (the western end of Lake Ontario, Luther Marsh at the headwaters of the Grand River

watershed, Manitoulin Island and near Sudbury) (Peck and James 1983, Armstrong 1987, Stout and Nuechterlein 1999, Sandilands 2005, Harris 2007). The eastern border is in the south-west of Québec, perhaps at c. 78° W. Here, in the south-west of the province, the birds breed locally in the Abitibi-Rouyn-Noranda region (Pelletier, Fiske and Osisko Lakes) (Godfrey 1986, Stout and Nuechterlein 1999, Redpath Museum 2007, Van der Haeghe and Gagnon 2010).

The southern border runs from Québec through the south-east of Ontario to Wisconsin and Minnesota. A southern and isolated breeding place was recorded in Michigan by Chamberlin (1977). In 1975 he found a breeding pair in the Cedarville Bay in northern Lake Huron at c. 46° N and c. 84° W. There have been no confirmed nesting records since, indicating that Red-necked Grebes breeding in Michigan must be a very rare event.

The birds breed in Wisconsin in the north-west of the state (formerly Lakes Twin and Oakridge in St. Croix County, in Polk County and Crex Meadows State Wildlife Area in Burnett County) and in the south-east (Grassy Lake in Columbia County, Lake Maria in Green Lake County, Rush Lake in Winnebago County, Beaver Dam Marsh in Waukesha County, Eldorado Marsh in Fond du Lac County and a place in Dane County) (Eichhorst 1985, Evrard 1988, Gieck 1988, Stout and Nuechterlein 1999, Brooks 2006, Mueller 2007, Bielefeldt 2011).

In Minnesota, the Red-necked Grebe nests primarily in the north-western, central, and east central regions; it occurs sparingly in the other parts of the state. There are breeding records from as far east as Lake Vermilion in St. Louis County, and as far south as Swan Lake in Nicollet County, Albert Lea in Freeborn County, and Heron Lake in Jackson County (Green and Janssen 1975). Hanson (1978) described a population breeding on Lake Edward in Crow Wing County (central Minnesota), and Nuechterlein *et al.* (2003) studied the dynamics of nesting dispersion in a population of 160-200 birds on Lake Osakis in Douglas and Todd counties (central Minnesota). Thompson (1947) stated that the birds were common on Lake Calhoun in Kandiyohi County (south-east of Douglas County) near Spicer.

From Minnesota the southern border runs through North Dakota and the southern parts of Saskatchewan to Alberta and the north-west of Montana. Red-necked Grebes nest mainly in the north-central portion of

North Dakota, especially in the Turtle Mountains at the border of Manitoba (Johnsgard 1979, Stout and Nuechterlein 1999, Sauer *et al.* 2014). There is an isolated breeding place in the extreme north-east of South Dakota (Stout and Nuechterlein 1999).

Smith (1996) describes the distribution of the species in Saskatchewan as follows: “The whinnying of the Red-necked Grebe is a fairly common sound of lake-margin marshes of central Saskatchewan and the Cypress Hills. The species’ abundance decreases markedly on the sterile lakes of the Precambrian Shield. Except for nestings on the comparatively fresh waters of the Cypress Hills, Last Mountain Lake, Wascana Lake and Condie Reservoir, the species is generally only a rare transient on the predominantly saline lakes of the prairies.”

The Red-necked Grebe nests throughout Alberta and is found in every natural region (Semenchuk 1992, Semenchuk *et al.* 2007).

The species nests in northwest Montana (Silloway 1902, Stout and Nuechterlein 1999, Johnsgard 2009), and is a common breeder south of Glacier National Park (Anonymous 2001). It breeds (isolated) in northwest Wyoming (Stout and Nuechterlein 1999, Johnsgard 2009).

From Montana the border continues its way through northern Idaho to the north-east of the state of Washington. In Idaho the Red-necked Grebe is a rare breeding bird (Burleigh 1972); it occurs in the north of the state (Hayden Lake and Lake Pend Oreille region), in the Upper Snake region (Henrys Lake area), and on isolated wetlands in the vicinity of Lake Cascade (Anonymous 2005).

The southernmost (isolated) breeding water is the Upper Klamath Lake at *c.* 42° N in the south of Oregon (Watkins 1988, Stout and Nuechterlein 1999).

The species breeds locally common on lakes in the north-east part of the state of Washington (Paulson 2013). Yocom *et al.* (1958) stated that most known breeding records are from Blue Lake, Park Lake, and Lake Lenore in the Grand Coulee of Grant County.

The range extends west to the north-east of the state of Washington, the western part of British Columbia, the south-west of the Yukon Territory and the west of

Alaska. The breeding distribution in British Columbia is relatively widespread across the central and southern areas east of the Coast Mountains, and rather sparse across the north, except in the Peace River lowlands where it is more widespread (Howie 2015).

It is fairly common in southern Yukon, and uncommon in central Yukon north to the Dawson area. North of there, it is regularly seen only at Old Crow and Old Crow Flats (Sinclair *et al.* 2003). The westernmost breeding place is found on the Seward Peninsula in Alaska at *c.* 166° W.

10.2 Winter Range

Both races are highly maritime in winter. Most birds disperse or migrate to tidal waters outside the breeding season. They use estuarine or coastal waters, and are often seen in inlets and bays, but also over shallows located well offshore. In smaller numbers they winter on large inland freshwater lakes (Cramp *et al.* 1977, Delany *et al.* 1999, Stout and Nuechterlein 1999, Vlug 2002a, Fjeldså 2004, Delany and Scott 2006).

10.2.1 Winter Range of the Population in Europe-West Asia

The principal non-breeding areas in north-western Europe are the Baltic Sea and the Danish Belts (Durinck *et al.* 1994, Skov *et al.* 2000, Garthe *et al.* 2003, Helcom Red List Bird Expert Group 2013), the Atlantic coasts of central Norway (Folkestad 1978, Pirot 1989, O’Donnel and Fjeldså 1997) and the sea off the Danish part of the Wadden Sea (Durinck *et al.* 1994). In the Baltic Sea and the Danish Belts, large concentrations are observed in the north-western Kattegat, the Pomeranian Bay and the south-western part of the Gulf of Riga (Durinck *et al.* 1994, O’Donnel and Fjeldså 1997, Skov *et al.* 2000, Vlug 2002a, Sonntag 2009).

The Red-necked Grebe is a regular but scarce wintering bird along the North Sea coasts of The Netherlands. The birds occur concentrated at some locations in the Dutch delta area. In severe winters, the numbers are higher (Camphuysen and Leopold 1994).

The species is also a rather scarce but annual non-breeding visitor to Britain and Ireland from continental Europe (Brown and Grice 2005, Balmer *et al.* 2013). The winter distribution shows a strong bias to the North Sea coast from Angus to Kent and along the south coast of

England (Balmer *et al.* 2013). Occasional influxes occur in hard weather (Chandler 1981, 1986). In Ireland, it is found mainly at a small number of coastal locations (Hutchinson 1989, Balmer *et al.* 2013).

Outside the breeding season, the birds are seen regularly in small numbers at the north-west coast of France (English Channel or La Manche). The species is also recorded at the coasts of the Atlantic Ocean and the Bay of Biscay (Commeccy 1991, Dubois *et al.* 2001, 2008, Deceuninck *et al.* 2015). In Spain, it is almost annual in winter along the north-western coast (Galicia) and the Biscay coast (Asturias, Cantabria and Basque Country), but is not seen in Portugal (De Juana and Garcia 2015).

Podiceps grisegena is observed in small numbers along the Spanish and French Mediterranean coasts and in the north Mediterranean Sea (Bonaccorsi 1994, Snow and Perrins 1998, Dubois *et al.* 2008, Deceuninck *et al.* 2015, De Juana and Garcia 2015) and it seems a scarce to rare winter visitor to the south side of the Mediterranean (Bannerman 1959, Snow and Perrins 1998). Perhaps, it is not rare in the Adriatic and Aegean Seas (O'Donnel and Fjelds  1997, Snow and Perrins 1998, Delany *et al.* 1999, Brichetti and Fracasso 2003, Fjelds  2004, Delany and Scott 2006).

Kirwan *et al.* (2008) stated that the Red-necked Grebe in Turkey is rarely recorded in winter, most frequently in the Mediterranean Sea but also in Marmara.

Significant numbers can be found in the Black, Caspian, and Aral Seas (Kuro kin 1985, O'Donnel and Fjelds  1997, Delany *et al.* 1999, Fjelds  2004, Delany and Scott 2006).

Some birds winter on inland waters, especially on the larger lakes in Switzerland and south Germany (Bezzel 1985, Winkler 1999), such as Genfersee (Lac L man, Lake Geneva) (G roudet 1987, Maumary *et al.* 2007), Bodensee (Lake Constance) (G nner 1999, Maumary *et al.* 2007) and Z richsee (Lake Z rich) (Maumary *et al.* 2007).

On passage, an exceptional concentration of 150 birds was recorded at Burdur G l  (Lake Burdur), Turkey, on 1-3 September 1980 (Kirwan *et al.* 2008).

In winter, Red-necked Grebes are not rare on inland waters of Azerbaijan (Kuro kin 1985), and they are found in this season in large numbers on Lake Issyk-Kul, Kyrgyzstan (Janu evi  *et al.* 1959, *cited in* Kuro kin 1985).

In the non-breeding season, the birds are observed in Iranian S st n (Seistan) (Porter and Aspinall 2010, Rasmussen and Anderton 2012).

The population nesting in the Balkhash-Alakol' area in South-East Kazakhstan and Kyrgyzstan (Oz. Sonkel) (*Podiceps grisegena* "balchaschensis" or "balchashensis") has a small wintering population in north-eastern Afghanistan (Kabul area), northern and central Pakistan and an increasing one in north-western India (Roberts 1991, O'Donnel and Fjelds  1997, Grimmett *et al.* 1998, Fjelds  2004, Wetlands International 2006, Rasmussen and Anderton 2012, Wetlands International 2015).

Vagrant birds of the nominate race (rare visitors seen far beyond the normal geographical range) are observed in Svalbard (Spitsbergen), Greenland, Iceland, Faeroes, Balearic Islands, Cyprus, Syria, Lebanon, Israel, Saudi Arabia, Egypt, Tunisia, and Algeria (Palmer 1962, O'Donnel and Fjelds  1997, Snow and Perrins 1998, P tursson and Kolbeinsson 2004, Porter and Aspinall 2010, De Juana and Garcia 2015).

10.2.2 Winter Range of the Population in East Asia

The Red-necked Grebe winters along the coasts of eastern Kamchatka, the Aleutian Islands, the Kuril Islands, Ussuriland and Sakhalin (Kuro kin 1985, Fjelds  2004, Shimba 2007, Brazil 2009). It is certainly a fairly common winter visitor in Japanese coastal waters from Honshu south to Kyushu. Although it can be found in reasonable numbers also in Hokkaido at this season, it rarely occurs in anything other than very small numbers (Brazil 1991). It occurs in winter along the coasts of Korea (Kuro kin 1985, Shimba 2007, Brazil 2009). In China, it winters on the Yellow Sea (Kuro kin 1985, O'Donnel and Fjelds  1997) and along the coasts of the East China Sea to the northern part of the South China Sea. Sometimes it is also found inland south to Fukien (Fujian) ( tch copar and H e 1978, Kuro kin 1985, Meyer de Schauensee 1989, O'Donnel and Fjelds  1997, MacKinnon and Phillips 2000, VlUG 2002a, Fjelds  2004, Brazil 2009).

10.2.3 Winter Range of the Population in North America

Summary

The species winters primarily on marine waters along the Atlantic and Pacific coasts and, to a limited extent, on the Great Lakes (Stout and Nuechterlein 1999). It is relatively rare to very rare on other freshwater lakes.

Details

Along the Pacific coast we find wintering birds from the Pribilof and Aleutian Islands, Kodiak Island, southern and south-eastern Alaska to central California (Monterey County), and rarely to southern California (Palmer 1962, Cogswell 1977, Armstrong 1983, Johnsgard 1987, Stout and Nuechterlein 1999, Sibley 2000). Most birds winter from the southern coast of Alaska to northern Oregon. They are especially abundant around southern Vancouver Island, the Juan de Fuca Strait, the Strait of Georgia, and Puget Sound (Campbell *et al.* 1990, Stout and Nuechterlein 1999, Paulson 2013).

Along the Atlantic coast, the grebes winter from Newfoundland south to North Carolina, but mostly in Nova Scotia and New Brunswick south to Long Island, New York (Stout and Nuechterlein 1999). The abundance for the Atlantic wintering population centres along the coast of the Bay of Fundy (Nova Scotia, New Brunswick, and Maine) (Root 1988, *cited in* Stout and Nuechterlein 1999). The species is rare in winter from South Carolina to Florida (Howell 1932, Pearson *et al.* 1942, Burleigh 1958, Palmer 1962, Potter *et al.* 1980, Stout and Nuechterlein 1999, Sibley 2000).

Band recoveries and contaminant data in eggs suggest that the breeding ranges of the Atlantic- and Pacific-wintering populations diverge somewhere in western Saskatchewan (Forsyth *et al.* 1994, Stout and Nuechterlein 1999).

A number of birds winter on the Great Lakes (McPeck *et al.* 1994, Sandilands 2005). However, the distribution and the size of the winter population are poorly known. In severe winters, irruptions of Red-necked Grebes into inland and coastal areas south and east of the Great Lakes following the freeze-up of the Great Lakes suggest that the numbers of wintering Red-necked Grebes may range from hundreds to a few thousand individuals (Bull 1974, Kaufman 1994, Stout 1995, Stout and Nuechterlein 1999, McWilliams and Brauning 2000).

With the exception of the Great Lakes, wintering Red-necked Grebes are relatively rare to very rare on freshwater bodies in North America. However, as stated above, after the freeze-up of the Great Lakes, higher numbers can be recorded on many inland lakes and rivers throughout much of interior eastern North America (Kaufman 1994, Stout 1995, McWilliams and Brauning 2000, Carolina Bird Club 2014, McCormac 2014).

In Canada, the birds are sometimes found on freshwater lakes while they remain open (Godfrey 1986). In the interior of British Columbia, the largest aggregations occur in the Okanagan valley (Campbell *et al.* 1990). In Alberta, overwintering has been observed at Wabamun Lake (Semunchuk 1992). The species has been recorded in December at Regina and Squaw Rapids in Saskatchewan (Smith 1996). In Ontario, where it is usually present in winter only on the Great Lakes (see above), it is very rarely seen on smaller water bodies (Sandilands 2005).

While in the northernmost part of the United States, in the Northern Tier, wintering birds are relatively rare, they are very rare in the southern United States interior and the Gulf coast from Nevada, Utah, Colorado, Kansas, and Missouri south to southern California interior, Arizona, New Mexico, and the Gulf coast states (Howell 1932, Lowery 1974, Stout and Nuechterlein 1999, Sibley 2000).

In North America, vagrant American birds are observed outside the breeding range in the Hudson Bay (Southampton Island) (Palmer 1962), Labrador (Makkovik, Spotted Island) (Godfrey 1986), Bermuda (Amos 1991, *cited in* Stout and Nuechterlein 1999), Bahamas (New Providence) (Raffaele *et al.* 1998, *cited in* Stout and Nuechterlein 1999), and the Gulf of Mexico (Santa Rosa Sound near Pensacola, Wakulla Bay near St. Marks, Pepperfish Keys and Cedar Keys) (Howell 1932, Duncan 2001).

Podiceps griseigena holboellii of North America and eastern Asia is a casual visitor to the Hawaiian Islands, Greenland, Iceland, Scotland, France and Spain (Witherby *et al.* 1947, Palmer 1962, O'Donnel and Fjelds  1997, Stout and Nuechterlein 1999, P tursson and Kolbeinsson 2004, Kehoe 2006, Dubois *et al.* 2008, De Juana and Garcia 2015).

11. Population Trends, Numbers and Status; Population Regulation, Demographic Factors and Life-history Features

11.1 Problems in Counting Breeding Birds

The first step in any study of bird populations is to count the birds reliably. It is not possible to study the global population of the Red-necked Grebe and the majority of other species. Instead the researcher has to work within a defined area, whose occupants form a tiny part of the much wider world population. Individuals may move freely in and out of the study area, and the grebes which



breed there occupy other areas outside the breeding season. Hence, population studies of *Podiceps grisegena* and most other birds have been concerned with the numbers found in defined areas at specific times. The general applicability of the conclusions from such localized studies depends partly on how typical the study area of the grebe's range is as a whole, and on whether the area is big enough compared with the scale over which the factors influencing overall population levels operate (Newton 2013).

The most accurate estimate for breeding pairs of Red-necked Grebes is obtained by halving the maximum number of grebes counted before the time of egg laying. During the courtship period and when exploring nesting areas, i.e. before egg laying, the birds are easy to count because they confidently expose themselves to view and are often on open water. In Central Europe, this means that the best census period is from the end of April to mid-May. During the incubation period and a short time after hatching, it is difficult to get a good estimate of the number of birds because they may live very secretly, not frequently exposing themselves to observation (Bäsecke 1948, Fjeldså 1977b, Lammi 1983, Vlug 1985, Südbeck *et al.* 2005).

Because ornithologists use different counting methods, their data are not completely comparable. One of the problems is that some authors consider all adult Red-necked Grebes in suitable nesting waters as breeding birds while others exclude the birds which seemingly do not nest, the so called “non-breeders”. It is often supposed that these “non-breeders” are Red-necked Grebes in their second calendar year which do not attempt to breed for physiological reasons (*cf.* Simmons 1974). Walser and Barthel (1994) discovered that most birds in their second calendar year, in their first summer plumage, can be aged reliably by their iris; the clearly visible yellow outer ring of the iris of the juvenile does not become completely dark brown before the summer of the second calendar year (see 3.2.4 and 3.2.6). Now it is known for certain that (most?) Red-necked Grebes are physiologically capable of breeding at one year of age. There are records of Red-necked Grebes breeding successfully in their second calendar year (Schleswig-Holstein, Germany) (Vlug 2000). But in spite of that, one-year-old birds do not usually breed, probably partly due to social interactions in the population. It is believed that they normally spend the summer away from the

breeding waters (Vlug 1985, 2000). Only 3.5% of 266 Red-necked Grebes in April and May 1995 in breeding waters in Schleswig-Holstein were in their second calendar year (Koop 1996).

In many cases it turns out that the “non-breeders” in the regular breeding range of the species really are “late breeders” (those that have been considerably delayed in nesting by unfavourable environmental conditions), “would-be breeders” (those that have been totally prevented from breeding) and “failed breeders” (Struwe 1985, Vlug 1985).

However, single individuals (one-year-old birds?) or, less often, pairs spend the summer (without breeding) in many countries outside the regular breeding range of the species, sometimes in suitable breeding habitats. The recorded number of summering Red-necked Grebes is low. The establishment of a breeding pair or small nesting population outside the regular breeding range may be heralded by displaying summering birds (see 13.2.2 for more details).

11.2 Patterns that Emerge from Studies of Bird Populations

The patterns that emerge from studies of bird populations depend partly on the timescale over which the studies are made, and partly on the changes in landscapes, food sources etc. that occur in that time. They also depend on the spatial scale (Newton 2013).

In the Red-necked Grebe, the number of breeding birds in larger areas may remain fairly constant through several decades. An example of such stability is provided by the birds in Schleswig-Holstein, Germany (see 11.2.1). However, there are also examples of declining breeding bird numbers in larger areas since c. 1980 (e.g. Sachsen, Saxony) or growing numbers (e.g. Niedersachsen, Lower Saxony) (Vlug 2002a, Gedeon *et al.* 2014, Krüger *et al.* 2014). After c. 2000 the numbers in Poland and Latvia showed a marked decline (European Environment Agency 2013). Considering periods of 50 years or more, most *grisegena* populations fluctuate substantially.

11.2.1 Population Regulation

Where habitats are not disturbed, the numbers of Red-necked Grebes and most other bird species remain relatively stable in abundance over long periods. Their

breeding numbers may fluctuate from year to year, but within narrow limits compared to what their reproductive and mortality rates would allow (*cf.* Lack 1954 and Newton 2013). This implies that their breeding numbers are regulated in some way. Mechanisms regulating the size of a population such as competition for food and nesting places, predation, disease and parasites are called density-dependent. Without the operation of stabilizing density-dependent mechanisms, populations could increase without bounds or collapse to zero. The Red-necked Grebe is a territorial and highly pugnacious bird, and it must be supposed, that the population regulation in the species is for a significant part density-dependent. The relatively stable numbers in e.g. Schleswig-Holstein (see below) are probably regulated by territorial behaviour, and the number of new breeders recruited from the non-breeding surplus in any one year possibly depends largely on the number of vacancies created by the loss of previous breeders (*cf.* Newton 2013).

The fact that many of the populations of Red-necked Grebes that have been monitored over several decades have changed greatly in abundance does not argue against regulation. It highlights the fact that environmental conditions change (*cf.* Newton 2013). In the period from 1985 to 2014 the number of breeding pairs in Schleswig-Holstein remained fairly constant and fluctuated from *c.* 500 to *c.* 700 pairs. Although the population between 1969 and 1978 was smaller, it was also relatively stable, and the number of breeding pairs fluctuated around 350 (with a roughly estimated range of 330 to 370 pairs) (Vlug 2005; J J Vlug). This probably means that the circumstances for breeding 1985-2014 were better (higher carrying capacity) than in 1969-78 (lower carrying capacity). It can be assumed that the population in the 1980s increased by changing environmental conditions which altered the population level around which density-dependent regulation occurred.

However, numbers of Red-necked Grebes sometimes decline because other factors (such as extreme weather, oil spills or drainage and disturbance of wetlands) affect a population regardless of its size. These disasters, so called density-independent factors, may act so severely as to override any density-dependent compensation possible (Newton 2013). An example is an oil-spill in the Danish coastal waters, near the island of Samsø in the Kattegat in January 1979. About 400-800 Red-necked Grebes were killed, and the breeding populations in Sjælland

(Zealand), Denmark and Skåne (Scania), South Sweden were reduced by *c.* 50% after this severe oil-spill and needed at least five years to recover (Larsen 1979, O'Donnel and Fjeldså 1979, Larsen, *cited in* Berndt and Busche 1981, Fjeldså 1982*a*, Karlsson and Kjellén 1984, Vlug 2000, 2002*a*, Fjeldså 2004).

While density-dependent factors tend to stabilize populations around an equilibrium, density-independent factors tend to destabilize them, causing large, unpredictable fluctuations. The size and fluctuations of *grisegeta* and other bird populations are determined by all the factors that impinge on it, whether or not they are influenced by density (Newton 2013).

11.2.2 Demographic Factors (Brood Success, Brood Size, Life Span and Survivorship)

Although there are data of brood success and family size on the breeding grounds, all that we can say about the population regulation in the Red-necked Grebe is hardly more than an educated guess because we know almost nothing about the demographic factors of the species such as annual survival or mortality rates, immigration or emigration and the number of non-breeding summering birds.

Brood Success (Percentage of Pairs Raising at Least One Young)

Europe

The mean brood success (= percentage of pairs raising at least one young) of European Red-necked Grebes is 41% ($n = 19,020$ pairs; however, the sample of Schleswig-Holstein, 14,976 pairs, is highly over-represented).

The brood success varies significantly from one European area to another (range of regional means 17% to 80%), but the data obtained by different authors are often not directly comparable, since there is no consistent method of measurement. Sometimes all the birds on the breeding waters (breeders and birds that have been totally prevented from breeding) are included in the calculations and sometimes only the birds proven to have bred there. Few authors have documented how many pairs leave the breeding area early without producing any young.

The brood success in the different areas in Europe was:

1. Schleswig-Holstein (1969-2014) 38% of 14,976

pairs on the breeding waters (including grebes that had been prevented from breeding) (J J Vlug)

2. South-eastern Denmark (1990) 38% of 68 pairs (H E Jørgensen)
3. Vejlerne, Denmark (1989-2003) 17% of 1,414 pairs (Kjeldsen 2008)
4. Uckermark, Brandenburg (1965-2005) 78% of 1,231 pairs (Dittberner and Dittberner 2006)
5. Sachsen (Saxony) (1955-82) 54% of 457 pairs (Vlug 2002a, calculated from Hummitzsch 1975, Tuschcherer 1981; P Hummitzsch)
6. The area around Leipzig ("Bezirk Leipzig"), Sachsen (1955-79) 63% of 245 pairs (Tuschcherer 1981)
7. Skåne (Scania), southern Sweden (1970-96) 60% of 351 pairs (Vlug 2002a, calculated from Tallroth and Axelsson 1991, Axelsson 1997; P Axelsson)
8. South-eastern Skåne (1987-96) 56% of 209 pairs (Axelsson 1997)
9. Lublin Province, south-eastern Poland (1993-99) 66% of 163 pairs (Kloskowski 2000)
10. The Volga delta, European Russia (1961-62) 80% of 360 pairs (Markuze 1965)

North America

In North America (1969-96) on average 60% of the pairs are successful ($n = 1,125$ pairs) (Vlug 2002a, calculated from Kevan 1970, Riske 1976, De Smet 1987, Fournier and Hines 1998). Brood success in Pine Lake, Alberta (25%) (Riske 1976) was the lowest, and in the Northwest

Territories, Canada (72%) (Fournier and Hines 1998) the highest of all the studied areas in North America.

The brood success in the different areas in North America areas was:

1. Yellowknife, Northwest Territories (1986-96) 72% of 652 pairs (Fournier and Hines 1998)
2. Turtle Mountain Provincial Park, Southern Manitoba (1980-81) 51% of 114 pairs (De Smet 1987)
3. Astotin Lake, Alberta (1969) 58% of 89 pairs (Kevan 1970)
4. Pine Lake, Central Alberta (1971-76) 25% of 207 pairs (Riske 1976)
5. Potholes in the Pine Lake area, Central Alberta (1970-76) 65% of 63 pairs (Riske 1976)

Range of Annual Means of Brood Success

Everywhere in its distribution area brood success of *grisegena* not only varies between the areas, but also between the years, e.g. from 14% to 68% in the period 1969-2014 (= 46 years) in Schleswig-Holstein (J J Vlug), from 3% to 51% in the period 1989-2003 (= 15 years) in Vejlerne, Denmark (Kjeldsen 2008), and from 51% to 85% over 11 years in the Northwest Territories (Fournier and Hines 1998).

The breeding results (annual brood success and brood size) of the Red-necked Grebe in Schleswig-Holstein and Hamburg 1969-2014 (J J Vlug) were:

Year	Total number of breeding pairs	Pairs with known breeding result	Pairs with one or more older young (= number of families)	Brood success (= % of pairs raising at least one young)	Total number of older young	Young per family (= brood size)
1969	340.5	125.5	49.5	39.44	77	1.56
1970	364.5	179.0	90.0	50.28	164	1.82
1971	362.5	139.0	46.0	33.09	79	1.72
1972	349.0	186.5	55.5	29.76	115	2.07
1973	348.5	197.5	104.0	52.66	168	1.62
1974	339.0	47.5	31.5	66.32	58	1.84
1975	347.5	106.0	59.0	55.66	96	1.63
1976	346.5	43.5	12.0	27.59	16	1.33
1977	342.5	105.0	34.0	32.38	57	1.68
1978	343.0	118.0	59.5	50.42	90	1.51
1979	272.5	76.5	50.0	65.36	109	2.18
1980	300.5	91.5	48.5	53.01	86	1.77
1981	329.0	163.5	111.0	67.89	200	1.80

Year	Total number of breeding pairs	Pairs with known breeding result	Pairs with one or more older young (= number of families)	Brood success (= % of pairs raising at least one young)	Total number of older young	Young per family (= brood size)
1982	423.0	253.5	118.0	46.55	212	1.80
1983	486.5	365.5	207.5	56.77	344	1.66
1984	466.5	311.5	60.0	19.26	87	1.45
1985	511.5	325.5	126.5	38.86	178	1.41
1986	543.5	396.5	215.5	54.35	371	1.72
1987	590.5	479.5	232.0	48.38	355	1.53
1988	605.5	458.5	252.0	54.96	394	1.56
1989	680.5	517.0	152.5	29.50	232	1.52
1990	726.0	509.5	127.0	24.93	169	1.33
1991	699.0	500.5	123.5	24.68	165	1.34
1992	621.5	428.0	157.0	36.68	245	1.56
1993	568.0	392.0	63.0	16.07	88	1.40
1994	605.5	419.0	168.5	40.21	255	1.51
1995	615.5	464.0	146.5	31.57	214	1.46
1996	524.5	353.0	50.0	14.16	82	1.64
1997	584.5	438.0	183.5	41.89	314	1.71
1998	630.0	440.5	183.0	41.54	357	1.95
1999	628.5	430.0	230.5	53.60	387	1.68
2000	667.0	443.0	132.5	29.91	198	1.49
2001	693.0	458.0	186.0	40.61	306	1.65
2002	656.0	414.5	158.5	38.24	256	1.62
2003	672.0	387.5	126.0	32.52	192	1.52
2004	690.5	381.0	99.0	25.98	142	1.43
2005	698.5	395.0	155.0	39.24	219	1.41
2006	717.0	408.5	156.0	38.19	239	1.53
2007	696.0	400.5	169.5	42.32	272	1.60
2008	720.0	409.0	113.5	27.75	164	1.44
2009	703.5	373.0	74.5	19.97	103	1.38
2010	703.0	367.5	157.5	42.86	249	1.58
2011	646.0	319.0	128.5	40.28	189	1.47
2012	684.5	387.0	138.0	35.66	215	1.56
2013	690.5	400.0	184.0	46.00	272	1.48
2014	681.0	371.0	145.0	39.08	203	1.40
Total 1969-2014		14,975.5	5,670.5	37.87	8,983	1.58

Brood Size (Family Size, Young per Successful Pair or Young per Family)

Europe and the western part of Asia

The majority of the successful pairs in Europe are observed with 1 or 2 young of at least a few weeks old.

The following data are from Germany:

1. In Schleswig-Holstein, northern Germany, 52% of the successful pairs had 1 chick, 37% 2, 9% 3 and almost 2% 4. Only 0.2% (= 6 pairs) were accompanied by 5 young ($n = 3.261$ families in the period 1969-2002) (Vlug 2005). Very exceptionally, a pair with 6 large chicks was observed on a pond near Rastorf in 2002 (R K Berndt and J J Vlug).

2. In Sachsen (Saxony), eastern Germany, 47% of the successful pairs were seen with 1 young, 36% with 2, 13% with 3 and 4% with 4 ($n = 385$ families) (Vlug 2005, calculated from Melde 1978, Köcher and Kopsch 1979, Tuchscherer 1981, Melde 1986, Müller 1991, Höser *et al.* 1998).
3. In the Uckermark, Brandenburg, eastern Germany, 25% of the families were seen with 1 young, 48% with 2, 22% with 3 and almost 5% with 4. Two pairs (= 0.4%) had 5 young ($n = 545$ families) (Dittberner 1996).

In Europe the mean number of (larger but still dependent) young per successful pair (= young per family or brood size) is 1.73 ($n = 8,783$ families; the majority, 5,671 families is from Schleswig-Holstein).

The mean brood size differs from area to area (range of regional means 1.11-2.80).

In the different European and West-Asiatic areas the brood size (young per family) was:

1. Schleswig-Holstein (1969-2014) 1.58 ($n = 5,671$ families with larger but still dependent chicks) (J J Vlug).
2. South-eastern Denmark (1990) 1.27 ($n = 26$ families) (H E Jørgensen)
3. Mecklenburg-Vorpommern (Mecklenburg-western Pomerania) in the 1980s 1.80 ($n = 267$ families) (Vlug 2002a, calculated from Eichstädt *et al.* 1987, Zimmermann 1987, Zimmermann and Schieweck 1988, Fiedler and Freitag 1989)
4. Lewitz fish ponds, Mecklenburg-Vorpommern (1968-87) 1.64 ($n = 144$ families) (Zimmermann and Schieweck 1988)
5. The area around Güstrow, Mecklenburg-Vorpommern 2.01 ($n = 74$ families) (Neubauer 2004)
6. Brandenburg (1960-93) 2.07 ($n = 610$ families) (Vlug 2002a, calculated from Schulze and Thinius 1982, Schmidt 1983, Dittberner 1996)
7. Uckermark, Brandenburg (1965-93) 2.07 ($n = 545$ families) (Dittberner 1996), and (1965-2005) 1.95 ($n = 956$ families) (Dittberner and Dittberner 2006)
8. Sachsen (Saxony) (1948-89) 1.74 ($n = 481$ families) (Vlug 2002a, calculated from Wobus 1964, Hummitzsch 1975, 1977, Melde 1978, Köcher and

Kopsch 1979, Tuchscherer 1981, Melde 1986, Müller 1991, Höser 1993; P Hummitzsch)

9. The area around Leipzig ("Bezirk Leipzig"), Sachsen (1955-79) 1.71 ($n = 155$ families) (Tuchscherer 1981)
10. Grimma, Oschatz and Wurzen in the Leipzig area, Sachsen (Saxony) (1960-76) 1.71 ($n = 58$ families) (Köcher and Kopsch 1979)
11. Oberlausitz, Sachsen (Saxony) (1948-77) 1.92 ($n = 77$ families) (Melde 1986)
12. Skåne (Scania), southern Sweden (1967-96) 1.83 ($n = 263$ families) (Vlug 2002a, calculated from Ahlén 1970, Tallroth and Axelsson 1991, Axelsson 1997; P Axelsson)
13. South-eastern Skåne (Scania) (1987-96) 1.85 ($n = 117$ families) (Axelsson 1997)
14. Lublin Province, south-eastern Poland (1993-99) 1.94 ($n = 108$ families) (Kloskowski 2000)
15. Milicz, south-western Poland 1.11 ($n = 27$ families) (Ławniczak 1982)
16. The Volga delta, European Russia (1961-62) 2.80 ($n = 288$ families with 806 young: 120 families with 336 young in 1961, and 168 families with 470 young in 1962) (Markuze 1965)
17. Naurzum Lakes, North-Kazakhstan 1.5 (Gordienko 1980)
18. The southern part of the Murmansk Region, European Russia (2000-01) 2.3 ($n = 12$ families) (Bakkal *et al.* 2002)

North America

The majority of the successful pairs (families) in North America (as in Europe) are observed with 1 or 2 young of at least a few weeks old:

1. Six pairs in British Columbia were seen with exceptionally large broods: 4 pairs had 6 young and 2 had 8 young, but the majority of the families had 1 or 2 young: 31% had 1 young, 45% 2, 16% 3, 4% 4, and 2% 5 ($n = 577$ families) (Campbell *et al.* 1990).
2. On Astotin Lake, Alberta, 44% of the successful pairs were observed with 1 young, 33% with 2, 17% with 3, 6% with 4 and 5 ($n = 70$ families) (Kevan 1970).

In North America (1936-96) the mean number of dependent young per successful pair was 1.95 (range of regional means 1.31-2.05, $n = 1.328$ families).

The brood size (young per family) in the different areas in North America was:

1. Yellowknife, Northwest Territories (1986-96) 1.99 ($n = 470$ families) (Fournier and Hines 1998)
2. Turtle Mountain Provincial Park, southern Manitoba (1980-81) 1.85 ($n = 58$ families) (De Smet 1987)
3. Astotin Lake, Alberta (1968-69) 1.87 ($n = 70$ families) (Kevan 1970)
4. Pine Lake, Central Alberta (1971-76) 1.37 ($n = 51$ families) (Riske 1976)
5. Potholes in the Pine Lake area, Central Alberta 1.63 (1970-76) ($n = 41$ families) (Riske 1976)
6. British Columbia 2.05 ($n = 577$ families) (Campbell *et al.* 1990)
7. Marsh behind a dyke near Duck Lake, Creston, British Columbia (1983-84) 1.31 ($n = 26$ families) (Ohanjanian 1986)
8. British Columbia (1936-41) 1.86 ($n = 35$ families) (Munro 1941)

Range of Annual Means of Brood Size

In the whole distribution area of the species brood size not only varies between the areas, but also between the years, e.g. from 1.33 to 2.18 in the period 1969-2014 (= 46 years) in Schleswig-Holstein (J J Vlug, see above), and from 1.59 to 2.25 over 11 years (1986-96) in the Northwest Territories (Fournier and Hines 1998).

Life Span and Survivorship

Chick mortality

The majority of the successful pairs are observed with 1 or 2 young of at least a few weeks old. However, complete clutches usually consist of 3, 4 or 5 eggs (Vlug 2002a) (see 16.3.4). Many factors are responsible for the difference between clutch size and brood-size. Partial clutch abandonment during hatching is frequently observed, especially in food shortage (Stout and Nuechterlein 1999, Vlug 2002a, Kloskowski 2003a). During the first days after hatching, the chicks are very vulnerable to chilling; damp, cool, and stormy weather is a major source of mortality, especially when food is scarce (Wobus 1964, Vlug 1985, Dittberner 1996, Vlug 2002a, Vlug 2005).

So, it is understandable that the mortality is the highest during the first 5-10 days after hatching, and there is little mortality after the first month (De Smet 1983, Ohanjanian 1986, Stout and Nuechterlein 1999, Kloskowski 2000). The age-specific mortality of Red-necked Grebe chicks was determined for a marsh behind a dyke near Duck Lake, Creston, British Columbia in 1983 and 1984. In both years mortality was greatest in the first 7 days after hatching – 48% and 67% of the chicks that died did so during this time. This dropped to 9% and 11% in the second week. In 1984 a slight increase was observed in the third week and no mortality occurred that year among chicks older than 22 days. In 1983, however, 2 chicks died in their fifth week. No mortality occurred in 1983 in chicks older than 35 days. In 55% of the broods at least one young survived up to the fledgling stage, and in the remaining 45%, all the chicks died earlier ($n = 47$ broods) (Ohanjanian 1986). In Turtle Mountain Provincial Park, Manitoba, 24% of the Red-necked Grebe chicks died during their first month ($n = 48$ families). As in other areas, the survival rates were much higher beyond the first month. Only one chick disappeared among 82 observed up to an age of 40 days, and none died among 51 observed up to 50 days of age (De Smet 1983).

Survival rates of adult birds

Although we know something about brood success, family size and chick mortality on the breeding grounds, we know almost nothing about the survival rates of the adult birds and of the young birds after leaving the breeding waters. Annual survival rates in birds are usually measured from ringing (but there are major uncertainties in the measurements results). From survival rates, mortality rates can be readily calculated, for when expressed on a percentage scale, both together add up to 100%. However, the number of recoveries of ringed Red-necked Grebes is very low. Konter and Konter (2006) could obtain data of only four young and seven older European birds of the species.

Some studies in particular areas involve checking to find what proportion of birds present in one year are still there the next. This method does not tell us where or when particular individuals die, nor does it separate deaths from permanent emigration (Newton 2013). The annual rates of colour-banded adults returning to Lake Osakis, Minnesota, over 5 years ranged from 61% ($n = 69$) to 100% ($n = 9$), suggesting high annual survival rates for adult Red-necked Grebes (Stout and Nuechterlein 1999) (see also 16.6.4).

11.2.3 Life-history Features

Red-necked Grebes have a surplus of stable and predictable survival habitats [marine moulting, summering (non-breeding) and wintering areas] at their disposal, but their breeding habitat (shallow wetlands) is fairly limited and unpredictable. So, it is likely that they have long life expectancies and rather confined prospects for successful breeding. Selection generally leads in such situations to allocation of energy to survival adaptations (K-selection) (Alerstam and Högstedt 1982, Fjeldså 1986). The contribution to the future gene pool of Red-necked Grebes is likely to be a matter of the total long-life production, rather than annual productivity, i.e. Red-necked Grebes most likely belong to the K-strategists among the grebes (Vlug 2005, 2012).

The description of *Podiceps grisegena* as a K-strategist is consistent with the facts. As already stated (see 11.2.2) the birds show a relatively small reproductive potential (relatively small clutch and brood sizes, low brood success). Their young are dependent on the parents for a long time and have a deferred age of first breeding (though one year old birds are sexually mature, they rarely breed before they are two years old, see 11.1) (Vlug 2005). The survival rates of adult Red-necked Grebes are probably large (Stout and Nuechterlein 1999) but can be easily reduced by a high investment in rearing their offspring (Clutton-Brock 1991, Bennett and Owens 2002), especially in poor habitats. This was indicated by a study of Kloskowski *et al.* (2017). They examined variation in body mass and commonly used haematological indices in incubating and chick-rearing Red-necked Grebes in Poland. Scaled body mass was lower in brood-rearing grebes than in incubating grebes. Probably, the drop in body mass during brood rearing is evidence of a deteriorated physical condition due to reproductive workload, indicating that parents suffered costs in the form of loss of body reserves (but for another possibility see Kloskowski *et al.* 2017). Disparities in habitat quality (and thus reproductive effort) were reflected in the erythrocytic profiles of Red-necked Grebes. In poor habitats, parents finished the breeding season in inferior physiological condition relative to breeders in high-quality habitats.

The adult birds have developed behaviour patterns to increase prospects for their own survival at the breeding sites, e.g. leaving the nests for extended periods at night

(by leaving their nests at night, the birds may be decreasing their exposure to nocturnal predators that prey on adults) (Nuechterlein and Buitron 2002), the defence of large territories which means that established pairs have more food available than the bare necessities (Vlug 2005), and early departures from the breeding waters to the moulting sites (Vlug 1996).

Red-necked Grebes which make food flights often have a lower than normal brood success and a smaller brood size. However, these adult birds do have large feeding areas (sea or large lake) at their disposal. The large bodies of water offer them more predictable conditions, too, so, the long life expectancies of these grebes are high. Probably, Red-necked Grebes breeding near large bodies of water follow the strategy of living a long life with a high total lifetime reproduction, even more so than those breeding in small ponds (Vlug 2005).

11.3 Breeding Population and Population Trends

11.3.1 Breeding Population and Population Trends in Europe-West Asia

Finland

Palmén (1876) stated that the Red-necked Grebe was a truly rare breeding bird in the southern part of Finland, but that it nested relatively often from 63° N in the central part of the country and bred frequently up to 65° N; in Lapland it was found as far north as Kittilä (67° 40' N).

In the 1950s, Merikallio (1958) estimated the population in Finland at around 2,000 pairs. He wrote that the main population occurred in Järvi-Suomi and in the northern part of Suomenselkä. From here, it extended as a broad belt across Lounais-Suomi through Tampere and Hämeenlinna to the neighbourhood of Uusikaupunki, where a population of about 100 pairs had been observed.

In the late 1970s the population was estimated at 2,500–3,000 pairs (Lammi 1983). However, the numbers given by Lammi (1983) and Merikallio (1958) were probably underestimates. The species nested patchily in the southern half of Finland. It was common only in a few localities in the south-eastern and south-western parts of the country, breeding mainly in single pairs or in small groups on scattered waters, but as many as 40 pairs could breed on the most suitable lakes. The distribution area in the late 1970s was the same as in the 1950s (Lammi 1983, Koskimies 1989).

The numbers increased considerably from the 1980s onwards (early 1990s: 5,000-7,000 breeding pairs) (Lammi *cited in* VlUG 1997, Väisänen *et al.* 1998, BirdLife International/European Bird Census Council 2000). During the periods from 1999 to 2001 and 2006 to 2010 6,000-8,000 pairs bred in Finland (BirdLife International 2004, Valkama *et al.* 2011). The majority of the birds were still found in the southern parts of the Finnish lake area (Väisänen *et al.* 1998). In the period from 2008 to 2012 the population was estimated at 6,000-9,400 pairs (European Environment Agency 2013). However, Pöysä *et al.* (2013) stated that the numbers of *P. grisegena* in the country increased during the period 1986-96 but declined in the period 1997-2011. Population changes in the Kukkia lake complex in southern Finland were in line with these nationwide trends: 1986-87 26, 1998-99 85, 2003-04 104 and 2012 60 pairs (Virkkala 2016).

Sweden

In Sweden and other countries in north-western Europe, the Red-necked Grebe is considered rare in the 17th and 18th centuries (Thomasson 1956), and Linnaeus (1758, 1766) did not mention the species. From about the middle of the 19th century it became increasingly common.

From the mid 1970s to the early 1990s c. 600 pairs bred in Sweden (Grenmyr 1984, Svensson *et al.* 1999, BirdLife International/European Bird Census Council 2000). After that period the population increased. Around the year 2000 the population was estimated at 700-800 pairs (SOF 2002, *cited in* Ottosson *et al.* 2012, BirdLife International 2004), and c. 10 years later Ottosson *et al.* (2012) mentioned c. 1,100 pairs. A national survey in 2011 resulted in an estimation of about 1,300 pairs (range 1,109-1,680) (Norevik 2014).

Podiceps grisegena in Sweden breeds especially on artificial water bodies, natural inland water bodies and coastal bays. The distribution is separated into two distinct areas: 1. Norrland (the northern part of the country with c. 580 pairs in 2011) and 2. Götaland (the southern part of Sweden with c. 712 pairs in 2011). In the area between, Svealand, the species is scarce (c. 103 pairs in 2011) (Norevik 2014). It is possible that the northern population was founded by immigrants from the (north-) east (through Finland) and the southern population by birds from the south-west (through Denmark) (Ekman 1922, *cited in* Grenmyr 1984, Curry-Lindahl 1959, Svensson *et al.* 1999).

1. Norrland

The majority of the breeding birds in northern Sweden are found in Västerbotten and Norrbotten. On the basis of surveys, mainly carried out during the 1970s, the size of the breeding population in these two provinces was estimated at c. 400 pairs (Grenmyr 1984). In the national survey in 2011 the population in Västerbotten and Norrbotten was calculated at c. 425 pairs, and in the whole of Norrland at c. 580 pairs (Norevik 2014).

2. Götaland

Most breeding birds in southern Sweden are found in Skåne (Scania), and in two lakes (Lake Tåkern and Hornborgasjön).

2a. Skåne (Scania)

In 1960 the number of breeding pairs in Skåne was estimated at more than 50, and in 1968 c. 28 were counted (Ahlén 1970). A census in the years 1978 and 1979 revealed 102 pairs (Karlsson and Kjellén 1984). In the early 1980s the number of breeding pairs was 40-60 (Risberg 1990, Svensson *et al.* 1999). Then the numbers began to rise. In 1998 at least 95 pairs bred in Skåne (SkOF 1998, *cited in* Bengtsson and Green 2013), and in 2011 the population peaked with 250-275 pairs (Bengtsson 2011, Ottosson *et al.* 2012, Bengtsson and Green 2013, Norevik 2014).

2b. Lake Tåkern

This lake in Östergötland is a shallow, nutrient-rich lake that was partly drained in the 19th century, allowing extensive reed-beds to colonize about one third of the total area. The shallow waters (average depth 0.8 m) are rich in aquatic flora. The lake is 12 km long and 8 km wide and is 5,620 ha large (Lindell *et al.* 2000). All five European species of grebes are found here. The breeding and feeding Red-necked Grebes were mainly found near the small pools and channels of the reed beds (Jacobsson 1975). Breeding on Lake Tåkern was recorded in 1925. In the 1950s the species was present in large numbers (Druid 1990). In 1970 at least 6 pairs bred on the lake. After that year the numbers grew spectacularly: 1972 25-30, 1973 c. 40, 1974 c. 70, 1975 c. 70, 1976 70-80, 1977 105-120, 1978 c. 75, 1979 c. 100, 1980 c. 120, 1981 120-130, and 1982 c. 120 pairs (Jacobsson 1974, 1975, 1977, Bergengren 1982, Druid 1990). In the period after 1987 the numbers never reached those of the early 1980s. In 1989 the estimation was 80-90 pairs (Druid 1990), in 1999 c. 60 pairs were recorded (SOF 2002, *cited in* Ottosson *et al.* 2012) and in 2011 c. 50 (Norevik 2014).

2c. Hornborgasjön

This is a shallow (max. depth 2 m) calcareous lake in Västergötland. It has undergone extensive restoration work, involving water-level management (Lindell *et al.* 2000). The surface area is 28 km². Like Lake Tåkern, all five European species of grebes are found here. In 1993 six pairs of Red-necked Grebes bred on the lake. Then the numbers increased enormously. In 1996 40-60, 1998 c. 80, 1999 c. 120, 2007 c. 180 and in 2011 175-180 pairs were observed (Fält and Johansson 1999, Lindell *et al.* 2000, Norevik 2014, Anonymous 2016).

Norway

Possibly the species bred near Oslo in the 19th century (Sundevall 1885, *cited in* Dement'ev and Gladkov 1951/1969). From the late 1960s onward there are observations of birds in the summer period (e.g. Haftorn 1971, Gjershaug *et al.* 1994, Reinsborg 2009), but the first confirmed breeding record was not until 1998. In that year a pair with one young was observed in Balsfjord, Troms in northern Norway (Solbakken *et al.* 2003). Artsdatabanken (2014, *cited in* Norevik 2014) stated that only a few breeding records for Norway exist.

Denmark

In Denmark, the Red-necked Grebe mainly occurs in smaller eutrophic lakes, pools created by peat digging, forest lakes, marshes and peat-bogs (Preuss 1969, Olsen 1992, Grell 1998). During the whole of the 19th century the species was probably a common breeding bird in the eastern part of the country (the islands), but also locally rather common in Jylland (Jutland) (Dybbro 1976, Ferdinand 1980, Palm 1988). In the first half of the 20th century it was considered a fairly common Danish breeding bird, with a rather scattered distribution but in (relatively) large numbers occurring at various places (Preuss 1969).

Preuss (1969) stated that during the period from 1960 to 1967 350-400 pairs bred in Denmark. The majority of the birds were found on the islands, especially Sjælland (Zealand). Although there were only a few breeding places in Jylland (Jutland), Preuss (1969) did not know that a large number Red-necked Grebes (probably 60-100 pairs) bred in Vejlerne, north-west Jylland (see below). Between 1971 and 1974 the Danish population was estimated at 600-800 pairs. The distribution was about the same as in the 1960s, but new breeding places were occupied on Jylland (Jutland) (Dybbro 1976, Meltofte and Fjeldsø 1989).

In the late 1980s the numbers were still higher, and 800-1,000 pairs nested in the country, most of them on the islands Sjælland, Lolland, Falster and Langeland. Large numbers were also observed in Vejlerne (75-80 pairs) in north-west Jylland (Jutland) (see below) and the Ribe district in south-west Jutland (65-70 pairs) (Olsen 1992).

In the 1990s the breeding population in Denmark was estimated at 1,500-2,000 pairs (Grell 1998, Dybbro 2004). However, Meltofte *et al.* (2009) studied many small wetlands and found in these "small biotopes" many breeding pairs which were not known by Grell (1998). They concluded that the Danish breeding population was c. 38% larger and consisted of 2,230-2,600 pairs.

After a long period of growth, it is possible that the Danish population began to decline. The number of breeding pairs in 2011 was estimated at 1,400 breeding pairs (Dansk Ornitologisk Forening 2015). However, this number is not based on data of a national census but on point counts.

Vejlerne

Vejlerne originated from two former shallow estuarine inlets of the brackish Limfjord which has been embanked by dikes since 1868. The area is a wet – and nowadays freshwater – area with channels, dikes, reed-beds, marshes and meadows. Until the mid 1960s a large population of Red-necked Grebes bred in Vejlerne, probably 60 to 100 pairs. Following a water level lowering after 1965 a large decline in numbers was observed, and by 1978 and 1979 only 13-14 pairs bred in the area. Since then the population has steadily increased: 1984 72, 1990 87, 1995 103 and 1999 141 pairs. The majority of the birds nested in smaller lakes within the reed-beds of the northern parts of Bygholm Vejle (Kjeldsen 2008).

Germany

The Red-necked Grebe in Germany predominantly inhabits small, shallow water bodies with abundant emergent and submerged vegetation. It can also be found in well-vegetated bays of large lakes. As breeding sites it chooses flooded meadows, fens, ponds, oxbow lakes, sedimentation ponds, sewage farms as well as marl pits and other abandoned pits and quarries that are filled with water. The majority of the breeding waters are found in the north-eastern German Plain, northeast of the rivers Elbe and Saale. About half of the population of Germany nests in Mecklenburg-Vorpommern (Nicolai 1993, Gedeon *et al.* 2014). The German breeding population

between 2005 and 2009 was estimated at 1,800-2,600 pairs. The general population trend in the period 1985-2009 is regarded as positive. Since the late 1990s, however, the numbers of breeding Red-necked Grebes seem to be stable, with some regional differences (Gedeon *et al.* 2014).

1. Schleswig-Holstein and Hamburg

The numbers of breeding pairs in Schleswig-Holstein and the state of Hamburg are often taken together. However, in Hamburg the species is rare and only c. 1-4 pairs bred in the period from 1964 to 2011 (Holzapfel *et al.* 1982, Vidal 1984, Vlug 1986, Mitschke and Baumung 2001, Mitschke 2012).

The species was already in the 19th century a common breeding bird in Schleswig-Holstein (Boie 1819, *cited in* Scholl 1974, Naumann 1838, Kjærboelling 1852, *cited in* Scholl 1974). The breeding population dynamics in Schleswig-Holstein were investigated between 1969 and 2014 (Scholl 1974, Vlug 1986, 2000, 2002a, 2005; J J Vlug) (see discussion 11.2.1). The majority of the breeding places are found in the eastern part of the country in the young moraine area. Here the grebes nest especially in fish ponds, lagoons and natural and (new) man-made shallow waters (Vlug 1993, Berndt *et al.* 2002, Vlug 2005, 2011, Koop and Berndt 2014). Scholl (1974) stated that in the early 1970s at least 200-220 pairs bred in Schleswig-Holstein. However, this estimation was too low. Between 1969 and 1978 the breeding population was c. 350 pairs (with a roughly estimated range of 330 to 370 pairs) (J J Vlug). The lowest number (272 pairs) was recorded in 1979 following an oil-spill in the Danish coastal waters, near the island of Samsø in the Kattegat in January 1979, causing the death of 400-800 Red-necked Grebes. Although the population in Schleswig-Holstein was less affected than the populations in Sjælland (Zealand), Denmark and Skåne (Scania), South Sweden, the number of breeding pairs still decreased by 20%, from 343 in 1978 to 272 in 1979 (Larsen 1979, O'Donnell and Fjeldså 1979, Larsen, *cited in* Berndt and Busche 1981, Fjeldså 1982a, Karlsson and Kjellén 1984, Vlug 2000, 2002a, Fjeldså 2004, Vlug 2005). From then on, the population increased continuously until c. 1990 (1980 301, 1985 512 and 1990 726 pairs). Then it did not change essentially (1995 616, 2000 667, 2005 699, 2010 703, 2014 681 pairs). Thus, the population remained fairly constant through several decades, and fluctuated

between c. 500 and c. 700 pairs in the period from 1985 to 2014 (J J Vlug).

Many (small) breeding waters on the mainland of Schleswig-Holstein are occupied by one, two or three pairs, but there are also a number of (often) larger nesting sites with a larger number of pairs, e.g. on a pond near Wittenberg (1 ha) 8 pairs were seen in 1990 (Vlug 1993). Thirty or more pairs were also recorded, e.g. on two ponds near Lebrade (with a total area of 69 ha) 56 pairs in 2006 and 2010, and on a pond near Kühren (40 ha) 35 pairs in 2012 and 2014 (B Koop and J J Vlug).

New artificial or natural shallow waters are often colonized quickly after flooding by large numbers of Red-necked Grebes. The populations increase sharply after flooding, but after a number of years a large decline usually occurs (Vlug 2000, Vlug 2011). An example is the Struckteich, 14 ha. In 1998, a few months after flooding, 25 pairs bred on this lake. The maximum number, 54 breeding pairs, was recorded in 2000. From then on, the numbers declined sharply: 2001 35, 2002 26 and 2003 7 pairs. In the period between 2004 and 2017 only 0-3 pairs were seen. Another example is the Dodauer See (Lake Dodau), 17 ha. This pond was flooded in 2002-03. In the first year, 2003, 24 pairs nested on this water body. The maximum number, 35 pairs, was observed in 2005. The numbers in 2009 and 2011 were 11 pairs (Vlug 2011), and in 2016 only 1 pair was recorded (I Fahne, D Heldt, J J Vlug).

Large numbers of breeding Red-necked Grebes are found on lagoons and other shallow wetlands separated from the Baltic Sea by a barrier beach or dyke, especially on the island of Fehmarn (Vlug 1993, 2009). The adult grebes make food flights to the adjacent sea and do not depend on the food supply of the breeding-waters. They achieve extremely high population densities here. Although it seems that the majority of the pairs on the lagoons actually breed, it is likely that a number of the birds are prevented from nesting and breeding by social interactions. Because it is impossible to follow the fate of the individual birds, the term "breeding pairs" is used here, although "potential breeding pairs" is perhaps a better term. Probably, Red-necked Grebes from other areas may visit the lagoons, which makes the situation even more difficult.

At a lagoon near Hohenfelde in the district of Plön on the mainland of Schleswig-Holstein 14 pairs bred (or at

least tried do so) in 2008. This lagoon has an area of 1.5 ha, thus the population density of the species was 9.3 breeding pairs/ha (see Fig. 33). At the Niobe-lagoon, Grüner Brink, a breeding water of 4 ha on the island of Fehmarn, in many years large numbers are seen, up to 32 pairs in 1989 and 2010 (= 8.0 breeding pairs/ha), and at a pond near Westermarkelsdorf, Fehmarn, 3 ha, 26 pairs were found in 1989 (= 8.7 breeding pairs/ha), 38 pairs in 2014 (= 12.7 breeding pairs/ha) and 40 pairs in 2017 (= 13.3 breeding pairs/ha (see Fig. 32). Nowhere in the whole breeding range of the Red-necked Grebe have such high densities ever been recorded (Vlug 1993, 2009; R K Berndt, B Koop, J J Vlug).

The numbers of breeding grebes on the island of Fehmarn in the 20th century show large fluctuations (Vlug 1986, 2000, Berndt *et al.* 2005). During and shortly before World War I the numbers of breeding Red-necked Grebes were very high, c. 450 pairs nested on the island in 1914 (Reichling, *cited in* Thiel 1953). Reichling (*cited in* Heinroth 1919) stated in December 1918 at the meeting of the German Ornithological Society that there were c. 120 nests of *Podiceps grisegena* on the ponds of Wallnau in the south-western part of the island. From that time on the population of Fehmarn underwent a marked decrease and in the 1950s the numbers on the island were low (1952 and 1953 12-15, 1954 25-26, 1956 31-35, 1958 25-27 pairs) (Thiel 1953, Schmidt, *cited in* Wobus 1964, Vlug 2000, Berndt *et al.* 2005). Although the numbers recovered, they have never achieved the former size (1970 95, 1980 70, 1986 142, 1990 235, 1995 149, 2000 75 and 2014 139 pairs) (Vlug 2000, Berndt *et al.* 2005; J J Vlug).

2. Mecklenburg-Vorpommern (Mecklenburg-western Pomerania)

Wüstnei and Clodius (1900) described the species as a rare breeding bird in Mecklenburg. Kuhk (1939) stated that the Red-necked bred on numerous lakes and was spread over the whole country. Krägenow (1977) estimated the population in Mecklenburg-Vorpommern at c. 200 breeding pairs. Zimmermann (1987) wrote that during the period from 1978 to 1982 c. 400 pairs bred in the state. The population increased further by the colonization of new breeding waters or newly created water bodies (Zimmermann 2006, Vökler 2014). In the period from 1994 to 1998 600-1,500 (Zimmermann 2006), and between 2005 and 2009 700-1,400 pairs nested in Mecklenburg-Vorpommern (Vökler 2014).

Many (small) breeding waters in the state are occupied by one or a few pairs, but there are also a number of nesting sites with c. 30 or more pairs, e.g. Stuerscher See (53-55 pairs in 2006) (Müller 2010), fish-ponds in the Lewitz (45-50 pairs in 1971) (Zimmermann and Schieweck 1988, Zimmermann 2008), Polder Rodde (36 pairs in 2007) (Müller 2011), Dambecker Seen (28-32 pairs between 1970 and 1975) (Spillner 1981), Peene-Polder Anklam to Neuhof (31 pairs in 2002) (Müller 2005) and Nonnensee, Rügen (29 pairs in 1996) (Helbig 1997).

3. Brandenburg and Berlin

The numbers of breeding pairs in Brandenburg and the state of Berlin are often taken together. The number of nesting Red-necked Grebes in Berlin fluctuated from 3 to 10 pairs between 1990 and 2000 (Otto and Witt 2002).

Schalow (1919) stated that the species was found in suitable breeding grounds over the whole Mark of Brandenburg, but in most areas, it apparently occurred in much smaller numbers than the Great Crested Grebe. The number of breeding pairs in Brandenburg in the mid 1970s was estimated at 100-500 (Schmidt 1983, Ryslavy *et al.* 2011, Gedeon *et al.* 2014), and in the mid and late 1990s at 200-300 pairs (Ryslavy 2001, Schonert 2001, Ryslavy and Mädlow 2008, Ryslavy *et al.* 2011). In the period from 2005 to 2009 c. 285 pairs were found in the state (Ryslavy *et al.* 2011). The numbers have probably been declining (sharply) since the 1970s (Ryslavy *et al.* 2011, Gedeon *et al.* 2014).

A considerable part of the population (at least 100 pairs) is found in the Uckermark, a district in the north-eastern part of Brandenburg (Schonert 2001). Large numbers in this district were observed on the Felchowsee (Lake Felchow) (40 pairs in 1968) (Dittberner 1996), and on the Landiner Haussee (c. 30 pairs in 1968, 1969 and 1991) (Dittberner and Dittberner 2006).

4. Sachsen (Saxony)

The breeding numbers of *Podiceps grisegena* in Sachsen have been declining since c. 1900 (Heyder 1952, Höser *et al.* 1998, Steffens *et al.* 2013). In the former district of Leipzig c. 100 breeding pairs were found around 1910, but only 9-18 pairs in the period from 1978 to 1989 (Höser *et al.* 1998).

Höser *et al.* (1998) stated that between 1978 and 1989 at least 54-93 pairs nested in the Free State. In the mid 1990s 80-100 pairs were found here (Steffens *et al.* 1998).

The numbers declined, among other things because of the intensification of fish farming. In the period from 2004 to 2007 50-70 pairs were observed (Steffens *et al.* 2013), and in 2008 the estimation was only 30-40 pairs (Rau *et al.* 2009).

Important breeding waters in Sachsen are (or were) the Eschefelder Teiche (fishponds near Eschefeld) (c. 50 pairs in 1917) (Wichtrich, *cited in* Heyder 1952), the Zschornaer Teiche (fishponds near Zschorna) (19-22 pairs in 1972) (Hummitzsch 1975), Königswartha (15-20 pairs) (Paulick, *cited in* Höser *et al.* 1998) and Werbeliner See (at least 16 pairs in 2008) (Schulz, *cited in* Rau *et al.* 2009).

5. Sachsen-Anhalt (Saxony-Anhalt)

In the period from 1990 to 1995 28-40 pairs bred in the southern part of Sachsen-Anhalt (Stenzel 1997). In the whole state of Sachsen-Anhalt, the breeding population was investigated between 2001 and 2013 (Fischer and Dornbusch 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2014a, b). In 2001, 2002 and 2003 the estimated number of breeding pairs was 30. From then on, the numbers increased continuously and in 2010 the population peaked with 75-80 pairs. The largest numbers were found in the nature reserve of Stremel in Havelberg (18 pairs in 2010).

6. Niedersachsen (Lower Saxony) and Bremen

In the first half of the 20th century more breeding pairs were found than in the 1960s and 1970s (Frantzen 1978, Krüger *et al.* 2014). In the 1970s only c. 5 breeding pairs were observed (Frantzen 1978, Südbeck and Oldekop 1999). Then the numbers increased: 1980 c. 5-10 pairs (Heckenroth 1985), 1985 9-16 pairs (Heckenroth and Laske 1997), 1997 and 1998 c. 20 pairs (Südbeck and Oldekop 1999), and 1999 27 pairs (Degen 2006). In the period from 2005 to 2008 20-25 pairs bred in Niedersachsen (23 pairs in 2005) (Krüger *et al.* 2014), and in 2014 25 pairs were seen (Krüger and Nipkow 2015).

There are no records of breeding Red-necked Grebes in the state of Bremen (Heckenroth 1985, Heckenroth and Laske 1997, Gedeon *et al.* 2014).

Thüringen, Nordrhein-Westfalen (North Rhine-Westphalia), Hessen (Hesse), Rheinland-Pfalz (Rhineland-Palatinate), Saarland, Baden-Württemberg and Bayern (Bavaria) are beyond the regular breeding range of the species.

7. Thüringen (Thuringia)

In Thüringen the Red-necked Grebe is only a rare breeding bird (Gierth 1986). There are a few breeding records since the early 1980s (Rost 1998, Rost and Grimm 2004).

8. Nordrhein-Westfalen (North Rhine-Westphalia)

The Red-necked Grebe is an occasional breeder in Nordrhein-Westfalen. Herkenrath (1984) recorded in three consecutive years a successful breeding pair near Bönen (district of Unna): 1938 (3 chicks), 1939 (4 chicks) and 1940 (3 chicks).

In the period from 2000 to 2005 the species colonized the Möhnesee (Möhne Reservoir) in the district of Soest. A single bird established a territory in 2000. In the following year the first unsuccessful breeding attempts took place. The highest number of breeding pairs was recorded in 2003, when three pairs established a territory. In 2004 only three birds were present, but due to a partner exchange during the breeding season breeding attempts were made in two territories. Also, in 2005 three birds were recorded. Large fluctuations in the water level forced the birds to build several new nests during the breeding season and all breeding attempts were unsuccessful (Hegemann 2005, Sudmann 2013).

9. Hessen (Hesse)

Müller (*cited in* Gebhardt and Sunkel 1954) saw in 1887 one or two adult Red-necked Grebes with chicks on the Albacher Teich (Pond of Albach) near Lich in the district of Gießen.

In the period from 1986 to 1991 a solitary Red-necked Grebe was observed on the Edersee (Eder Reservoir) near Herzhausen in the district of Waldeck-Frankenberg. In 1986, 1987, 1989, 1990 and 1991 the bird defended a territory against Great Crested Grebes, showed nest-building and was highly vocal (Burkhardt 1995, Hessische Gesellschaft für Ornithologie und Naturschutz 2010; R Enderlein). Solitary birds defending a territory were also recorded in the area of the Borkener Seen in the district of Schwalm-Eder (since 1990), and in Lahnaue in the district of Gießen (since 2007) (Hessische Gesellschaft für Ornithologie und Naturschutz 2010).

Although Hessen is beyond the regular breeding range of the species, there is a breeding outpost of the species in the nature reserve Teufelsee und Pfaffensee near Echzell in the district of Wetterau. In the period from 2001 to 2007 one pair bred on the Pfaffensee (c. 25 ha)

(Roland 2001, Hessische Gesellschaft für Ornithologie und Naturschutz 2010). In 2008, 2009 and 2010 three to five pairs were recorded (Hessische Gesellschaft für Ornithologie und Naturschutz 2010). Although the breeding success was low because many nests were washed away during periods of high winds, the numbers increased further. In 2014 c. 7 and in 2015 c. 9 pairs were seen (T Sacher and S Stübing, ornitho.de). The Pfaffensee has (almost) no fish and abundant invertebrate and amphibian faunas (Roland 2001, Hessische Gesellschaft für Ornithologie und Naturschutz 2010).

10. Rheinland-Pfalz (Rhineland-Palatinate)

A number of authors stated that Maximilian Prinz zu Wied observed the species breeding on larger ponds of the Westerwälder Seenplatte in the middle of the 19th century (Mildenberger 1982, Pickel 1983, Kunz and Simon 1987). However, Maximilian Prinz zu Wied (1841, manuscript published by Kunz 1995) recorded only migratory birds (“*C. subcristatus* L. Graukehliger Taucher. Einzeln jung auf dem Zuge”) (Kunz 1995, Pickel 1997).

In 1993 a pair attempted to breed on the Wiesensee in the Westerwald (nest building) (Fahl and Pickel 1994).

Since the late 1990s there is a breeding outpost of the species on the Dreifelder Weiher (100 ha), Westerwälder Seenplatte, in the district of Westerwald (Dietzen 2015). The first breeding was seen in 1997 when a pair raised 2 young (Kunz and Schäfer 1998). Breeding pairs were recorded in each year of the period from 1998 to 2015 with a maximum of c. 5 pairs (Müllen *et al.* 1999, Dietzen *et al.* 2002, 2003, 2004, 2005, 2006, Dietzen and Folz 2008a, b, Dietzen *et al.* 2011, Dietzen 2015; A. Kunz, ornitho.de). In contrast to the breeding outpost in Hessen (see above) the breeding success on the Dreifelder Weiher was high.

On the Haidenweiher (16 ha), near the Dreifelder Weiher, a pair raised 3 young in 2005, showed breeding attempts in 2006 and was recorded with 3 chicks in 2007 (Dietzen *et al.* 2006, Dietzen and Folz 2008a, b).

A solitary Red-necked Grebe defended a territory against Great Crested Grebes and showed nest building on the Sangweiher near Daun in 2009 (Dietzen *et al.* 2011).

11. Saarland

There are no records of breeding Red-necked Grebes in the state of Saarland (Bos *et al.* 2005).

12. Baden-Württemberg

Landbeck (1834, *cited in* Hölzinger *et al.* 1970) stated that the species bred on the Federsee near Bad Buchau in the district of Biberach. In the early 20th century a breeding pair was possibly found in Öhringen in the Hohenlohekreis (district of Hohenlohe) (Niethammer 1942).

One successful pair was registered in the Wagbachniederung in northernmost Baden-Württemberg in 1997 (Konter, *cited in* Vluc 2002a, and *cited in* Hölzinger *et al.* 2011).

There are two confirmed breeding records and one possible nesting record from the Bodensee (Lake Constance). A pair with one chick was observed in the Ermatinger Becken, Untersee, in 1982 (Gönner 1999, Winkler 1999, Maumary *et al.* 2007), and a pair possibly bred in the Eriskircher Ried in 2001 (Maumary *et al.* 2007, Hölzinger *et al.* 2011). These two records are from the German part of the lake (Baden-Württemberg). The third one is from the Austrian part of the Bodensee (Rheindelta, Rhine delta of Vorarlberg) where an adult Red-necked Grebe and two small chicks were observed in 1994 (Gönner 1999, Winkler 1999, Maumary *et al.* 2007).

13. Bayern (Bavaria)

Bandorf (1982) mentioned a number of (possible) breeding records from the first half of the 20th century. Gengler (1912 and 1913, *cited in* Bandorf 1982) asserted that in the Weihergebiet (region of ponds) in Oberfranken (Upper Franconia) breeding pairs were observed during the whole summer (around 1910). The species nested near Scheerau in Mittelfranken in 1920 (Gengler 1925, *cited in* Bandorf 1982). Wüst (1931, *cited in* Bandorf 1982) wrote that around 1923, in May, a male bird and one chick were shot on the Starnberger See. The young bird was still unable to fly. Stark (1941, *cited in* Bandorf 1982) stated that a pair nested and cared for chicks on the Weiherhammer Weiher (Pond of Weiherhammer) in the Oberpfalz in 1939.

Bandorf (1982) believed that these records do not prove that the species bred in Bayern. However, it should be stressed that the species shifts the boundaries of its geographical breeding range continually. So, we found newly established breeding outposts in Rheinland-Pfalz, Hessen and The Netherlands from the late 1980s and 1990s onwards, and in Niedersachsen the number of breeding pairs changed significantly after the first half of the 20th century.

A pair of Red-necked Grebes built a nest on a pond in the district of Cham in 1978, and a clutch was laid. However, no chicks were observed, and the birds deserted the nest and left the pond (Zach 1978, Bezzel *et al.* 2005). After this breeding attempt there are no records of breeding Red-necked Grebes in Bayern (Rödl *et al.* 2012, Gedeon *et al.* 2014).

The Netherlands

Albarda (*cited in* Eykman *et al.* 1941) stated in 1884 that the species bred once near Tietjerk in the province of Friesland.

In the period from 1918 to 1980 the Red-necked Grebe was an occasional breeder in The Netherlands. From this period only three confirmed breeding records are known (Teixeira 1979, Vlug 2002a). The first record concerns a pair that raised 4 young in Brielle in the province of Zuid-Holland in 1918 (Snouckaert van Schauburg 1918). The second one is the observation of an adult Red-necked Grebe with a nest with 5 eggs on a pond near the River Vecht near the border of the provinces of Noord-Holland and Utrecht in 1927 (De Vries 1928). The third record was made near Rotterdam in the province of Zuid-Holland where a breeding attempt took place in 1966 (Duiven 1967). The nest with eggs washed away during a period of high winds and one or two weeks later one of the adult birds died.

A pair probably raised young in 1966 and 1967 on the Rottemeren in the province of Zuid-Holland (Vogelwerkgroep Avifauna West-Nederland 1981).

The number of summering records increased in the 1970s and 1980s (Vlug 2002a, b). The species probably bred every year in the Netherlands in the period from 1985 to 2015, with a maximum number of 13-15 pairs (Bijlsma *et al.* 2001, Vlug 2002a, Van Dijk *et al.* 2006, 2007, 2008, 2009, 2010, Boele *et al.* 2011, 2012, 2013, 2014, 2015, 2016, 2017).

The majority of the nesting birds were found in the province of Drenthe (Diependal near Smilde and Oranje, Dwingelderveld near Dwingeloo and Ruinen, Boerenvense Plassen near Hoogeveen, Bargerveen near Emmen) (Bijlsma *et al.* 2001, Vlug 2002b).

In Diependal the birds established a breeding outpost with a small population. The first confirmed breeding here was recorded in 1988 (Van der Veen 1997). In 1999 4 (Van der

Veen 2000) and in 2000 3-5 pairs nested here (Haanstra and Van der Veen, *cited in* Vlug 2002b). However, it is possible that the number of breeding pairs was higher than stated in the literature. On 30 June 2000, for example, 17 adult Red-necked Grebes were counted on the pond (Vlug 2002b), and it is conceivable that all these birds tried to settle but failed in their breeding attempts. In the period from 2001 to 2005 6-8 breeding pairs were recorded in Diependal (maximum 8 pairs in 2004), from 2006 to 2012 4-7 pairs (maximum 7 pairs in 2011 and 2012) and from 2013 to 2015 5-7 pairs (maximum 7 pairs in 2015) (Van Dijk *et al.* 2006, 2007, 2008, 2009, 2010, Boele *et al.* 2011, 2012, 2013, 2014, 2015; SOVON).

On Dwingelderveld, another area with small water bodies in the province of Drenthe with a small breeding population, 1-5 breeding pairs were seen in the period from 2002 to 2015 (maximum 5 pairs in 2008) (Van Dijk *et al.* 2006, 2007, 2008, 2009, 2010, Boele *et al.* 2011, 2012, 2013, 2014, 2015; SOVON).

Although there are every year observations of summering birds in the whole country of The Netherlands, confirmed breeding records outside the province of Drenthe are rare (Van Dijk *et al.* 1994, Bijlsma *et al.* 2001, Vlug 2002b). The real number of nesting birds is undoubtedly considerably higher than the given number of confirmed breeding records, because the birds may live very secretly during the incubation period and shortly thereafter.

Two breeding records are known from the province of Friesland: on the Westerplas on the island of Schiermonnikoog a female bird sat two months on a nest with infertile eggs in 1996 (Bijlsma *et al.* 2001, Vlug 2002b), and the species bred on the island of Ameland in 2014 and 2015 (Slaterus *et al.* 2015; SOVON).

Four confirmed breeding records are from the province of Groningen: a pair built a nest in Westerbroekstermadepolder in 2010 (Boele *et al.* 2012); two pairs with young were seen in Kropswolderbuitenpolder in 2012, and one pair nested in Westerpolder near Kolham and raised one young in 2014 (Boekema 2016).

Belgium

An unsuccessful breeding attempt was recorded on a clay pit (2.6 ha) at Brecht-St.-Lenaarts in the province of Antwerp in 1979 (nest with eggs, but no young hatched) (Voet and Maes 1981). Another unsuccessful breeding

attempt was observed at Lochristi in the province of Oost Vlaanderen (East Flanders) in 1985 (pair with nest with 6 infertile eggs) (Bultinck, *cited in* Vlug 2002a; P Bultinck and P Boesman).

After the breeding attempt in 1985 the species is not mentioned as breeding bird in Belgium (Vermeersch *et al.* 2004, Jacob *et al.* 2010).

England

Records of the Rare Breeding Birds Panel have shown an increase in the number of individuals summering in Britain in the 1980s, culminating in a record of probable breeding in England and the first confirmed breeding attempt in this country (Spencer *et al.* 1989, 1990, Donald 1993).

The probable breeding record concerns the observation of a pair of Red-necked Grebes accompanied by a very young juvenile at a site in England in August 1987. It is only thought probable that the birds could have bred in the area and *successful* breeding in England has not yet been proved (Spencer *et al.* 1989, Donald 1993).

The first confirmed breeding attempt took place in Cambridgeshire. During the summers of 1987-90, what seemed to be the same individual Red-necked Grebe defended a territory against Great Crested Grebes at a flooded gravel-pit in Cambridgeshire. In 1988, a mate appeared, eggs were laid, but failed to hatch after being incubated beyond the normal period. A different partner appeared in 1990 but died before eggs were laid. The 1988 attempt in Cambridgeshire coincided with one in Scotland (Anonymous 1989) and together these were the first recorded instances of breeding by Red-necked Grebes in Britain (Parslow-Otsu and Elliott 1991). Since then only single birds or, less often, pairs have summered in England. On occasion, birds have been reported displaying, copulating or building nesting platforms (Brown and Grice 2005, Balmer *et al.* 2013).

Scotland

Since the early 1970s, summering has become a regular event, particularly in the eastern parts of central and southern Scotland (Thom 1986, Murray 2003). The first nest was built by a pair at Black Springs, Threipmuir Reservoir in the region of Lothian in 1980; however, although birds sat on the nest and covered it when leaving, apparently no eggs were laid (Thom 1986, Forrester *et al.* 2007).

From 1981 to 1989, at least one bird was present in summer at Bavelaw Marsh in Lothian; and in 1985 and 1986 a pair built a nest but, again, egg-laying was not confirmed (Forrester *et al.* 2007).

In 1988, a pair laid eggs at a third site, Gladhouse Reservoir in Lothian (Forrester *et al.* 2007). They used an old Great Crested Grebe nest platform. Both Red-necked Grebes were nest-building on 18 June and the next day there was one egg. On 20 June the nest contained two eggs, one a fresh pale blue and the other stained which suggested that incubation had started. On 30 June the nest was empty. Only one adult was seen, and it too had apparently left by 3 July. It was speculated that predation by American Mink *Mustela (Neovison) vison* was the cause of the nest failure (Anonymous 1989).

From 1989 to 1999 a pair summered at Lindean Reservoir in the region of Borders; but, although display, copulation and nest-building occurred in most years, it was never certain that eggs were laid (Forrester *et al.* 2007).

In 1998, as pair built a nest at a site in north Fife but they left before egg-laying (Forrester *et al.* 2007).

The first successful breeding in Scotland (and Britain) was recorded in 2001 (Ogilvie *et al.* 2003). In that year, a pair built a nest on an undisclosed loch in Borders. On 8 July Murray (2003) saw both adults with a brood of two juveniles. The young were approximately half the length of the adults. The author supposed that the young had hatched out by 21 June. Sometime later, one juvenile apparently disappeared, the other was last seen to reach adult size and presumably fledge (Murray 2003). This breeding in Borders in 2001 was the only successful breeding record in Scotland and England (Balmer *et al.* 2013).

Various other freshwater sites have held Red-necked Grebes in spring and early summer, usually single birds. The concentration of summering records on fresh water in south and central Scotland may suggest that breeding birds come from the Firth of Forth wintering population (Forrester *et al.* 2007).

Ireland

Parslow (1973), Hutchinson (1989) and Donald (1993) give no breeding records of the species in Ireland, but Hillis and O'Sullivan (2012, *cited in* Balmer *et al.* 2013 and *cited in* Hobbs 2015) stated that *Podiceps grisegena* has bred at least once in 2003.

France

In France the species is a rare breeding bird, and a small number of breeding records are known since 1900, all from the north-eastern part of the country. As in The Netherlands, Britain and other countries outside the regular breeding range, summering birds are sometimes observed on inland water bodies (Dubois *et al.* 2008) and it is highly probable that more Red-necked Grebes nest than the known confirmed breeding records suggest.

Gengler (1925) visited the Meurthe-et-Moselle department in the region of Lorraine during World War I in 1916 and 1918. Near Longuyon he saw a family of Red-necked Grebes with three relatively small young on a marshy brook in July. He believed that more pairs bred in this department.

It took 60 years before another breeding case was recorded. A pair nested in 1978 on the Étang de Galetas, a lake of c. 100 ha in the department of Yonne, 150 km south-east of Paris. The first egg of a clutch of three was laid on 15 May. The nest was destroyed by human activities just after a chick hatched. This chick grew up normally (Tostain *et al.* 1981).

Ten years later, in 1988, a breeding pair reared one chick on a lake of c. 80 ha in Argonne in the department of Marne (Siblet 1995, Dubois *et al.* 2001).

Probably, a pair bred on Lac Amance in the department of Aube in 1990 (observation of a bird on a nest) (Croset and Thiollay 2007), and another pair on a gravel pit lake in Douzy, department of Ardennes, in 2002 (record of two adults with two just flying young) (R Dujardin).

There is only one lake where breeding was proved in more than one year: on Lac d'Orient (Orient Lake), an artificial lake of c. 2,700 ha in Aube, a pair reproduced successfully in 2005 (2 young), 2006 (1 young) and 2007 (3 young) (Croset and Thiollay 2007). Breeding was observed regularly here until at least 2012 (Deceuninck *et al.* 2015).

A solitary Red-necked Grebe in the department of Yonne built a nest in May 2011 (Deceuninck *et al.* 2015).

Switzerland

There are no records of breeding Red-necked Grebes in Switzerland. However, almost every year summering birds are seen, and the species bred in the German and

Austrian parts of the Bodensee (Lake Constance) (Maurmary *et al.* 2007), so it is very possible that the species occasionally nests in the country.

In June 2012, at the Weissenau, Thuner See (Lake Thun), a Red-necked Grebe displayed courtship behaviour to a Great Crested Grebe near a nest, but the latter did not respond. This courtship behaviour was also observed here in 2010 and 2011 (Schuster *et al.* 2014).

Italy

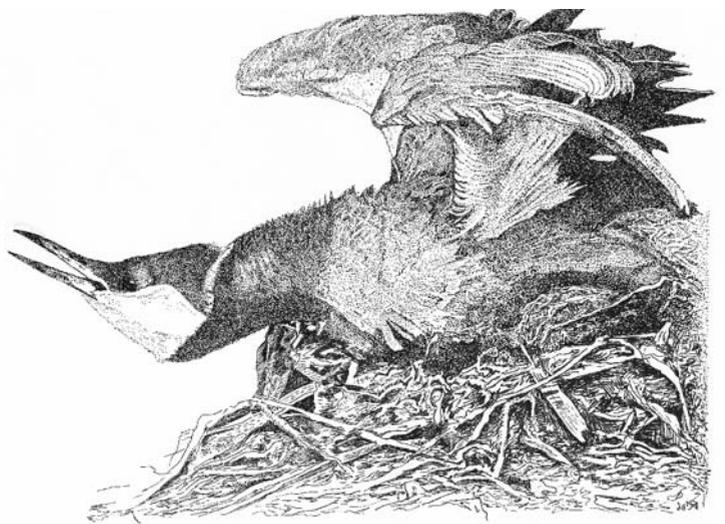
There are no confirmed breeding records in Italy (Brichetti *et al.* 1992, BirdLife International/European Bird Census Council 2000, BirdLife International 2004); only some observations of birds in summer are known (Brichetti 1992). Old reports of nesting in Lombardia (Lombardy) and in the Veneto Region are unreliable (Brichetti and Fracasso 2003).

Austria

The Red-necked Grebe bred at least occasionally in the 19th century in the riverside forests of the Donau (Danube) near Wien (Vienna) (von Oesterreich and Brehm 1879, von Oesterreich *et al.* 1879), and probably also on the Neusiedler See (Zimmermann 1943).

From the first half of the 20th century no confirmed breeding records are known. In the 1950s the species bred at least twice in the country: in June 1952 an adult at nest was found and photographed by Makatsch, but the exact location was not mentioned (Ferguson-Lees 1957), and on 11 September 1955 Ausobsky (*cited in* Tratz 1960) saw unfledged chicks on the Wallersee near Salzburg. Because the young birds were still unable to fly, it is very probable that the birds bred on this lake.

The species is an occasional breeder in Austria from c. 1970 onwards. Breeding is often concluded by observations of adult(s) with young. Although it is possible that a number of those grebes bred elsewhere, for example in Hungary (P Sackl), this appears normally not the case because the adults depart from the breeding lakes up to 4 weeks before their young (Wobus 1964, Scholl 1974, Riske 1976, Vlug 1996, Stout and Nuechterlein 1999). Adults with young were seen on the Haidlacke in Seewinkel near the Neusiedler See in 1970, on the Neusiedler See near Illmitz in 1972 (Löffler 1974, Prokop 1978, Dvorak *et al.* 1993), in the Steiermark (Styria) in 1972 and 1973 (Dvorak *et al.* 1993), on the Längsee in Kärnten (Carinthia) in 1979 (Rokitansky 1980), and on the Ruster Bucht of the



Neusiedler See on 24 June 1983 (adult bird with two chicks) (Dvorak *et al.* 1993).

A peculiar observation was made on a pond near Brunn am Gebirge, southwest of Wien (Vienna), where a Red-necked and a Great Crested Grebe showed courtship behaviour in May. A nest was discovered in June and the birds took turns to sit on it (incubating eggs?). However, the grebes deserted the nest and no chicks were seen (Dvorak *et al.* 1993).

There is one confirmed breeding record of the Austrian part of the Bodensee (Lake Constance): an adult Red-necked Grebe with two small young (c. 1-2 weeks old) was seen in the Rheindelta (Rhine delta) of Vorarlberg in 1994 (Schmid *et al.* 1998, Gönner 1999, Winkler 1999, Maumary *et al.* 2007).

There are no confirmed breeding records since c. 1995 (BirdLife International 2004).

Czech Republic

In the Czech Republic (Bohemia and Moravia) the Red-necked Grebe was a regular and locally numerous breeding bird in the 19th century, and to some extent it was regular until the first years of the 20th century (Wobus 1964, Cramp *et al.* 1977, Hudec 1994, VlUG 1997). It became a rare breeding species during the first half of the 20th century (Kren 2000).

From 1800 to 1860 the species was really common in Bohemia, especially in the areas with many ponds near Budějovice, Pardubice, Kopidlno, Trěboň and Chlumec (Hachler, *cited in* Wobus 1964). Around 1900 some areas were already deserted, and other places were more sparsely populated (Urbánek, *cited in* Wobus 1964). The breeding numbers in Moravia showed a similar decline from around 1900 (Wobus 1964). On the ponds near Náměšť in central Moravia more Red-necked (1886-94 4 pairs) than Great Crested Grebe pairs were seen until 1894, but after 1913 *grisegena* was not recorded for almost 50 years (2 pairs showed breeding attempts in 1959) (Fiala 1974).

Only irregular breeding attempts in the Czech Republic have been recorded since the 1920s (Hudec, *cited in* Cramp *et al.* 1977, Šťastný *et al.* 1987, Hudec 1994, Cepák and Musil 1997). The number of breeding pairs in the 1990s was estimated at 0-5 (VlUG 1997, Kren 2000).

Cepák and Musil (1997) stated that the only regular breeding site in the Czech Republic at the beginning of the 1990s was found in the district of Ústí nad Labem. The total number of breeding pairs in the republic around 2000 was estimated at 1-5 (BirdLife International 2004).

Slovak Republic

The Red-necked Grebe is a rare breeding bird in Slovakia. There are only a few confirmed breeding records known from the 20th century, until c. 1985 (Wobus 1964, Šťastný *et al.* 1987, Hudec 1994). Since c. 1985-90 the species regularly nests in low numbers in the country (Snow and Perrins 1998, Danko 2002). The population was estimated at 5-20 breeding pairs for the period from 1980 to 1999 (BirdLife International 2004).

As a rule, the breeding waters are occupied by one pair. However, five to six nests were found on an area of 40 x 160 m in a pond at Senné, eastern Slovakia, in 1985 (Danko 2002).

Hungary

Naumann (1838) stated that numerous Red-necked Grebes were found in Hungary. From the period around 1900 some data are known from Velencei-tó (Lake Velence) in Central Hungary. Von Homeyer (*cited in* Hennicke 1903) found some nests of the Red-necked Grebe, together with nests of the Black-necked Grebe, within a large Black-headed Gull *Larus (Chroicocephalus) ridibundus* colony on the lake. The majority of the nests of *grisegena* were built at one side of the gull colony, and those of *nigricollis* at the other side. Chernel de Chernelháza (1907) wrote that the Red-necked Grebe bred more especially at the south end of Velencei-tó, but in much smaller numbers than the Great Crested and Black-necked Grebes.

Niethammer (1942) described the species in Hungary as a regular, but sparsely distributed breeding bird.

Máté (1958) stated that *Podiceps grisegena* rather irregularly occurred in the country. In the county of Fejér in Central Hungary he found three breeding ponds. In many years these ponds were not occupied, but in the years of occupation the number of nesting pairs was 1-3. However, on a moor pond near Dinnyés (in the neighbourhood of Velencei-tó), where normally one or two pairs lived, Máté (1958) observed 12-15 breeding pairs in 1937. On Velencei-tó the author never saw Red-necked Grebes.

In the early 1970s the number of breeding pairs in Hungary was estimated at 50-60 pairs. The birds bred not on any of the large lakes but were found on the numerous fish ponds (Horváth, *cited in* Sage 1973). From the 1970s the number of breeding pairs in Hungary increased (temporarily?) (Haraszthy 1984, Gorman 1996, Haraszthy 2000). Snow and Perrins (1998) gave the number of 100-150 breeding pairs for the period from 1979 to 1993, and the number was 80-150 pairs in 1998 (BirdLife International/European Bird Census Council 2000), of which a great deal in the Hortobágy (60 pairs in 1982, but only 20-30 pairs in the 1990s) (Haraszthy 2000).

Slovenia

Podiceps grisegena is a rare breeding bird in Slovenia. In the period from 1990 to 2000 3-6 pairs bred in the country (Snow and Perrins 1998, BirdLife International 2004). The first breeding record (2 or 3 pairs) was in 1990 at Lake Cerknica, an intermittent lake in Inner Carniola (Geister 1991).

Croatia

The species nests in Slavonia (the north-eastern part of Croatia) (Niethammer 1942, Makatsch 1950, Vlug 1997). The total nesting population in Croatia was estimated at 1-10 pairs in 2002 (BirdLife International 2004).

Bosnia-Herzegovina

The Red-necked Grebe is rare in Bosnia-Herzegovina and it possibly breeds in the northern part of the country (Vlug 1997).

Serbia and Montenegro

The species is a breeding bird in Serbia. The majority of the birds nest in the northern part of the country (Vlug 1997), especially in the Vojvodina (Jegrička, Obedska Bara, Carska Bara) (Wobus 1964, Puzović and Grubač 2000, Marsh 2005; J J Vlug). The total number in Serbia and Montenegro was estimated at 10-20 breeding pairs in the period from 1990 to 2002 (BirdLife International 2004). However, Puzović and Grubač (2000, p. 731 of Volume 2) stated that along a narrow, 60 km stretch of the Jegrička River with fringing reed *Phragmites* 400-500 *grisegena* pairs bred in 1997. The authors remarked that members of the Bird Protection and Study Society of Vojvodina undertook intensive ornithological research here between 1989 and 1997.

Macedonia

Ilić (*cited in* Makatsch 1950) found a nest in the marshes of the Crna Reka River (Logovardsko Blato) in 1940, and

supposed that the species also bred in Struško Blato near Struga and Ohridsko Ezero (Lake Ohrid).

The species is still very rare in Macedonia and the total number of breeding pairs in the country was between 0 and 10 in 1990-2000 (BirdLife International 2004).

Greece

Red-necked Grebes used to breed in the Nestos delta up to the early 1960s, but following drainage and land reclamation over much of the area, this small breeding population (*c.* 10 pairs) ceased to exist (Cramp *et al.* 1977, Handrinos and Akriotis 1997). A record of a pair possibly nest-building at Lake Ismaris (8 May 1991) (Atkinson, *cited in* Handrinos and Akriotis 1997), suggests that perhaps isolated pairs may still nest occasionally in the north-eastern part of Greece (Handrinos and Akriotis 1997).

Bulgaria

At the end of the 19th and the first half of the 20th century the Red-necked Grebe was a sparse breeding bird in Bulgaria with isolated nesting sites. The population was almost entirely destroyed by large-scale draining of marshes during the first half of the 20th century and the species was considered as extinct around 1950 (Patev 1950, *cited in* Iankov 2007), but then a partial recovery took place. Around 1980 the number of nesting pairs did not exceed 50 and the largest population (20-25 pairs) was found at Belene Island, an island formed by the Danube River in the northern part of Bulgaria (Ivanov 1985, *cited in* Iankov 2007). The total population in Bulgaria at the end of the 20th and the beginning of the 21st century was estimated by Iankov (2007) and BirdLife International (2004) at 30-70 pairs, with decreasing numbers. However, Petkov (2006) stated that the breeding population in this period was only 10-30 pairs, with the most important breeding sites along the Danube River. Many former breeding sites are lost, including the Aldomirovsko Marsh and Kremikovtsi deposit basin in the Sofiya (Sofia) area, the Belene Marshes (Belene Island, see above) in the northern part of Bulgaria, and the Burgas and Varna Lakes near the Black Sea Coast (Petkov 2006).

Romania

Dombrowski (1912) stated that the species was much rarer than *Podiceps cristatus* in the marshes of Romania; you could nevertheless consider it as a bird occurring in large numbers.

BirdLife International/European Bird Census Council (2000) estimated the population in the country at 1,000 to 3,000 breeding pairs, and Snow and Perrins (1998) at 2,000-3,000 pairs in 1986-92.

Danube delta

The majority of the birds nest in the Danube delta and Razelm-Sinoe complex. This is the most extensive wetland in Europe after the Volga delta, comprising three arms of the Danube interspersed with marine and river sandbanks, fields, marshes, lakes and canals. Reedbeds *Phragmites* cover large areas (totalling 160,000 ha) and include a type of floating reed habitat known as "plauri". In 1996 at least, c. 2,000 *grisegena* pairs nested in this wetland (Munteanu 2000). Goriup *et al.* (2007) stated that a minimum of 2,200 birds bred in small lakes of the lower Danube and Danube delta in Romania and Ukraine.

Moldova

According to Snow and Perrins (1998) and BirdLife International/European Bird Census Council (2000) 350-500 pairs nested in Moldova in 1990.

Poland

Tomiałojć (1976) described the species in Poland as a scarce breeder in the lowlands. It nested in small or very small numbers in all lowland parts of the country. It was locally more numerous, for example on the fishponds near Milicz, near Pińczów and Busko, Łowicz, Pruszków, Parczew and Gryfino. In the 1970s at least 540 and perhaps up to 1,000 pairs bred in the country (Cramp *et al.* 1977).

It appears that the numbers increased in the 1980s. Tomiałojć (1990) gave the figure of 1,630-2,000 pairs for the country, and Bauer and Berthold (1996) 2,500-3,500 pairs. Tomiałojć and Stawarczyk (2003) considered the species as widespread in the lowlands, but less numerous and locally absent in the northern belt of mostly oligotrophic lakes and in the southern hilly part of the country. The authors estimated the total population in Poland at 2,000-3,000 pairs. According to BirdLife International (2004) and Bauer *et al.* (2005) 3,000 to 4,000 pairs bred in the country between 1990 and 2000.

Górecki and Stajszczyk (2007) wrote that in the period from 1985 to 2004 the largest populations were in the Szczecin (Stettin) region, Mazowsze (Mazovia) and the Lublin region. The species was locally also common in Śląsk (Silesia) and Małopolska (Lesser Poland), but rare in central Pomorze (central Pomerania), in the Gdańsk

(Danzig) region, and in the extreme north-eastern part of Poland. On and around large fish farms local populations could exceed 60-100 breeding pairs, but the numbers tended to fluctuate greatly. The authors remarked that trends are difficult to assess with certainty and gave a population of 2,000-3,000 pairs for the whole country. After c. 2000 the numbers showed a marked decline, and in the period from 2008 to 2012 only 700-1,000 pairs bred in Poland (European Environment Agency 2013).

1. Śląsk (Silesia)

Censuses between 1983 and 1985 in Śląsk revealed 600-800 breeding pairs (Dyrzc 1991). Later Tomiałojć and Stawarczyk (2003) stated that 520-660 pairs nested here. Many pairs were found on the fish-ponds in the Barycz (Bartsch) valley in the 1980s (281 pairs in 1982 and 273 in 1983) (Dyrzc 1991), but numbers declined thereafter (Milicz fish ponds: c. 200 pairs in 1982, 1983 and 1984, and c. 30-50 between 1998 and 2010) (Witkowski and Orłowska 2012).

2. Mazowsze (Mazovia, Warsaw province)

The breeding population of Mazowsze with the southern part of Podlasie was estimated at 520-590 pairs between 1986 and 1990 (Tomiałojć and Stawarczyk 2003).

3. Wielkopolska (Greater Poland, Poznań province)

A number of at least c. 350 pairs bred in Wielkopolska in the period from 1980 to 1995 (Kupczyk 2000, Tomiałojć and Stawarczyk 2003). A large population was found on the Przygodzice fish-ponds (70 breeding pairs in 1992).

4. Małopolska (Lesser Poland, Cracow, Kielce and Rzeszów provinces)

A maximum number of 330 breeding pairs were observed in Małopolska. The breeding sites were recorded almost exclusively in the Małopolska upland and Podkarpacie (Mielczarek 1992).

5. Lubelszczyzna (Lublin province)

Tomiałojć and Stawarczyk (2003) give a maximum number of c. 150 pairs for Lubelszczyzna.

6. Warmińsko-Mazurskie (province of Warmia-Masuria)

This region contains the southern part of the historic Prussian province of East Prussia (Ostpreußen). Around 1940 15 pairs were known to breed in this region (Tischler 1941), but around 2010 c. 150 pairs bred here (Alex 2011).

Kaliningrad Area

Around 1940 c. 25 pairs bred in the Kaliningrad Region (Königsberger Gebiet) (Tischler 1941) and around 2010 22-30 pairs were found in this area (Alex 2011).

Estonia

The number of breeding pairs in Estonia increased in the 20th century. Onno (1960, 1966) gave c. 100 for the period between 1951 and 1957. In the 1950s-1960s the breeding population was estimated at 120 pairs of which up to 35 bred on Lake Porkuni, 30 on Lake Maardu, and 20 on Lake Linnulaht (Onno 1971, Veromann 1994). In 1991 150-200 pairs nested in the country (Snow and Perrins 1998), in 1998 200-300 pairs (Lõhmus 2001, BirdLife International 2004) and in the period between 2008 and 2012 300-400 pairs (European Environment Agency 2013).

Latvia

The Red-necked Grebe is relatively common in Latvia (Von Transehe 1965, BirdLife International 2004). The population was estimated at 1,500-2,000 breeding pairs in the 1980s (Snow and Perrins 1998) and in the 1990s (BirdLife International 2004), but numbers declined thereafter. In the period between 2008 and 2012 only 304-657 bred in Latvia (European Environment Agency 2013). The majority of the birds nest in the western part of the country (Priednieks *et al.* 1989).

Lake Engure

Large numbers nest on Lake Engure, a shallow and heavily eutrophic freshwater lake (coastal lagoon) with seven islands, separated from the Gulf of Riga by a narrow (1.5-2.5 km) strip of land. The lake is covered by vast expanses of emergent vegetation (mainly *Phragmites*, *Typha* and *Scirpus*) covering about 65% of the lake's surface (in 2004). Around 600 pairs of *grisegena* bred on the lake between 1994 and 2004 (Račinskis 2000, BirdLife International 2015b).

Lithuania

Around 150 to 200 nests were found in 12-13 localities (Snow and Perrins 1998). BirdLife International/European Bird Census Council (2000) estimated the population of the whole country at 200-300 pairs between 1996 and 1998, and the European Environment Agency (2013) at 200-250 pairs in 2008 to 2012.

Belarus (Belorussia)

The species is rare in Belarus (Fedyushin and Dolbik 1967). The breeding population was estimated at 50-100

pairs for the period from 1997 to 2000 (BirdLife International 2004).

Ukraine

A large number of Red-necked Grebes breed in the Ukraine. The population for 1988 was estimated at 7,000-12,000 pairs (BirdLife International/European Bird Census Council 2000) and for the period from 1990 to 2000 at 5,000-9,000 pairs (BirdLife International 2004).

In the western part of the Ukraine c. 1,200 pairs nested (Kuchinskaya 2001), and in the southern part of the country 2,500-3,000 pairs (Koshelev *et al.* 1998). Large numbers nest in fish-ponds, river deltas and river lowlands and forelands. In the Ukrainian part of the Danube delta and the Stentsovskii flats (river forelands) 400-500 breeding pairs were found, in the delta of the Dniestr (Dnestr, Dniester) 300-400, in the delta of the Dniro (Dnepr, Dnieper) 300-500 and in the river forelands of the upper reaches of the Kakhovskii Reservoir 50-100 (Koshelev *et al.* 1998). The species also nests in the Syvash (Sivash), a large system of shallow lagoons on the west coast of the Sea of Azov. In the western Sivash 50-100 and in the eastern Sivash 30-350 pairs nested (Koshelev *et al.* 1998).

In 2010, about 250 pairs nested on the island of Ermakov near Vilkovo in the Ukrainian part of the Danube delta (M Zhmud).

European Russia

No thorough surveys of the population in European Russia exist. In river deltas in the southern part of the country numerous Red-necked Grebes may breed. In the fish ponds of Yamat (690 ha) and Mayachnuii (270 ha) in the Volga delta 241 nests were found in 1962 (Markuze 1965), and in the delta of the river Don 1,000-1,500 pairs bred in 1997 (Sviridova 2000). The total breeding population in European Russia is roughly estimated at 12,000-25,000 pairs for the period 1990-2000 (BirdLife International 2004).

Georgia

The species is present in Georgia, but the number of breeding pairs is not known (BirdLife International 2004).

Armenia

In Armenia the Red-necked Grebe is an uncommon species (Adamian and Klem 1997), and only 2-8 pairs bred in the period 1997-2002 (BirdLife International 2004).

Turkey

In Turkey the Red-necked Grebe is seemingly an uncommon and rather local breeding bird, largely to Inner and East Anatolia (Kasperek 1992, Kirwan *et al.* 2008), but also to immediately adjacent areas of other regions, including the extreme northeast Black Sea coastlands and perhaps the central part of the same region, at Kızılırmak delta. It is probably scarcer in the western part of its Turkish range (Kirwan *et al.* 2008). The breeding population of the whole country was estimated at 280-350 pairs in 2001 (BirdLife International 2004).

Morocco

There are old records of many birds being present on the Ras el Doura lakes in Morocco (Favier, *cited by* Irby 1875, Bannerman 1959) (see 10.1.1 for more details).

Western Siberia

It breeds in West Siberia north to Surgut, and east to the Barabinskaya Step' and Kulundinskaya Step' (Dement'ev and Gladkov 1951/1969, Koshelev 1981, Kuročkin 1985). No thorough surveys of the population in Western Siberia exist.

Kazakhstan

The Red-necked Grebe is a common and widespread breeding bird in northern and south-eastern Kazakhstan (Wassink 2015). The number of breeding birds of some wetlands is known. In 1972-81 the population of the Naurzum nature reserve in the region of Kostanay ranged between 140 and 1,200 pairs (Bragin and Bragina 2002, *cited in* Wassink 2015). In the Tengiz-Korgalzhyn region, a large wetland complex in the steppe zone of Central Kazakhstan, up to 790 individuals were seen in the period 1999-2004 (Schielzeth *et al.* 2008). BirdLife International (2015c) wrote that 530 individuals were counted in the Korgalzhyn state nature reserve in the breeding-season 2006.

Kyrgyzstan (Kirghizia)

The species nests in Kyrgyzstan and was found on Lake Sonkel' (40-50 pairs), 3,016 metres above the sea level (Kuročkin 1985).

Breeding Population Density in Europe-Western Asia

In general, only one pair occurs on small breeding ponds, sometimes more, for example 11 pairs on a pond with an area of 6 ha in the West-Ukraine [= 1.83 breeding pairs (bp)/ha] (Buchko *et al.* 1995), 3 pairs on a pond of 1.1 ha in Estonia (= 2.73 bp/ha) (Onno, *cited in*

Wobus 1964), and 6 pairs on a pond of 2 ha in Brandenburg, Germany (= 3.00 bp/ha) (Schmidt 1983). High population densities were recorded in Schleswig-Holstein, Germany [8 breeding pairs on a fish pond of 1 ha on the mainland (= 8.00 bp/ha)] (Vlug 2000). Large numbers of breeding birds were found near the Baltic Sea in water bodies from which the adults make foraging flights to the sea: 13 breeding pairs on a lagoon of c. 2.75 ha (= c. 4.7 bp/ha) on the island of Als, Denmark (Nielsen and Tofft 1987), and up to 40 breeding pairs in 2017 on a pond of 3 ha (= 13.33 bp/ha) on the island of Fehmarn, Schleswig-Holstein (J J Vlug) (see 11.3.1 - Schleswig-Holstein and Hamburg).

Usually the population density is much lower, especially in large water bodies, mainly caused by the ratio of the lake surface area to the length of the shore line; e.g. the maximum number of breeding pairs on the Selenter See (Lake Selent, Schleswig-Holstein, 2,239 ha) was 31 in 2008 (= 0.01 bp/ha) (J J Vlug), and up to 50-80 pairs (= c. 0.13 bp/ha) bred on the most suitable lakes in Finland (E Lammi). On Lake Porkuni (68 ha), northern Estonia, up to 35 breeding pairs were found (= 0.51 bp/ha) (Onno, *cited in* Wobus 1964).

About 250 *grisegena* pairs bred in 1962 on 960 ha fishponds in Volga delta (= c. 0.26 bp/ha) (Markuze 1965). 400-1200 pairs (in various years) bred on the Naurzum Lakes, North-Kazakhstan (Gordienko 1981); the population density there was 0.3-1.4 bp/ha suitable marsh vegetation (Gordienko 1980). However, because Gordienko (1980) did not use the lake surface area in his calculations, his data are not comparable with other studies. On a lake in Barabinskaya Step' (West-Siberia) 80 pairs bred on 600 ha (= 0.13 bp/ha) (Kuročkin 1985).

Breeding Population Estimates of the Red-necked Grebe in Europe-West Asia

Wetlands International (2006, 2015) discerns four populations of *Podiceps grisegena grisegena* and gives population estimates:

1. Birds breeding in East Europe (14,000-20,000 pairs) and wintering in coastal north-western Europe: 42,000-60,000 individuals (including immature birds)
2. Birds breeding in East Europe and West Asia (14,000-36,000 pairs) and wintering on the Black and Mediterranean Seas: 41,000-107,000 individuals

3. Birds breeding in West Asia and wintering on the Caspian Sea: 15,000 individuals
4. Birds breeding in Central Asia (the Balkhash-Alakol' area in South-East Kazakhstan and Kyrgyzstan) (*Podiceps grisegena* "balchaschensis" or "balhashensis") and wintering in southern Asia: 1-10,000 individuals

The total population of the nominate *grisegena* (Europe-West Asia) was estimated at 98,000-192,000 individuals (including immature birds) (Wetlands International 2006, 2015) and at 50,000 breeding pairs (Vlug 2002a).

11.3.2 Breeding Population and Population Trends in East Asia

No thorough surveys of the population in East Asia exist. On Lake Khanka, a freshwater lake located on the border between Primorskiy Krai, Russia and in the province of Heilongjiang, China, c. 250 breeding pairs were found (Knystautas and Šibnev 1987). Eremin *et al.* (1986) recorded 140-160 pairs on two lakes (Nevskoe and Ainskoe Lakes) on the island of Sakhalin in 1983-84. It was estimated that less than 100 pairs bred in Japan (BirdLife International 2015a).

The population of *Podiceps grisegena holboellii* in East Asia was roughly estimated at 50,000 individuals (including immature birds) (Wetlands International 2006, 2015). Almost nothing is known about population trends.

11.3.3 Breeding Population and Population Trends in North America

The occurrence of the Red-necked Grebe in North America is sporadic and limited to suitable water bodies. *Podiceps grisegena holboellii* breeds on small and shallow lakes in the northern prairies, western parklands, and forests.

Alaska

In Alaska, the Red-necked Grebe nests north to near the northern limit of trees. It is a common breeding bird in central Alaska, but it is uncommon in the south-eastern, south-coastal and western parts of the state. In the south-western part it is rare in summer (Armstrong 1983). During the year 2006, the birds were surveyed on 79 lakes in south-central Alaska [Anchorage area, Mat-Su (Matanuska-Susitna) Valley and Kenai Peninsula]; 36 lakes were occupied by the species while only 16 supported chicks to fledged (Mills 2007).

The breeding population in Alaska was estimated at about 12,000 birds (= c. 6,000 breeding pairs) (Stout and Nuechterlein 1999).

Yukon Territory

The Red-necked Grebe is fairly common in southern Yukon, and uncommon in central Yukon north to the Dawson area. North of there, it is regularly seen only at Old Crow and Old Crow Flats (Sinclair *et al.* 2003).

In the south, it has been recorded at small and large lakes across the region, and nesting has been confirmed at numerous locations from Beaver Creek east to Scoby Lakes near the Coal River (Sinclair *et al.* 2003). In central Yukon, it is a common breeder at the McQuesten Lake wetland, where 17 broods were counted in one season (Sinnott and Mossop 1998, *cited in* Sinclair *et al.* 2003), and nesting has also been confirmed at Gravel and Fair-weather lakes (Sinclair *et al.* 2003). Frisch (1987, *cited in* Sinclair *et al.* 2003) did not record the species on the Yukon section of the Dempster Highway, but there is an observation from the Blackstone Uplands. In the north, small numbers nest near Old Crow and at Old Crow Flats, and courtship behaviour was also noted at Trout Lake on the Coastal Plain. Along the North Coast, there are only four records, all of single birds between Clarence Lagoon and the Babbage River (Sinclair *et al.* 2003).

Northwest Territories

Fournier and Hines (1998) studied an area near Yellowknife in the period 1986-96. Breeding Red-necked Grebes were recorded on 110 of 575 ponds available in the study area. The yearly mean number of breeding pairs was 59 (range of annual means 50-72 pairs) (Fournier and Hines 1998). The authors stated that the population of the Northwest Territories probably exceeded 5,500 breeding birds (Fournier and Hines 1998).

Saskatchewan

The northern limit of the breeding range passes through the extreme north-eastern part of Saskatchewan (the species breeds near Fond-du-Lac). The Red-necked Grebe is fairly common on lake-margin marshes of central Saskatchewan and the Cypress Hills. The species' abundance decreases markedly on the sterile lakes of the Precambrian Shield (Smith 1996).

Manitoba

Red-necked Grebes nest in central (Thompson Junction, Thicket Portage) and south Manitoba (Lake Winnipeg-

sis, Turtle Mountain Provincial Park), but they do not breed in the north-eastern third of the province (Bent 1919, De Smet 1983, Godfrey 1986).

De Smet (2003) gave some details and stated that Red-necked Grebes breed locally across the southern two-thirds of the province; they prefer large open marshes, shallow lakes, and secluded bays on large lakes. They are most often found in aspen parkland and the southern half of the boreal forest and are particularly common just south of Riding Mountain National Park, in Turtle Mountain and Duck Mountain Provincial Parks, and on Lake Winnipegosis. The northernmost known breeding localities are Sisipuk Lake and Pikwitonei; there are three early-June records of stray migrants at Churchill. Breeding Bird Survey records extend east to Bissett and north to Cranberry Portage, but numbers are too low to detect population trends.

Early observers found the Red-necked Grebe to be common on both prairie sloughs and boreal lakes. Factors contributing to reduced numbers across the prairies include wetland drainage and the removal of shoreline emergent vegetation by grazing cattle and summer cottagers. This grebe's fish-rich diet also makes it susceptible to pesticide residues (De Smet 2003).

De Smet (1983) studied the Red-necked Grebe in Turtle Mountain Provincial Park, southern Manitoba, during 1980 and 1981. In the Turtle Mountains, single pairs of Red-necked Grebes nested in lakes ranging from 1.8 to 25.9 ha in size. The maximum breeding densities were found on Morins Lake (3 pairs within 8.8 ha = 0.34 bp/ha) and Bella Lake (8-9 pairs within the 22.6 ha south arm and southwest bay = 0.38 bp/ha). The densest nesting population was found on North Breadon Lake during 1980, however, where 9 pairs held territories within an area of about 20 ha on the west side (= 0.45 bp/ha) and 4 occupied territories within an area of less than 4 ha in the westernmost end (= 1.00 bp/ha) (De Smet 1983).

Ontario

In Ontario, the Red-necked Grebe generally occurs in small numbers, but locally dense populations of as many as 50 pairs breed in rich marshes. It is rare to locally uncommon in the province and most abundant in the Lac Seul to Lake of the Woods area (Harris 2007). De Smet (1982, *cited in Sandilands 2005*) suggested that there were approximately only 200 breeding pairs in Ontario, and Austen *et al.* (1994, *cited in Sandilands 2005*) also

felt that the Ontario breeding population was about 200 pairs. However, the number of nesting pairs more than doubled between *c.* 1983 and *c.* 2003. The increase was primarily in the Northern Shield region where most of the breeding population occurs, but no significant range shift occurred (Harris 2007).

Whitefish Lake

On Whitefish Lake (3,015 ha) in the district of Thunder Bay, one to three pairs bred in the 1930s (Dear 1940, *cited in Harris 2007*). Wheeler (2001) studied the breeding population of Red-necked Grebes at this lake in 1993 and 1994 and found a breeding population of 59 pairs in 1993 and of 39 in 1994. The population was strongly associated with uncultivated Wild Rice *Zizania palustris* stands in shallow bays of the lake. The mean inter-nest distance for nearest neighbour was only 27.2 m, range 1.5-185.0 m ($n = 148$ nests), and Wheeler (2001) considered this population to be semi-(or loosely-) colonial.

Québec

In Québec, the species breeds only in the south-west of the province (see 10.1.3 for more details).

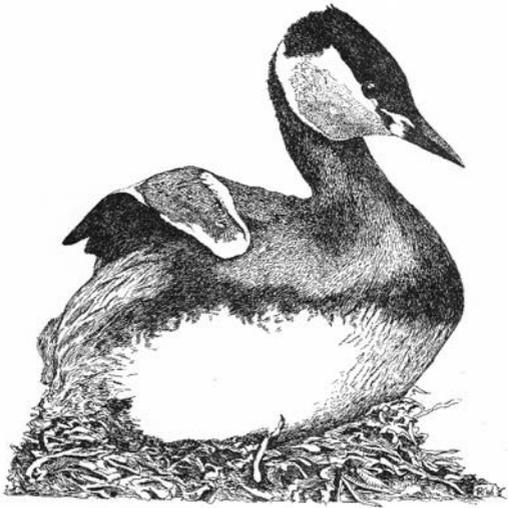
On Lake Pelletier 11 adults were seen in the breeding season 2010, on Lake Fiske 5 and on Lake Osisko 16 (Vander Haeghe and Gagnon 2010).

Michigan

An isolated southern breeding place was recorded in Michigan by Chamberlin (1977). In 1975 he found a breeding pair in the Cedarville Bay in northern Lake Huron. There have been no confirmed nesting records since, indicating that Red-necked Grebes breeding in Michigan must be a very rare event.

Wisconsin

Wisconsin is on the fringe of the breeding range of the species, and it is a rare and local nester (Brooks 2006). It breeds in the north-west of the state (formerly Lakes Twin and Oakridge in St. Croix County, in Polk County and Crex Meadows State Wildlife Area in Burnett County) and in the south-east (Grassy Lake in Columbia County, Lake Maria in Green Lake County, Rush Lake in Winnebago County, Beaver Dam Marsh in Waukesha County, Eldorado Marsh in Fond du Lac County and a place in Dane County) (Eichhorst 1985, Evrard 1988, Gieck 1988, Stout and Nuechterlein 1999, Brooks 2006, Mueller 2007, Bielefeldt 2011). A 1983 breeding survey of 13 former breeding areas found nesting at only 3 sites;



45-65 pairs at Rush Lake, 5 pairs at Oakridge Lake and 1 pair at Grassy Lake (Gieck 1988). It appeared that c. 25-30 pairs nested in Wisconsin annually in the period from 2000 to 2005 (Brooks 2006).

Rush Lake

Rush Lake supported the largest population of Red-necked Grebes in Wisconsin. This lake is a shallow, prairie pothole wetland located in the south-western corner of Winnebago County and the north-western corner of Fond du Lac County. It has an area of 1,245 hectares and an average depth of only 60 centimetres. The lake was once largely covered with Hardstem Bulrush *Scirpus (Schoenoplectus) acutus* and scattered islands of Cattail (Bulrush) *Typha latifolia* and Lesser Bulrush *T. angustifolia*. Unfortunately, this emergent vegetation is steadily disappearing due to high water levels maintained by a dam that was constructed at the outlet of the lake in 1953 (Ziebell 1999), and after 1994 the remaining Hardstem Bulrush beds began to be overwhelmed by Cattail (Ziebell 2008).

The number of breeding Red-necked Grebes on Rush Lake in 1971 was estimated at 55, in 1972 and 1975 at 37, in 1976 at 42, and in 1977 and 1978 at 40 breeding pairs (Strohmeier, cited in Gieck 1988). Ziebell (cited in Gieck 1988) recorded in 1980 up to c. 22, in 1981 up to c. 26 and in 1982 up to c. 24 pairs. Eichhorst (1985) estimated a minimum of 55 breeding pairs in 1983, and Gieck (1988) wrote that 45-65 pairs bred on the lake in that year.

The numbers showed large fluctuations, with the lowest numbers recorded in very dry and/or low water level years: in 1984 c. 57 pairs were reported (Ziebell, cited in Gieck 1988, Ziebell 1999), but in 1986 c. 10 and 1988 c. 3 pairs bred on the lake (Ziebell 1999). In 1993 more than 50 pairs were seen. In the following year 1994, which was neither a dry or low water year, the numbers plummeted to c. 3 breeding pairs, perhaps by winter casualties (many Red-necked Grebes were found grounded in late January and early February 1994, Kaufman 1994). In 1997 c. 25 pairs were reported (Ziebell 1999).

In the period 1998-2015 the numbers were not only changing annually, but also declining, perhaps caused by changing water levels, fluctuating water transparency and turbidity, (growing) carp populations, and quantity and composition of emergent and submergent vegetation (Ziebell 2008; T Ziebell).

In the 1970s, 1980s and 1990s researchers voiced their concern about the continued loss of emergent vegetation on Rush Lake. Ziebell (2008) wrote that by 1998, emergent vegetation covered about 25% of the lake, but by 2005, this vegetation only covered about 10%. From 1994 onwards, the remaining Hardstem Bulrush *Scirpus (Schoenoplectus) acutus* beds began to be overwhelmed by Cattail *Typha*. In 1998, many of the once pure *Scirpus* beds were 70% to 80% *Typha*, and by 2005, the *Scirpus* beds were completely covered by Cattail. Only a few small, sparse stands of pure *Scirpus* remained on the lake. Ziebell (2008) stated that this is significant because many of the birds that nest on the lake, such as the Red-necked Grebe, prefer Hardstem Bulrush.

In 1998 9 nests with 20 eggs were documented by Ziebell. In 2000 c. 8, in 2001 c. 14, in 2002 c. 16 and in 2003 c. 7 pairs were seen on the lake by him. In 2004 no nests or young were found, but on 18 June 2005 c. 10 pairs with 14 young, and on 15 June 2006 c. 8 pairs were reported by Ziebell. In 2007, a dry year, only one adult Red-necked Grebe was observed on the lake. In 2008 c. 6 pairs were seen.

In 2009 only c. 2 pairs (with 3 young) were counted, although the water level was normal, the water "crystal clear", and there was an abundance of submergent vegetation (*Chara*), and numerous small minnows (Cyprinidae) were present. In 2010, Ziebell reported a similar situation as in 2009, but there was no indication of nesting and he counted only c. 4 pairs on the lake. In 2011 1, and in 2012 2-3 pairs were observed, and in 2013 no Red-necked Grebes were seen. In 2015 Ziebell reported 3 adults and 3 young on Rush Lake.

Minnesota

Hanson (1978) described a population breeding on Lake Edward (1,151 ha) in Crow Wing County (central Minnesota); 75 adults and 38 young were recorded in July 1978.

During 1995-98 Nuechterlein *et al.* (2003) studied the nesting dispersion in a population on Lake Osakis, a large (2,537 ha) lake in Douglas and Todd counties (central Minnesota). They counted c. 80-100 breeding pairs.

Thompson (1947) stated that Red-necked Grebes were common (at least 15 pairs in 1947) on Lake Calhoun in Kandiyohi County (south-east of Douglas County) near Spicer.

North and South Dakota

Red-necked Grebes nest mainly in the north-central portion of North Dakota, especially in the Turtle Mountains at the border of Manitoba (Johnsgard 1979, Stout and Nuechterlein 1999, Sauer *et al.* 2014).

Montana and Wyoming

The Red-necked Grebe nests in northwest Montana (Sil-loway 1902, Stout and Nuechterlein 1999, Johnsgard 2009), and is a common breeder south of Glacier National Park (Anonymous 2001). It breeds (isolated) in northwest Wyoming (Stout and Nuechterlein 1999, Johnsgard 2009).

Alberta

The species nests throughout Alberta and is found in every natural region (Semenchuk 1992, Semenchuk *et al.* 2007).

The populations of the Red-necked Grebe have suffered substantially since the end of the 19th century, from pot-hole drainage, land clearing, environmental contamination and human recreational activities on lakes. The species is still reasonably common and is probably Alberta's most common grebe (Semenchuk 1992). About half of Canada's breeding adults of the species reside in Alberta (De Smet 1982, *cited in* Semenchuk 1992). The Breeding Bird Survey did not find an abundance change for the Red-necked Grebe in the province, or in the whole of Canada, during the period 1985-2005 (Semenchuk *et al.* 2007).

Semenchuk (1992) wrote that the largest nesting concentrations occurred near Edmonton, Calgary, and Lesser Slave Lake. After the early 1990s, the species became less common in central Alberta between Edmonton, Whitecourt, and Athabasca, but more common in south Alberta, in the Grassland between Brooks, Medicine Hat, and Taber (Semenchuk *et al.* 2007).

Riske (1976) studied the grebes in the Pine Lake area in central Alberta. During 1970-76 a maximum of 60 Red-necked Grebe pairs were recorded on Pine Lake (402 ha).

Idaho

In Idaho, the Red-necked Grebe is a rare breeding bird (Burleigh 1972). It occurs in the Panhandle, the Upper Snake region (Henrys Lake area), and isolated wetlands in the vicinity of Lake Cascade. The population size is unknown, although it is estimated that 500 adults breed in the Northern Rockies Bird Conservation Region. Of

these, approximately 100 breed in Idaho at 4-6 different locations, including Henrys Lake and Hayden Lake (Anonymous 2005).

Oregon

The Upper Klamath Lake in Klamath County is an isolated breeding water in the south of Oregon (Watkins 1988, Stout and Nuechterlein 1999). A survey conducted from March-July 1988 showed that 13 adult Red-necked Grebes raised six young on Pelican Bay of this lake (Watkins 1988). The Oregon Department of Fish and Wildlife (2015) stated that 5-20 birds at Rocky Point (Pelican Bay) in the Upper Klamath Lake National Wildlife Reserve form the only consistent breeding population in Oregon.

Washington

The species breeds locally common on lakes in the north-east part of the state of Washington (Paulson 2013).

British Columbia

In British Columbia, the breeding distribution is relatively widespread across the central and southern areas east of the Coast Mountains, and rather sparse across the north, except in the Peace River lowlands where it is more widespread. The breeding range during the period 2008-12 appears to be much the same as in the 1980s (Howie 2015).

The Red-necked Grebe appears nowhere common in British Columbia, but it seems most likely to be found in the Central Interior, southern Sub-boreal Interior, and northern extremes of the northern Boreal Mountains and Taiga plains ecoprovinces, and in a narrow zone in the southern Rocky Mountain Trench. During 2008-12 (Howie 2015), the species appeared to be less frequently found in the far south-central portions of the province than indicated in Campbell *et al.* (1990).

On Stump Lake, Quilchena, 64 nests were recorded in 1983 (Campbell *et al.* 1990), on Swan Lake, Vernon, 40 pairs were counted in 1930 and 55 pairs in 1939 (Munro 1941, Campbell *et al.* 1990), and on Duck Lake (1,300 ha) near Creston, 55 pairs were seen in 1982 (Campbell *et al.* 1990).

Breeding Population Density in North-America

In North-America, Red-necked Grebes may inhabit ponds as small as 0.1 ha, e.g. near Yellowknife in the Northwest Territories (Fournier and Hines 1998). High

densities are found in Turtle Mountain Provincial Park, southern Manitoba, for example on Morins Lake (3 pairs on 8.8 ha = 0.34 bp/ha) (De Smet 1983).

Bays of large lakes can have high densities; 4 pairs occupied territories within an area of less than 4 ha in the westernmost end of North Breadon Lake, Turtle Mountain Provincial Park (= 1.00 bp/ha) (De Smet 1983). However, populations densities of entire large water bodies are much lower. On Whitefish Lake (3,015 ha) in the district of Thunder Bay, Ontario, 59 pairs bred in 1993 (= 0.02 bp/ha) (Wheeler 2001), on Lake Edward (1,151 ha) in Crow Wing County, central Minnesota, c. 38 pairs in 1978 (= c. 0.03 bp/ha) (Hanson 1978), on Lake Osakis (2,537 ha) in central Minnesota, c. 90 pairs during 1995-98 (= c. 0.04 bp/ha) (Nuechterlein *et al.* 2003), on Duck Lake (1,300 ha) near Creston, British Columbia, 55 pairs in 1982 (= 0.04 bp/ha) (Campbell *et al.* 1990), and on Rush Lake (1,245 ha), Winnebago County in Wisconsin, c. 57 pairs in 1984 (= 0.05 bp/ha) (Ziebell, *cited in* Gieck 1988, Ziebell 1999).

Usually the population density is higher in smaller lakes, mainly caused by the ratio of the lake surface area to the length of the shore line. During 1970-76 a maximum of 60 Red-necked Grebe pairs were recorded on Pine Lake (402 ha) in central Alberta (= 0.15 bp/ha) (Riske 1976).

Breeding Population Estimates of the Red-necked Grebe in North America

De Smet (1982, *cited in* Fournier and Hines 1998) calculated a conservative population estimate of 5,500+ breeding adult Red-necked Grebes in Canada, but suggested that more widespread and accurate population surveys would produce an estimate in excess of 20,000 breeding birds (= 10,000 breeding pairs). However, he had little information available to him, especially for northern portions of the breeding range. The North American population likely exceeds 45,000 individuals (Stout and Nuechterlein 1999; see also Wetlands International 2006, 2015); it is estimated that more than 70% of the population resides in Canada (Fish and Wildlife Service US FWS Gov. 2007).

11.3.4 World Breeding Population

The total population of the nominate *grisegena* (Europe and West Asia) was estimated at 98,000-192,000 individuals (including immature birds) (Wetlands International 2006, 2015) and at 50,000 or more breeding pairs (Vlug

2002a; J J Vlug). The population of *holboellii* (East Asia and North America) is probably greater than 100,000 birds (O'Donnel and Fjelds  1997).

Wetlands International (2006, 2015) estimated the global population at c. 193,000-287,000 individuals (including immature birds), and Jehl (2001) gave the number of c. 200,000 birds. Perhaps, the global population of *Podiceps grisegena* consists of c. 100,000 breeding pairs.

11.4 Wintering Population and Population Trends

11.4.1 Problems in Counting Wintering Birds

The Red-necked Grebe is strongly maritime in winter and is more attracted to the sea than the Great Crested Grebe (Durinck *et al.* 1994). It uses estuarine or coastal waters, often bays, inlets, estuaries and narrows, but is also frequently recorded over shallows located well offshore (Cramp *et al.* 1977, Campbell *et al.* 1990, Brazil 1991, O'Donnel and Fjelds  1997, Stout and Nuechterlein 1999). The number of birds and young recorded on the breeding waters is considerably higher than the number of birds counted on the wintering grounds. This is undoubtedly because counts of birds at sea produce underestimated figures.

Land-based counts (from the shore) can be unreliable and incomplete. In ideal circumstances, the birds can be recorded to a distance of approximately 2 km. However, accurate identification is often possible only within one kilometre from the shore. In addition, and more importantly, Red-necked Grebes often use areas further away from the coast than the Great Crested Grebe and are often out of sight from the shore (Scholl 1974, Durinck *et al.* 1993, Sonntag 2009).

Numbers of Red-necked Grebes in non-breeding plumage based on aerial counts may also give underestimated figures (Helcom Red List Bird Expert Group 2013).

Surveys of wintering *grisegena* made from ships are often more complete and more reliable than land-based or aerial counts, and thus necessary to cover the species (Skov *et al.* 2011, Helcom Red List Bird Expert Group 2013). However, the marine areas where Red-necked Grebe winter are enormous and so it is almost impossible to investigate regularly all the relevant areas.

Another problem with counting birds in winter is that during this period the birds, especially of the nominate race *grisegena*, are frequently solitary or in twos, and so the chance of being detected is not large.

11.4.2 Wintering Population and Population Trends in Europe-West Asia

On the basis of records and estimations of the number of breeding birds, we expect to find a winter population in coastal north-west Europe of up to 60,000 individuals (including immature birds) (Wetlands International 2015). However, as already stated (see 11.4.1) the number of recorded wintering birds is much lower.

The principal non-breeding areas in north-western Europe are the Baltic Sea and the Danish Belts (Durinck *et al.* 1994, Skov *et al.* 2000, Garthe *et al.* 2003, Helcom Red List Bird Expert Group 2013), the Atlantic coasts of central Norway (Folkestad 1978, Pirot 1989, O'Donnell and Fjeldså 1997) and the sea off the Danish part of the Wadden Sea (Durinck *et al.* 1994). Significant numbers can be found in the Black, Caspian, and Aral Seas.

The Baltic Sea and the Danish Belts

The Baltic Sea is a brackish non-tidal sea covering about 415,000 km² (including the Kattegat, the Danish straits, the Bothnian Bay, the Bothnian Sea and the Gulf of Finland). Although the maximum depth of the Baltic Sea is 459 m, it is a relatively shallow sea with a mean depth of about 55 metres. Furthermore, large parts are less than 25 m deep, especially in Danish, German and Polish waters, and a number of large very shallow semi-open lagoons with water depths of just 1 to 2 metres are found here (Durinck *et al.* 1994). The Red-necked Grebes have mainly been observed in offshore areas of 5 to 20 m water depth; most birds (81%, $n = 1,698$ Red-necked Grebes) were observed in waters up to 15 m depth. It seems that they often use areas further away from the coast than the Great Crested Grebe. A large winter concentration has been recorded in shallow parts of the north-western Kattegat (see below) (Durinck *et al.* 1993, 1994, Garthe *et al.* 2003, Sonntag 2009).

During the period 1988-93, an average number of *c.* 5,500 wintering Red-necked Grebes were counted in the Baltic Sea (including the Danish Belts), with concentrations in the north-west Kattegat (on average *c.* 2,350 birds, and with a maximum of 3,600 estimated birds in 1992), Pomeranian Bay (on average *c.* 1,250 birds), the

area between Rügen and Fehmarn-Kiel Bay (on average *c.* 780 birds) and the Gulf of Riga (on average *c.* 550 birds) (Durinck *et al.* 1993, 1994).

The results of a study undertaken in the period 2007-09 generated significantly smaller numbers of wintering Red-necked Grebes in the Baltic Sea (770 individuals) as compared to the 5,500 birds estimated during 1988-93, equivalent to a decrease of 86%. However, a part of this decline was caused by the lack of available data from several important Danish areas as no ship-based surveys, which are necessary to cover this species, were undertaken. Most importantly, the north-western Kattegat where more than 2,300 birds were found in 1988-93 was not covered (Skov *et al.* 2011).

The Helcom Coreset trend data for the period 1991-2001 revealed a stable trend of the Red-necked Grebe in the Baltic Sea, but this figure is based on coastal counts only and might thus be inappropriate for the species that also occur offshore. Assuming that numbers might be somewhat underestimated by Skov *et al.* (2011), the population decrease in the Baltic Sea is supposed to be lower than 80%, but higher than 50% (Helcom Red List Bird Expert Group 2013).

Atlantic Coasts of Central Norway

Along the coasts of central Norway, *c.* 2,500-3,000 birds winter in fairly exposed but shallow, coastal waters with a depth of 5-10 m, with islets and skerries (Folkestad 1978, Pirot 1989, O'Donnell and Fjeldså 1997). Many birds were seen around the island of Smøla, where up to 470 birds were counted, even though only parts of the area were covered (Folkestad 1978).

Danish North Sea Coast

The North Sea coast off south-west Denmark is a rather important wintering site of the species (Laursen *et al.* 1977, Stone *et al.* 1995, Helcom Red List Bird Expert Group 2013). About 1,000 birds were recorded at sea off the Danish part of the Wadden Sea (Durinck *et al.* 1994).

North Sea Coasts of The Netherlands

Along the North Sea coast of The Netherlands, Red-necked Grebes are scarce, but regularly observed from the second half of October to April, mainly between November and March (Camphuysen and Van Dijk 1983, Camphuysen and Leopold 1994). From ship-based surveys and sea-watching data, it is unlikely that more than a few hundred individuals occur in Dutch coastal waters

at any time (Camphuysen and Leopold 1994). The birds occur concentrated in some locations in the Dutch Delta area and in the Wadden Sea (SOVON 1987, Camphuysen and Leopold 1994, Bijlsma *et al.* 2001). It was estimated that c. 40 Red-necked Grebes wintered annually on the deeper parts of the Dutch Wadden Sea in the early 2010s (Schekkerman *et al.* 2015). Sometimes the birds concentrate near moles and dams off the North Sea coast, e.g. 56 birds near the harbour moles of IJmuiden on 17 February 1970 (Vogelwerkgroep Zuid-Kennemerland 2015), 55 on the North Sea near the Brouwersdam on 7 February 1985 and 71 at the place last mentioned on 18 November 1995 (Breedveld *et al.* 2004). Red-necked Grebes wash ashore annually, but usually in very small numbers. In severe winters, the birds strand more frequently because the wintering numbers are higher (Camphuysen and Leopold 1994), such as in February 1979, when more than 100 dead Red-necked Grebes were found at the Dutch beaches of the North Sea (SOVON 1987).

Coasts of Britain and Ireland

The species is also a rather scarce but annual non-breeding visitor to Britain and Ireland from continental Europe (Brown and Grice 2005, Balmer *et al.* 2013). The winter distribution shows a strong bias to the North Sea coast from Angus to Kent and along the south coast of England (Balmer *et al.* 2013). Approximately 200 birds are estimated to spend the winter around the United Kingdom, but the numbers may increase during cold spells over Europe as birds move west to ice-free waters (Chandler 1981, 1986, Barton and Pollock 2004). During the large and extremely widespread influx of the winter 1978-79, the numbers in most areas reached their maximum from 19 to 25 February 1979, with a grand total of 481 (Britain and Ireland, Chandler 1981).

At most sites, records often refer to just one or two individual birds. The Firth of Forth is the only area to support larger numbers in the non-breeding season on a regular basis, though numbers there have declined since c. 2000. In 1994-95 up to 100 birds were recorded, 1997-98 64, 1999-2000 67, 2000-01 29 and 2010-11 just 4 (Barton and Pollock 2004, Balmer *et al.* 2013).

In Ireland, it is found mainly at a small number of coastal locations (Hutchinson 1989, Balmer *et al.* 2013).

Coasts of France

Outside the breeding season, the birds are seen regularly in small numbers off the north-west coast of France

(English Channel or La Manche). The species is also recorded off the coasts of the Atlantic Ocean and the Bay of Biscay (Commecy 1991, Dubois *et al.* 2001, 2008). The maximum number of observed birds in France (at sea and on inland water bodies) in mid-January 2000-06 was 52 individuals, but this is very probably an underestimation (Dubois *et al.* 2008). In the northern and western parts of France 423 birds were recorded in January 1996 (Delany *et al.* 1999). Deceuninck *et al.* (2015) estimated the total French winter visitor population at only 10-30 Red-necked Grebes in 2010-13.

Mediterranean Sea

Podiceps grisegena is observed in small numbers along the Spanish and French Mediterranean coasts and in the north Mediterranean Sea (Bonaccorsi 1994, Snow and Perrins 1998, Dubois *et al.* 2008, De Juana and Garcia 2015), and it seems a scarce to rare winter visitor to the south side of the Mediterranean (Bannerman 1959, Snow and Perrins 1998). Perhaps, it is not rare in the Adriatic and Aegean Seas (O'Donnel and Fjeldså 1997, Snow and Perrins 1998, Delany *et al.* 1999, Fjeldså 2004, Delany and Scott 2006). Bricchetti and Fracasso (2003) wrote that the species is a regular winter visitor in Italy with an estimated population of 100-200 Red-necked Grebes at the end of the 20th century, with a maximum of 130 birds in 1997. The largest numbers were found off the northern coast of the Adriatic Sea in Friuli-Venezia Giulia; on the lagoons of Grado-Marano up to 95 birds were seen in 1997 and in Panzano Bay up to 19 individuals in 1996. No thorough surveys of the total winter population of the Mediterranean Sea exist.

Black, Caspian, and Aral Seas

As already stated, significant numbers can be found in the Black, Caspian, and Aral Seas, but there are no thorough surveys (Kuročkin 1985, O'Donnel and Fjeldså 1997, Delany *et al.* 1999, Fjeldså 2004, Delany and Scott 2006).

Inland Waters in Europe

Some birds winter on inland waters, especially on the larger lakes in Switzerland and southern Germany (Bezzel 1985, Winkler 1999), such as Lac Léman (Genfersee, Lake Geneva) (Géroudet 1987, Maumary *et al.* 2007), Bodensee (Lake Constance) (Gönner 1999, Maumary *et al.* 2007) and Zürichsee (Lake Zürich) (Maumary *et al.* 2007).

In southern Germany 113 birds were recorded in January 1995 (Delany *et al.* 1999). The mean mid-January numbers in Switzerland were 20 birds (9-37) in the period 1968-79, 51 (23-130) in 1980-91, and 57 (19-93) in 1992-2003 (Maumary *et al.* 2007).

Bodensee (Lake Constance)

Lake Constance is a lake situated in Germany, Switzerland and Austria near the Alps. It covers approximately 571 km² (57,100 ha) and has an average depth of 90 m. In the period 1974-83 a mean annual number of 45-50 wintering Red-necked Grebes were seen on the lake. Then this number tripled and in the period 1984-93 a mean annual number of 135-150 birds were counted, with a maximum of 310 birds in 1988 (Gönner 1999). In mid-January 1995 61 and in mid-January 2000 23 birds were counted on the lake (Schmid *et al.* 2001).

Lac Léman (Genfersee, Lake Geneva)

Lake Geneva is a lake on the north side of the Alps, shared between Switzerland and France. Its surface area is 580 km² (58,000 ha) and its average depth is 154 m. In the period 1979-86, a mean number of *c.* 28 birds (range 16-58) were counted on the lake in winter. The maximum numbers were 49 Red-necked Grebes (in mid-January 1983), and 58 (in mid March 1983) (Géroutet 1987). In the period 1991-2000 the maximum number of birds in January was 30 (1992) and the minimum 7 (1995) (Schmid *et al.* 2001). Near Excenevex, in the French part of the lake, up to 50 birds and more were seen (Géroutet 1987, Maumary *et al.* 2007).

Zürichsee (Lake Zürich)

Lake Zürich is a lake in Switzerland. It has a surface area of *c.* 89 km² (8,900 ha) and an average depth of 49 m. The maximum number of Red-necked Grebes seen in January 1991-2000 was 17 (in 1992) and the minimum 2 (in 2000) (Schmid *et al.* 2001).

Azerbaijan and Kyrgyzstan

In winter, Red-necked Grebes are not rare on inland waters of Azerbaijan (Kuročkin 1985), and they are found in this season in large numbers on Lake Issyk-Kul, Kyrgyzstan (Janušević *et al.* 1959, *cited in* Kuročkin 1985).

South Asia

There is a small wintering population in north-eastern Afghanistan, northern and central Pakistan and an increasing one in north-western India (see 10.2.1 for more details).

11.4.3 Wintering Population in East Asia

The Red-necked Grebe winters along the coasts of eastern Asia (see 10.2.2 for more details). It is certainly a fairly common winter visitor in Japanese coastal waters from Honshu south to Kyushu. Although it can be found in reasonable numbers also in Hokkaido at this season, it rarely occurs in anything other than very small numbers.

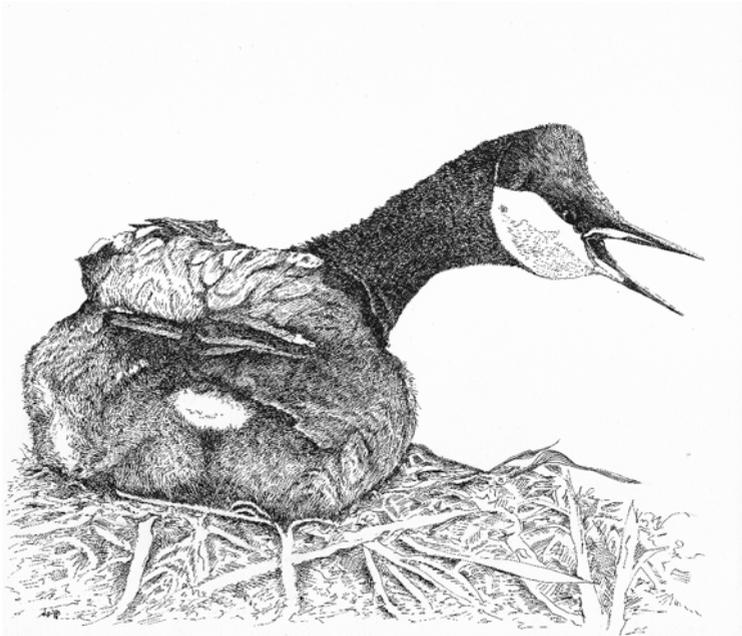
No thorough surveys of the winter population along the coasts of East Asia exist. The estimations are very rough: *c.* 50-1,000 wintering individuals in China and *c.* 1,000-10,000 wintering birds in Japan (BirdLife International 2015a). The expected number of Red-necked Grebes wintering along the coasts of East Asia is estimated at *c.* 50,000 birds (Wetlands international 2006).

11.4.4 Wintering Population in North America

The species winters primarily on marine waters along the Atlantic and Pacific coasts and, to a limited extent, on the Great Lakes (Stout and Nuechterlein 1999) (see 10.2.3 for more details).

Along the Atlantic coast, the grebes winter mostly in Nova Scotia and New Brunswick south to Long Island, New York. The abundance for the Atlantic wintering population centres along the coast of the Bay of Fundy (Nova Scotia, New Brunswick, and Maine). Annual (1990-94) August-November counts of eastern-wintering migrants through eastern Lake Superior (Whitefish Point Bird Observatory) have ranged as high as 18,739 individuals (Stout 1995, Stout and Nuechterlein 1999), and the minimum total number of wintering birds along the Atlantic coast is estimated at 20,000 birds.

Along the Pacific coast we find most wintering birds from the southern coast of Alaska to northern Oregon. They are especially abundant around southern Vancouver Island, the Juan de Fuca Strait, the Strait of Georgia, and Puget Sound. Surveys conducted in Prince William Sound, Alaska, in 1998 estimated 1,396 birds during winter (Irons *et al.* 2000, *cited in* Alaska Natural Heritage Program 2005). The Pacific wintering population is probably much higher than the Atlantic wintering population (Stout and Nuechterlein 1999), perhaps 25,000 birds or more.



12. Threats, Causes of Death in Young and Adult Birds, Nest and Egg Losses, Causes of Population Fluctuations

12.1 Vulnerability to Threats Relating to Life History Tactics

Podicipedidae face many threats. Dangers such as reduction of reed-beds and destruction of clutches and chicks by wave action are obvious. However, the life history tactics of individual species will determine the effect of various kinds of stress on the long-term development of a population. Thus, various hazards may have fundamentally different impacts on species with high breeding potential than on long-lived species with low annual recruitment (O'Donnel and Fjelds  1997).

Red-necked Grebes belong to the K-strategists, and thus show a relatively small reproductive potential, and developed behaviour patterns to increase prospects for their own survival. In general, the contribution to the future gene pool of *P. grisegena* is likely to be a matter of the total (long) life production rather than annual productivity (Vlug 2005). So, it seems that adult losses are a more serious threat to Red-necked Grebe populations than to populations of Little Grebes and other r-strategists. On the other hand, egg and chick losses are probably less serious in *grisegena* than in r-strategists.

12.2 Exposure to Drought and Bad Weather Conditions

12.2.1 Drought and Varying Water Levels

Naturally and artificially changing water levels may affect nesting populations of *grisegena* (for varying water levels caused by anthropogenic factors, see 12.3.4).

The Naurzum Lakes in North Kazakhstan are important breeding places of the Red-necked Grebe. The water levels of these lakes in the steppe zone are mainly determined by the quantity of melt water and the losses due to evaporation. The lakes are not deep, c. 1-2 m, and the depth of the largest lake does not exceed 3-4 m, while the area of the lakes is comparatively small. These factors lead to considerable annual and seasonal fluctuations in the water levels. In the second half of the 20th century, the hydrological regime of the lakes was affected by the economic development of the area (Inyutina *et al.* 2011). Gordienko (1980, 1981) observed large population fluctuations of Red-necked Grebes in the Naurzum Lakes

nature reserve (400 breeding pairs in 1972 and 1,200 in 1975) (Gordienko 1981). In 1972-81 the breeding population ranged between 140 and 1,200 pairs (Bragin and Bragina 2002, *cited in* Wassink 2015). Gordienko (1981) attributed the fluctuations, among other things, to varying water levels. Undoubtedly, not only the population of the Naurzum Lakes, but also of many other steppe lakes in Central Asia show unstable hydrological regimes, which may result in annual population fluctuations and occasionally in large scale movements of *grisegena*. Significant in this connection is, that the tendency of the Black-necked Grebe to increase on the western and northern edges of its distribution range (north-western and Central Europe) from the late 19th century is often ascribed to desiccation of wetlands in the centre of its breeding range, especially of the lakes in the steppe areas of the Caspian region, causing invasions in years of the greatest aridity (Cramp *et al.* 1977).

In some years, low water levels in fish-ponds in Schleswig-Holstein, caused by a shortage of precipitation, may lead to a decrease in breeding numbers of Red-necked Grebes. In these years many pairs cannot build a nest because the emergent vegetation is inaccessible to them, and they often leave the breeding water early in the season. Vlug (2000) stated that the number of pairs reduced from 616 (in 1995) to 524 (in 1996) due to a shortage of water in 1996.

The numbers of breeding pairs of the Red-necked Grebe in Rush Lake, a shallow, prairie pothole wetland located in Winnebago County, Wisconsin, showed large fluctuations, with the lowest numbers recorded in very dry and/or low water level years, such as 1986 and 1988: in 1984 c. 57 pairs were reported (Ziebell, *cited in* Gieck 1988, Ziebell 1999), but in 1986 c. 10 and 1988 c. 3 pairs bred on the lake (Ziebell 1999). In 1993 more than 50 pairs were seen (Ziebell 1999). In 2007, a dry year, only one adult Red-necked Grebe was observed on the lake (T. Ziebell).

12.2.2 Wave Action During the Breeding Period

Wave action during storms is a major cause of nest and egg losses in large breeding waters of Red-necked Grebes and other Podicipedidae, especially on wind exposed places without enough protective emergent growth (see also 16.3.5). Wave action not only causes egg losses but may also kill large numbers of small chicks. Lake size and reproduction are often negatively correlated, because the

destructive force of waves increases as the area of the lake grows (Vlug 1983, 2005).

Many authors, especially from North America, report nest losses by wave action in Red-necked Grebes. A European account is from Zimmermann and Schieweck (1988). They wrote that a windstorm (in June 1987) destroyed 17 *grisegena* nests on the Lewitz-fish ponds in Mecklenburg-Vorpommern (Mecklenburg-Western Pomerania), Germany.

The following reports are from Canada and the United States:

Speirs *et al.* (1944) stated that storms were responsible for the destruction of *holboellii* nests at Burlington on Lake Ontario during the breeding seasons of 1943 and 1944.

A severe storm destroyed a loose colonial aggregation of five *holboellii* nests at the west end of Wizard Lake, southwest of Edmonton, Alberta, on June 9, 1970. The nests, composed almost entirely of leaves and stalks of the Variegated Yellow Pond Lily (Bullhead Lily) *Nuphar variegata* and anchored in a large bed of the same species, were located in the open, and exposed to wind from all sites; the nest nearest shore was located 30 m from emergent bulrush (cattail) *Typha* there (Riske 1976).

Nuechterlein *et al.* (2003) studied a population of 80-100 breeding pairs of Red-necked Grebes on Lake Osakis, a large (2,537 ha), windblown lake in Minnesota. In every year of their study (1995-98), wave action caused by sporadic windstorms was responsible for the most failed nests. After severe windstorms, they saw that the nests were sunk or had disappeared, with the eggs sometimes located nearby on the lake bottom.

Riske (1976) discovered a high negative correlation ($r = -0.85$) between the average wind-force (during May, June and July in 1970-73) and the mean numbers of larger young per *holboellii* pair on Pine Lake, Alberta. In complete contrast to Pine Lake, the pothole-nesting birds (near Pine Lake) were almost immune to destruction of their nests by wind because of shelter afforded by adjacent topography and the small size of the water bodies, both of which contribute to preventing waves from being generated.

De Smet (1983, 1987) studied the factors influencing the reproductive success of Red-necked Grebes in Turtle

Mountain Provincial Park, Manitoba, during 1980 and 1981. Over 400 small to medium-sized lakes dot this Park. Wind speeds during the summer months of the study years were about 20% below normal, and accordingly, only 17 eggs (= 2%) of a total of 697 eggs (found in 179 regularly observed clutches) were lost by waves.

Ohanjanian (1986) studied Red-necked Grebes on Duck Lake, British Columbia, from 1982 to 1984. The population on this lake nested in the open on the lake. The nests were constructed on accumulations of submergent vegetation, principally Spiked Water Milfoil *Myriophyllum spicatum*. As the season progressed, the accumulations of Water Milfoil grew and effectively acted as breakwaters damping the action of waves and protecting nests constructed in or behind them. Over the three years of the study of Ohanjanian (1986) complete clutches were found only in areas where accumulated milfoil was of high or medium density. All nests constructed in May of 1981-83, prior to the build-up of substantial amounts of milfoil, were lost.

Species of grebes which prefer to breed on large open lakes (e.g. Great Crested and Western Grebes) may suffer severely by wave action, much more than birds nesting on open spaces in swamps and marshes such as Little and Pied-billed Grebes. Wind storms sometimes destroy whole breeding colonies of Great Crested Grebes, e.g. in Lake IJsselmeer in The Netherlands and in Lac Léman (Lake Geneva) in Switzerland, resulting in an exceedingly poor breeding success. For example, the mean number of reared young per pair (including the unsuccessful pairs) of about 400 Great Crested Grebe pairs which breed every year in the colonies in Lake Geneva varied during many years from 0.1 to 0.3 (Vlug 1983, 2005).

Massive nest and eggs losses by wind storms are observed in colonies of Western Grebes. Storer and Nuechterlein (1992) stated that nest losses by waves in this species are most extensive in low-water years, when areas with dense emergent vegetation are too shallow and inaccessible to grebes, and the birds have to build their nests in areas exposed to waves. In years of high water, the colonies tend to be larger and farther into the emergent vegetation.

12.2.3 Rainy and Chilly Weather Conditions During the Breeding Period

The ability of newly-hatched young of Red-necked Grebes and other Podicipedidae to regulate their body

temperature seems badly developed at first. In addition, the short down is not waterproof and isolates poorly. Thus, the newly hatched Red-necked Grebes are highly vulnerable to chilling and must remain on the parent's back, where they are brooded almost continuously during the first week after hatching. Until the thermoregulation ability develops in the second week, the young chicks are dependent on the production of body heat of their parents (Heinroth 1922, Onno 1960, Wobus 1964, Fjelds  1977b, Stout and Nuechterlein 1999). It is not surprising that chick mortality of Red-necked Grebes is highest during the first 5-10 days after hatching, and that there is little mortality after the first month (De Smet 1983, Ohanjanian 1986, Stout and Nuechterlein 1999, Kloskowski 2000). Large numbers of newly-hatched *grisegena* chicks may be killed in windstorms or cold, damp weather, especially when food is scarce (Wobus 1964, Vlug 1985, Dittberner 1996, Stout and Nuechterlein 1999, Vlug 2002a, 2005).

Vlug (2005) reported that the Atlantic Ocean has a growing influence on the climate in Schleswig-Holstein, Germany, since 1970, i. e. the averages of summer precipitation and wind activities increased from 1970 to 2002. The change of climate during this period coincides with a decrease in breeding success of Red-necked Grebes. In years with bad weather conditions, the brood success was low. In 1984 only 19% of 312 pairs raised one or more young, and in 1993 no more than 16% of 392 pairs were successful (the mean brood success, i. e. the percentage of pairs raising at least one young, from 1969 to 2002 was 39%, $n = 10,349$ pairs).

Not only in Red-necked Grebes but also in other Podicipedidae bad weather may kill many chicks, e. g. hundreds of young Western Grebes were found dead, washed up on the shores of Lake Manitoba after violent windstorms (Storer and Nuechterlein 1992).

12.2.4 Bad Weather During Migration and Icing of Wintering Waters (these topics are treated in more detail in 13.8)

Even adult Podicipedidae are affected by storms and frost periods in winter. Piersma (1988b) estimated that a healthy *grisegena* with average winter reserve levels can (only) survive a period of about eleven days without food in midwinter, and so it is likely that severe winters are an important factor influencing the numbers of the birds. Karlsson and Kjell n (1984) found that the breed-

ing numbers of Red-necked Grebes in Sk ne (Scania), southern Sweden, were inversely correlated with the winter severity in their wintering areas. However, Vlug (1986) could not find such a correlation in Schleswig-Holstein, Germany, and Norevik (2014) stated that no statistically significant relationship could be found between the harshness of the winter in the wintering areas and the observations of passage migrants at Ottenby,  land, south-east Sweden, but he wrote that an indirect effect of winter weather on the Swedish population can not be ruled out.

Snow- and ice-storms, rain, and fog can cause nocturnal migrants to become disorientated and force them to land on glistening wet or icy pavement, where they become grounded and unable to fly. Severe winters force the Red-necked Grebes to leave their interior wintering lakes, e.g. the Great Lakes on the Canada-United States border. These birds may become grounded during passage (Stout and Nuechterlein 1999, Vlug 2002a). Red-necked Grebes not leaving and remaining on the open water of large lakes during severe winters can be frozen into the ice because they are usually unable to rise in flight from a hard surface. Many cases are known in which birds have been caught by encroaching ice during sudden freeze-up of lakes. They were unable to escape death unless they chanced upon a permanent air hole, where they could survive until the return of milder weather (Wetmore 1924, Stout and Nuechterlein 1999).

Grounded Red-necked Grebes

Observations of stranded Red-necked Grebes in Europe are rare. However, in contrast to Europe, the number of reports in eastern North America is large.

With the harsh weather of the winter 1993-94 in eastern North America, the Great Lakes were frozen over almost completely, forcing out many waterbirds that ordinarily winter there. Almost certainly as a result of this, an unprecedented invasion of Red-necked Grebes moved east to the Atlantic Coast and south into the interior of the east and Midwest during February. The push of Red-necked Grebes was preceded in January by a southward flight of Slavonian Grebes, undoubtedly vacating the Great Lakes as the winter got worse. But the Red-necked Grebes appear to have held on as long as possible, so when they finally did leave the Great Lakes, they did it all together in large numbers.

Birders in the North encountered these birds mainly as failed migrants: at least six were picked up dead or grounded in New England during February; in southern Ontario, dozens of Red-necked and Slavonian Grebes were found grounded on roads in late January and early February. The total Hudson-Delaware region tally came to at least 850 Red-necked Grebes, and most appeared healthy (Kaufman 1994, see 13.8.2 and 13.8.3 for more details).

Grounded Black-necked Grebes in North America

Downings are not unique to Red-necked Grebes, but also reported from other Podicipedidae, especially Black-necked Grebes.

Early in the morning of 13 December 1928 residents of Caliente, Nevada, were awakened by a heavy thumping of something falling on the roofs of their houses. The next morning, several thousand Black-necked Grebes were found on the ground and flat roofs of business houses throughout the city (Cottam 1929). Marriage (*cited in* Cottam 1929), formerly secretary to the Cambridge University (England) Natural History Society, stated that “literally thousands of these birds were found in every portion of the town and outskirts. ... We saved thousands by putting them in the creek; most of those that died were crippled in some way; they were forced out of the air by the heavy density of the snow which bore them to the ground, thousands being buried under the snow, and working themselves out in the morning. I watched hundreds coming up through the snow. Many flew off at noon, going southwest. Hundreds were killed by hitting the wires, houses, and trees. Caliente had the main bunch, but they were scattered for twenty miles every way.”

On 10 December 1991 thousands of Black-necked Grebes departed Great Salt Lake en route to the Salton Sea, California, or Gulf of California, Mexico. Several hours into the flight, over southern and Central Utah, large numbers were forced down by a snowstorm along a 180 km stretch between Holden and Cedar City. The birds did not fall uniformly, but apparently were attracted to lights from towns and highway intersections. Many died when they crashed to earth; others were hit by cars on the highway, which they evidently mistook for open water. Thousands more were captured alive and released on whatever local water bodies remained open. About 14,000 birds died (Jehl 1993, 1996).

Influxes of Red-necked Grebes in Great Britain

A comparatively small number of Red-necked Grebes winter in Great Britain, but occasional influxes occur on the east coast in hard weather, as in 1937 and 1979.

At least some of the birds in these influxes die. By far the greatest number of dead Red-necked Grebes in the invasion of 1979 was found between 19 and 25 February, the week in which the greatest numbers were present in Britain. In two or three instances, birds were reported to have had empty stomachs apart from a small quantity of water-weed: since the species normally feeds on animal matter, this points to starvation as the most likely cause of death (Chandler 1981) (see 13.8.2 for more details).

The influx of 1979 was also recorded in The Netherlands. In February more than 100 dead Red-necked Grebes were found at the Dutch beaches of the North Sea (SOVON 1987).

12.2.5 Bad Weather and Food Shortage

Not much is really known about the relation between food and weather. As stated above (12.2.4), Piersma (1988*b*) estimated that a healthy *grisegena* with average winter reserve levels can (only) survive a period of about eleven days without food in midwinter. During the 1979 winter invasion in Great Britain, starvation by bad weather conditions was the most likely cause of death in at least some of the Red-necked Grebes found dead (see 12.2.4).

Vlug (2005) conjectured that a combination of food shortage and bad weather conditions cause high mortality among newly hatched Red-necked Grebe chicks.

Jehl *et al.* (2002) found that weather can cause food shortages in wintering Black-necked Grebes. The population of Black-necked Grebes in Mono and Great Salt Lakes in autumn 1997 was estimated to be 3.56 million birds (more than 99% of North American Black-necked Grebes stage at these lakes). The numbers crashed to 1.60 million in 1998, when hundreds of thousands starved in the Gulf of California as a result of a major El Niño. During ENSO (El Niño-Southern Oscillation) years, surface water temperatures are elevated. Jehl *et al.* (2002) suspect that this affected food supply either by killing it or by forcing prey to cooler waters below the efficient foraging depth of grebes.

12.3 Environmental Contamination and Other Effects of Human Activity

12.3.1 Oil-spills

Numerous cases have been published of grebes being affected by oiling, but the evidence is mostly anecdotal (Fjeldså 2004). More than 4,000 Slavonian Grebes were killed in an oil-spill in 1976 in Chesapeake Bay, east coast of the United States (Roland *et al.* 1977, cited in Stedman 2000). It was estimated that 30,000 birds died in the oil-spills caused by the Kuwait war in 1991, equally divided between grebes (Great Crested and Black-necked) and cormorants (Fjeldså 2004).

It is probable that the extensive winter ranges of *grisegena* often prevent catastrophes caused by oil-spills. However, because the birds sometimes show marked local concentrations in the marine environment, especially around the migratory periods, local populations are occasionally seriously affected. An oil-spill in the Danish coastal waters, near the island of Samsø in the Kattegat in January 1979, caused high mortality of Red-necked Grebes. About 400-800 birds were killed, and the breeding populations in Sjælland (Zealand), Denmark and Skåne (Scania), South Sweden were reduced by c. 50% after this severe oil-spill and needed at least five years to recover. Although the population in Schleswig-Holstein was less affected, the number of breeding pairs still decreased by 20%, from 343 in 1978 to 272 in 1979 (Larsen 1979, O'Donnel and Fjeldså 1979, Larsen, cited in Berndt and Busche 1981, Fjeldså 1982a, Karlsson and Kjellén 1984, Vlug 2000, 2002a, Fjeldså 2004).

When the oil-tanker Exxon Valdez went aground in Prince William Sound, Alaska, on 24 March 1989, the ensuing spill became the largest marine oil spill in the United States history. Marine birds, which are among the most conspicuous victims of oil spills at sea, experienced substantial mortality: nearly 30,000 carcasses were collected throughout the spill-affected area during the spring and summer of 1989. The total mortality was estimated at 375,000-435,000 birds. Murphy *et al.* (1997) conducted post-spill surveys during mid-summer (1989-91) in 10 bays that had been surveyed prior to the spill (1984-85). Species that were significantly less abundant during all 3 post-spill years than they were prior to the spill included Red-necked Grebes, Pelagic Cormorants *Phalacrocorax pelagicus*, and Pigeon Guillemots *Cephus columba*. Nineteen Red-necked Grebes were ob-

served in the pre-spill surveys and only one during the 1989-91 surveys. However, the authors question the biological significance of this apparent decline because this species generally is uncommon in Prince William Sound during summer and the statistical evaluations of annual changes are based on scant data.

12.3.2 Pesticides, Heavy Metals and Other Contaminants/Toxics

As predators in the aquatic ecosystems, grebes are likely to accumulate pesticides, heavy metals, and other contaminants (e.g. Prestt and Jefferies 1969, Riske 1976, De Smet 1987, Forsyth *et al.* 1994, Fjeldså 2004, Burger and Eichhorst 2005, 2007). Elevated levels of DDE (dichlorodiphenyldichloroethylene), PCB (polychlorinated biphenyl), polychlorinated dibenzodioxin, and dibenzofuran have been detected in eggs or body tissues of Podicipedidae in many areas. Although the effects of these chemicals are known, in general terms, their impact on grebe populations is less well known (Fjeldså 2004).

In Red-necked Grebes in North America, high levels of organochlorines, mercury, and other heavy metals were often found in adults, eggs, and young (Stout and Nuechterlein 1999).

Forsyth *et al.* (1994) analysed the eggs of Red-necked Grebes and other Podicipedidae from Manitoba, Saskatchewan and Alberta during 1982-87. All eggs in their study were collected in areas remote from industrial pollution. The fact that some of the highest concentrations of PCB were found in grebe eggs from inside or close to provincial and national parks suggests strongly that most of the contaminant burden in these birds was accumulated during winter or spring migration. The authors found a high PCB: DDE ratio (3:1) in eggs of Red-necked Grebes from Manitoba. This is similar to the 3:1 ratio that is characteristic of birds wintering or staging on the Atlantic coast and the Great Lakes, where elevated levels of the industrial contaminant PCB predominate. In contrast, the overall low PCB levels and approximately 1:1 PCB: DDE ratio found in eggs of Alberta-nesting Red-necked Grebes is typical of birds wintering on the Pacific coast. The presence of mirex at significant levels in all samples of Manitoba Red-necked Grebe eggs, as well as a sample of Saskatchewan, supports the hypothesis that these birds spent some time during migration on the lower Great Lakes, where mirex occurs consistently.

A tendency towards lower levels of DDE and PCBs as the nesting season progressed was observed for Red-necked Grebes in Alberta and Manitoba. This also suggests that the major intake of organochlorines occurs on migration and in wintering areas, and that body burdens decline through the transfer of residues into the eggs (Riske 1976, De Smet 1987).

Eggshells of Red-necked Grebe eggs were found to have indices of strength (“thickness”) that were inversely correlated with the levels of DDE and PCBs (Riske 1976, Forsyth *et al.* 1994). Analysis of historical Red-necked Grebe eggshell thickness data indicated that eastern populations (Manitoba-nesting) underwent reductions in shell thickness during the DDT era (1947-72) from which they had not yet completely recovered by 1983, whereas western populations (Alberta-nesting) maintained shell thickness throughout that time (Forsyth *et al.* 1994).

Substantial eggshell-thinning, inviable eggs and high mortality during hatching were primarily attributed to high levels of PCBs, DDE, dieldrin, and other organochlorines in the eggs of Red-necked Grebes in North America. Especially studies conducted in Central Alberta in 1971-1976 and in Southwest Manitoba in 1980-81 suggested that the effects of organochlorine contaminants contributed to a reduced productivity of Red-necked Grebes (Riske 1976, De Smet 1987, Stout and Nuechterlein 1999).

A slight decline in mean organochlorine residues (DDE and PCB) was noted in Red-necked Grebe eggs collected in Manitoba in 1986 compared to measurements on eggs collected in Manitoba in 1981 and Wisconsin in 1970 (Forsyth *et al.* 1994).

Regrettably, nothing is known about the organochlorine levels in Red-necked Grebe eggs and bodies after *c.* 1990.

It is also unknown whether organochlorines and other contaminants affect the productivity of Red-necked Grebes in Europe and Asia. Prestt and Jefferies (1969), however, found no evidence to suggest that organochlorine insecticide residues had any widespread effect on the breeding performance of Great Crested Grebes in Britain.

12.3.3 Changes in the Food Webs Chain: Eutrophication, Hypertrophication and Cyprinid Fish

From about the middle of the 19th century *Podiceps grisegena* and other Podicipedidae became increasingly

common in Europe and extended their northern distribution limits (see 9.1.6 for more details). This was once attributed to legal protection and climatic amelioration, but probably an even more important factor was the eutrophication caused by the use of fertilizers and incipient pollution (O’Donnell and Fjeldså 1997, Vlug 2000). As soil management improved, the wetlands became richer, with increasing biomasses of macrophytes. At the same time the biomasses of macroinvertebrates expanded. However, in many areas this increasing trend was reversed around the middle of the 20th century as intensive use of nitrate fertilizers leads to hypertrophic conditions in the wetlands. Many lakes went through a series of “trophic cascades”, until they reached a new equilibrium where large populations of cyprinid fish “control” the ecosystem (Fjeldså 2004) (see 9.1.5 and 9.1.6 for more details). Thus, advancing eutrophication caused an increase in numbers of cyprinid fish. However, Fjeldså (2004) wrote that it is important to note that even if the state of eutrophication remains constant, the wetland may shift between two distinctive equilibriums, according to the diversity of the fish fauna. Cyprinid introductions can profoundly alter the conditions in a lake, as these fish compete directly for food with Red-necked Grebes, and, in addition, they can impede indirectly the development of prey for the birds (see 9.1.5 for more details). As the macroinvertebrates are overgrazed by fish, the microplankton takes over, the turnover of nutrients accelerates, and the phytoplankton shades away the submergent macrophytes. In a very short time, another equilibrium in wetlands is established, which is characterized by short food chains (with much fewer macroinvertebrates): phytoplankton – micro-invertebrates – cyprinids – predatory fish/birds.

In many areas, these changes had a marked negative impact on the number of Red-necked, Black-necked and Slavonian Grebes:

Vlug (2000, 2002a, 2005) wrote that in ponds with very high number of Carp *Cyprinus carpio* or other cyprinids in Schleswig-Holstein, these fish impaired population density and breeding success of Red-necked Grebes (see also Steffens *et al.* 2013).

The Red-necked Grebe was locally a common breeder in the Czech Republic in the 19th century. During the first half of the 20th century it became rare. The breeding population of Black-necked Grebes in the Czech Repub-

lic also declined dramatically. The decline in numbers of both species has been related to an excess of nutrients due to fertilization in intensive agriculture (leading to hypertrophication), and high fish stocks in fish-ponds (see 9.1.5 for more details).

An assumed main cause of the decline of Slavonian Grebes in Sweden (46% between 1972 and 1996) was also food competition with cyprinid fish; as the eutrophication from agriculture increased, the cyprinid populations expanded (Douhan 1998, Stedman 2000).

Most negatively affected by fish populations are the species of grebes, which require shallow areas with clear water and rich submergent vegetation teeming with arthropods, such as Red-necked, Back-necked, Silvery and Hooded Grebes. For instance, the introductions of Rainbow Trout *Oncorhynchus mykiss* in Andean lakes drastically reduced the food supplies for Silvery Grebes (Fjeldså 2004). Rainbow Trout are also a problem to Hooded Grebes. These birds may only be able to breed successfully in wetlands where there are no fish. Lawrence (2012) wrote: “The main area where introduced Rainbow Trout are a problem is south of the Buenos Aires Plateau in the Strobel Plateau. The effect of the introduced trout there has been so great it has reduced Hooded Grebe breeding by more than 98% in the last 25 years. In addition to reducing food sources, the presence of trout leads to a change in the turbidity of the water, which prevents the growth of “vinagrilla” (= *Myriophyllum elatinoides*, JJV), the filamentous plant that provides indispensable nesting material for all the water birds that breed in the lagoons.”

When interpreting local and regional population trends in Red-necked Grebes, much more attention should be given to the role of fish populations, in addition to the external factors leading to eutrophication of the breeding waters.

12.3.4 Habitat Loss and Degradation

Artificially Changing Water Levels

In water bodies of which water levels can be controlled, changing water levels can degrade the habitat and affect the breeding population of grebes. In low water years many pairs cannot build a nest because the emergent vegetation is inaccessible to them. An example is Vejlerne in Denmark. This area originated from two former shallow estuarine inlets of the brackish Limfjord which has

been embanked by dikes since 1868. Vejlerne is a wet – and nowadays freshwater – area with channels, dikes, reed-beds, marshes and meadows. Until the mid 1960s a large population of Red-necked Grebes bred in Vejlerne, probably 60 to 100 pairs. Following a water level lowering after 1965 a large decline in numbers was observed, and by 1978 and 1979 only 13-14 pairs bred in the area (Kjeldsen 2008).

Drainage of Wetlands

The drainage of wetlands has been common practice in Europe for centuries, but the extent of this human intervention has increased significantly in the 20th century, and especially in the last 50 years of this century. Some two-thirds of the European wetlands that existed 100 years ago have been lost, leading to a substantial decrease in the number, size and quality of the natural habitats of large bogs, marshes, and small or shallow lakes (Silva *et al.* 2007). This has dramatically altered both the visual landscape and the number of breeding places for Red-necked Grebes and other Podicipedidae.

Desiccation and silting-up of wetlands caused by human factors and climatic changes led to a decrease in the number of breeding waters of Red-necked Grebes in Brandenburg, Germany, since the 1980s (Ryslavý *et al.* 2011).

Extensive drainage of wetlands also occurred in the pot-hole region of North America throughout the 20th century and likely reduced the populations of Red-necked Grebes in the southern part of its breeding range in North America (Stout and Nuechterlein 1999).

Riske (1976) wrote: “After land was initially cleared, many potholes and marshes have been actively drained at various times to provide more arable land. The total surface area of water useful to aquatic birds has therefore been declining. By 1950 agriculture in the United States had drained about one-half of the potholes in its portion of the “duck factory” pothole region of western North America (i. e. 60,000 square miles or 155,000 km²) (...). Canadian losses of aquatic habitat have, on a proportional basis, likely been similar.” As early as 1919, a warning for the welfare of grebes in Canada was sounded by Taverner (1919, cited in Riske 1976). He reported that “the drainage of many of their natural breeding grounds is continually reducing their numbers”.

Creation of Artificial Shallow Waters: Increasing and Decreasing Numbers

Not only drainage, but also road construction and building projects can result in loss of water bodies and marshes. In an effort to mitigate the impacts of this destruction, new wetlands are created, e. g. by flooding of meadows in northern Germany. These new artificial shallow waters are often colonized quickly after the inundation by large numbers of Red-necked Grebes and other waterbirds.

After the inundation the terrestrial plants die off and form a rich litter which constitutes a substrate for detritus feeding macroinvertebrates, and a complex aquatic food-web develops with many macrozoans (larger invertebrates and small vertebrates). They are important food organisms for Red-necked Grebes and many species of ducks. During the first years Red-necked Grebes have few competitors for this rich food source. It is also important that in the first years after flooding many marsh plants are abundant. This vegetation provides Red-necked Grebes with nesting places, and many macrozoans live among their underwater stems.

However, after a number of years a large decline in waterbird populations usually occurs. A number of factors are responsible for this decline. The detritus-based biomass of macroinvertebrates is substantially reduced when the plant litter from the first period has broken down. There is also a gradual increase in the number of invertebrate predators and of large fish which compete with Red-necked Grebes for food. However, it must be stressed that also without fish the decline of Red-necked Grebes and other waterbirds takes place. A number of years after the flooding a thick layer of mud often builds up, and the water turbidity increases. The result is that the submerged vegetation, in which macrozoans thrive, disappears. In many new ponds the emergent marsh plants also vanish after a few years, especially when there are large rising water levels (Vlug 2000, 2011) (see 9.1.4 for more details).

Destruction of Emergent Vegetation

Red-necked Grebes usually nest in flooded emergent vegetation. Destruction of this vegetation by dredging, burning, excavation of the rhizomes and roots, mowing during the summer, grazing of cattle and Greylag Goose *Anser anser* etc. often has a conspicuous and immediate local impact on the number of breeding birds (Vlug

2002a; J J Vlug). Removal of the emergent vegetation in fish ponds in Central Europe may decrease the number of breeding birds (Steffens *et al.* 2013).

12.3.5 Destruction of Clutches

There are reports of destruction of clutches of Red-necked Grebes in fish-ponds during the removal of the littoral vegetation in the breeding season, and of robbing of nests by humans (Markuze 1965, Kloskowski 2000, Dittberner and Dittberner 2006). Although the predation of eggs by man is only of local importance, it can sometimes cause serious losses, especially in fish-ponds.

The floating nests of Red-necked Grebes are vulnerable to boating activities; the wake generated by watercraft can sometimes wash eggs off nests (Semenchuk *et al.* 2007).

12.3.6 Disturbance of Incubating Red-necked Grebes, and Behaviour of the Birds in the Period After Egg-laying

Prior to breeding, Red-necked Grebes appear quite confident and usually behave conspicuously, often calling very loudly. During and after egg-laying, the birds suddenly become shy and may live very secretly, only now and then vocalizing from their hiding place in the vegetation. The skulking habits of Red-necked Grebes in the nesting period are described by Bent (1919), Bäsecke (1948), Fjeldså (1977b), Lammi (1983), Vlug (1985), and Südbeck *et al.* (2005).

Although this skulking behaviour diminishes the chance that the birds will be persecuted, and their eggs robbed, sporadic incidents of harassment and vandalism of course take place (see 12.3.5). It has been reported that human disturbance during laying and incubating the eggs causes the grebes to leave their nest and increases the predation risk (Onno 1960, Gordienko 1977, Dittberner 1996). However, many students systematically overstate the adverse effects of human disturbance and underestimate the significance of “habituation” and “tolerance”. Nesting Red-necked and Great Crested Grebes may be sensitive to disturbance early in the nesting cycle, but some pairs become extremely tolerant of repeated disturbance and may sit very tight when approached (Fjeldså 2004). Red-necked Grebes in water bodies near or in villages or towns do not care about people walking along the shore. The best examples of habituation to the presence of humans we find in the Great Crested Grebe

in The Netherlands. They often nest completely open to view in city channels, e.g. in Amsterdam. Along a landing stage in a yacht harbour in the town of Enkhuizen many pairs were nesting (c. 125 pairs in 2003). They were totally uninterested in the passing people (J J Vlug).

12.3.7 Hunting

Tens of thousands of Podicipedidae were shot for “fur” in the 19th and early 20th centuries (Vlug 2002a). Fjelds  (2004) stated: “One hundred years ago, hunting of birds for the lucrative women’s fashion industry was considered one of the principal threats to birds around the world – and was a direct motivation for the emergence of bird conservation movements (...). Few now living ornithologists and birdwatchers may realize the magnitude of this problem, which fortunately is history today. Grebes were hunted for their white “grebe-fur”, which is the dense, silky white belly plumage of mainly the larger species. It was especially used to make shoulder capes and mufflers (or “tippetts” in the original meaning of the word). Great Crested Grebes were killed commercially on a large scale to satisfy the demands of the millinery trade, and was quickly brought to the edge of extirpation in Western Europe.”

In “The Great Crested Grebe Enquiry, 1931” Harrison and Hollom (1932) wrote: “About the middle of the nineteenth century suddenly began a real interference with the Grebes in Britain. For a great many years there had been a regular traffic on the continent, and Grebe feathers, particularly the breast feathers as “grebe furs”, were fashionable in Britain. But not until 1857 did anyone realize that the market could, to some extent at least, be supplied from home. ... From 1857 onwards, there was a steady traffic in the birds, particularly in Norfolk, where many Broads were easily available for unscrupulous gunners. ... Writing in 1876, Johns remarks that it (Great Crested Grebe, JJV) was common thirty years ago in Norfolk, rare now. All the time shot-guns were improving enormously in efficiency and decreasing in price, so that they came within the practical scope of almost any man. Along with this came the increase in collecting, the mid-Victorian epoch of plumes and stuffed Kingfishers, the increased value of eggs as the species became more scarce. All this combined nearly wiped out the Grebes. Numbers in Norfolk, Stafford and Cheshire were greatly reduced, apparently none were left in Shropshire, and only one or two pairs stayed on at certain large private and protected lakes elsewhere.”

In the 1870s, c. 100,000 grebe skins were traded annually from Omsk in West Siberia (Fjelds  2004).

From the early 1890s until approximately 1906, tens of thousands of Western Grebes were shot for their “fur”, and large colonies such as that at Lower Klamath Lake, Oregon, were virtually wiped out by market hunters (Storer and Nuechterlein 1992). Writing about the Black-necked Grebe in North America, Bent (1919) remarked: “This species, as well as the western grebe, has suffered seriously from market hunting for the millinery trade, notably in the lake regions of Oregon and California, where thousands were shot every week during the breeding season; they were tame and easily killed. The breasts were stripped off, dried, and shipped to New York, where they were much in demand for ladies’ hats, capes, and muffers.”

As late as in 1924, three years after importation to the UK was banned, 135,956 skins of three grebe species were confiscated on one occasion (Fjelds  2004).

The use of Podicipedidae for clothing is in no way restricted to the 19th and early 20th centuries, and in some parts of Europe, Central Russia, and Kazakhstan grebes were still hunted for “fur” at least until the middle of the 20th century (Fjelds  2004).

In some places Red-necked Grebes are still being shot as they are accused of harming freshwater fisheries; until the 1960s this was normal practice in Central and East Europe. Blohm (1921), for example, received 108 freshly shot grebes (*P. cristatus*, *grisegena* and *nigricollis*) from the fish-ponds of Wallnau, Fehmarn, Germany, in May 1908, and later (May or June 1908) he participated in a hunt at Wallnau in which about 20 Red-necked Grebes were killed.

About 540 Red-necked Grebes were killed by shooting and drowning in nets in the fish-ponds of Yamat in the Volga delta in 1961 and 1962 (Markuze 1965).

12.3.8 Fishing Nets

In some areas, drowning in fishing nets represent a severe problem for grebes. Unfortunately, this problem is much overlooked, and the published evidence is mainly of anecdotal character (Fjelds  2004). There are records of drowned Red-necked Grebes in wintering areas such as Lake IJsselmeer, Netherlands (Piersma 1988b), and in

breeding areas such as Uckermark, Germany (Dittberner 1996). In the Baltic wintering areas, intense gillnet fisheries impose a high risk of entanglement and drowning for Red-necked Grebes and other diving birds. In the Pomeranian Bay, an important wintering area of Red-necked Grebes, intense set net fisheries are operated in the coastal zones as well as offshore and overlap with the resting and feeding areas of Red-necked Grebes. Hence, the birds are particularly susceptible to becoming entangled in the nets while diving for their preferred prey near the sea bottom (Helcom Red List Bird Expert Group 2013). According to Zydalis *et al.* (2009, *cited in* Helcom Red List Bird Expert Group 2013), tens to hundreds of Red-necked Grebes are caught annually in gillnets in the Baltic Sea, especially in Poland and Germany.

Markuze (1965) reported that many Red-necked Grebes, usually young ones, drowned in fishing nets in the fishponds of Yamat in the Volga delta. On some days 35 birds were found in the nets.

Because of the widespread introduction of monofilament fishing nets to provide protein in many developing countries, this threat to Podicipedidae may now spread rapidly. In the Lake Titicaca area in Peru/Bolivia, use of monofilament nets has escalated since about 1980. The locals report that many grebes drown in these nets, and the endemic Titicaca Flightless Grebes *Rollandia microptera* seem to have virtually disappeared from areas with intense mistnetting, and it may therefore now be critically endangered (Fjeldså 2004).

Similarly, the strong decline of Podicipedidae in East Africa since the 1980s may, to a large extent, be the result of introduction of *Tilapia* and the use of fishing nets almost everywhere. Use of fishing nets may also be one important factor contributing to the extinction of the Alaotra Grebe *Tachybaptus rufolavatus* (Fjeldså 2004).

12.3.9 Offshore Wind Turbines

In their wintering areas at sea, Red-necked Grebes mostly swim, but between different resting sites the birds generally fly. Migration movements usually occur at dawn, night and dusk, and the species has only low flight manoeuvrability. Hence, Red-necked Grebes are particularly at risk of colliding with offshore wind turbines and other obstacles, especially in unfavourable conditions with poor visibility (Helcom Red List Bird Expert Group 2013). The species scores high in the wind farm

sensitivity index (Garthe and Hüppop 2004, *cited in* Helcom Red List Bird Expert Group 2013).

12.4 Predation

12.4.1 Predation on Adults and Chicks

Predation on Podicipedidae is only infrequently recorded, but it may have played a significant role in shaping the behaviour of grebes. Their nocturnal migration may mainly be determined by predation risks relating to their poor manoeuvrability (Fjeldså 2004).

Eagle Owl *Bubo bubo*, Great Horned Owl *B. virginianus*, White-tailed Eagle *Haliaeetus albicilla*, Goshawk *Accipiter gentilis*, and Peregrine Falcon *Falco peregrinus* have been cited as likely predators of adults, which are most vulnerable during incubating the eggs (Wobus 1964, De Smet 1987, Stout and Nuechterlein 1999).

There are observations of White-tailed Eagles hunting Red-necked Grebes successfully at wetlands in Schleswig-Holstein (e. g. T Herfurth).

Eichhorst (1985) studied the Red-necked Grebe on Rush Lake, Winnebago County, Wisconsin. Great Horned Owls *Bubo virginianus* killed incubating adults at 9 of 138 nests. The owls left the carcasses on the grebe nests and consumed the grebes over a period of several days, until only the wings and some feathers remained. During one visit Eichhorst (1985) found the fresh remains of a decapitated Red-necked Grebe lying belly up on a nest.

Peregrine Falcons *Falco peregrinus* may represent a serious threat when grebes are in the air. In Iceland, Slavonian Grebes were occasionally taken by Gyrfalcons *Falco rusticolus* when flying between lakes in the light summer nights (Fjeldså 2004).

Goshawks *Accipiter gentilis* may take some young Red-necked Grebe chicks from forest ponds, and in more open wetlands the main aerial predators are Marsh Harriers *Circus aeruginosus*, Red Kites *Milvus milvus* and White-tailed Eagles *Haliaeetus albicilla* that take grebes out of the water by swooping low.

Perkins *et al.* (2005) used time-lapse video cameras to determine the causes of nest failure of Slavonian Grebes. The aquatic Eurasian Otters *Lutra lutra* were the most

frequent predator filmed. They took two clutches and an adult Slavonian Grebe plus chicks from nests.

A number of (semi aquatic) land predators such as Raccoons *Procyon lotor* and the American Mink *Mustela (Neovison) vison* may occasionally be a menace to grebes nesting or loafing in narrow vegetation zones near the shore line, or in water-bird colonies. Because of its aquatic habits, the American Mink can also threaten grebe nests in reed-bed mosaics and islands some distance from the shore. This is a serious predator on nesting Red-necked Grebes and other Podicipedidae in some areas in North America, South America and Europe, as it returns repeatedly to the colonies, taking birds off nest at night. Often the inverted skin with the legs of the killed bird, sometimes also with the wings or even sternum attached, is found near the nest (Storer and Nuechterlein 1992, Fjelds  2004).

The American Mink is a terrible danger for the already diminishing population of Hooded Grebes *Podiceps gallardoi*. One of the only five colonies found in 2011-12 was destroyed by one individual mink in a single event, leaving 33 adult Hooded Grebes dead and some 40 eggs abandoned (Imberti *et al.* 2011, Roesler *et al.* 2012).

Nuechterlein and Buitron (2002) discovered that many Red-necked Grebes on Lake Osakis, Minnesota, often abandon their nests for extended periods during the night. By leaving their nests, the birds may be decreasing their exposure to nocturnal predators that prey on adults, such as American Mink and Great Horned Owls *Bubo virginianus* (see 16.4.4 for more details).

Many aerial and some (semi aquatic) land predators may be a threat to grebe chicks, e.g. gulls *Larus*, crows *Corvus*, Marsh Harrier *Circus aeruginosus*, Red Kite *Milvus milvus*, Grey Heron *Ardea cinerea*, and American Mink *Mustela (Neovison) vison* (Wobus 1964, Vlug 2002a; J J Vlug).

When not on their parent's back, small grebe chicks may be taken by large predatory fish, such as Rainbow Trout *Oncorhynchus mykiss* or Pike *Esox lucius* (Simmons 1955, De Smet 1983, Stout and Nuechterlein 1999, Imberti *et al.* 2011). Although there are no observations of fish predation on Red-necked Grebe chicks, there are records of predation of Pike on Little Grebes (Bandorf 1970). Bannerman (1959), writing about Little Grebes, stated: "On water where pike are prevalent these voracious fish take toll of any young birds which come within their reach

and many are the little grebe ducklings – and their parents – which fall victim to them. On Fritton Lake in Suffolk, where the pike take a heavy toll, Ticehurst has recorded how a little grebe has been taken whole from the belly of one of these fish."

Imberti *et al.* (2011) stated that the introduction of Rainbow Trout *Oncorhynchus mykiss* on the breeding lakes of the Hooded Grebe *Podiceps gallardoi* is not only a problem because of competition for the grebe's main sources of food, but also because the trout voraciously prey on nests, chicks and possibly even adult Hooded Grebes.

12.4.2 Predation on Eggs

Egg losses caused by predators vary from area to area, but low breeding success of the Red-necked Grebe is rarely attributed to depredation. Predators on eggs of Red-necked Grebes and other Podicipedidae include crows *Corvus*, gulls *Larus*, Marsh Harrier *Circus aeruginosus*, Red Kite *Milvus milvus*, Coot *Fulica atra*, American Coot *F. americana*, Great Blue Heron *Ardea herodias*, American Mink *Mustela (Neovison) vison*, Raccoon *Procyon lotor*, Muskrat *Ondatra zibethicus*, Eurasian Otter *Lutra lutra*, Red Fox *Vulpes vulpes*, Stoat *Mustela erminea*, Pine Marten *Martes martes* and Wild Cat *Felis silvestris* (Onno 1960, Wobus 1964, Borrmann 1969, Gordienko 1977, Plath 1978, Zimmermann and Schieweck 1988, Dittberner 1996, Cullen *et al.* 1999, Stout and Nuechterlein 1999, Kloskowski 2000, Stedman 2000, Nuechterlein *et al.* 2003, Perkins *et al.* 2005).

Raccoons *Procyon lotor* have become significant predators on grebe, loon and diving duck nests since the 1940s because of their range expansion into the Canadian Prairie Pothole Region during this period. They appear to be the major predators on grebe eggs in the Manitoba potholes and in Minnesota. Feral populations of Raccoons, originating as escapees from fur farms, also appear to be an increasing threat to grebe eggs in Central Europe, especially of eggs in nests placed near the shore line (Stout and Nuechterlein 1999, Fjelds  2004).

Although Raccoons are significant predators on grebe eggs in some areas, the main egg predators in most districts are crows *Corvus* and gulls *Larus*. The incubating Red-necked Grebes defend their nests from egg predators by jabbing with their bill and giving a Hissing-call, but often in vain. Human disturbance during the egg pe-

riod causes the grebes to leave their nest and increases the predation risk by crows and gulls. There are reports of Carrion Crows *Corvus corone* specializing in robbing eggs in colonies of Great Crested Grebes after human intrusion (Vlug 1983). Eggshells, with a hole laterally, are usually found on land, sometimes on an open or somewhat elevated point on the adjacent shore meadow (Stout and Nuechterlein 1999, Fjelds  2004).

Since nest-sites near the shore are most vulnerable to mammalian predators while those far offshore are most exposed to wave action and egg-stealing gulls, these threats play against one another when grebes choose nest-sites. Eggs are easily replaced but especially mammalian predators threaten the lives of incubating adult grebes. Probably, the nest-site selection of grebes evolved primarily as a response to this threat and less to wave action (Fjelds  2004).

12.5 Losses by Inter- and Intraspecific Competition

12.5.1 Egg Losses

Egg Losses by Competition with Great Crested Grebes
In wetlands where Red-necked and Great Crested Grebes co-occur, abandonment of nests due to aggression by Great Crested Grebes may contribute to egg losses in Red-necked Grebes (Kloskowski 2000; J J Vlug).

Egg Losses by Intraspecific Conflicts

Egg losses are also attributed to intraspecific conflicts. Sometimes, incubating birds can be driven away from their nests by neighbouring pairs (see Fig. 97). An incubating bird disturbed by a threatening neighbour could possibly knock one of its eggs into the water as it hurriedly leaves its nest. High rates of intraspecific aggression are noted where nest densities are high and are believed to contribute to many eggs being found beside active nests at these sites (Kevan 1970, De Smet 1983).

12.5.2 Chick Losses by Intraspecific Conflicts

Chick Losses by Intraspecific Territorial Conflicts

Birds, especially in areas of high nesting densities, may spend a disproportionate amount of time in agonistic encounters during which chicks fall off their parent's back onto the water and are left unattended, and occasionally are killed by other pairs (J J Vlug, northern Germany). Ohanjanian (1986) wrote that attacks on

neighbouring chicks were observed frequently when, during clashes at territorial boundaries, the young followed the wrong adults in confusion. They were immediately pecked and although no mortality was directly observed the author saw that one chick appeared seriously hurt (Creston, British Columbia).

Infanticide by Own Parents

Parental aggression against small chicks sometimes occurs. Kloskowski (2003a) observed parent Red-necked Grebes pecking and chasing away their chicks in three two-chick broods in which later one of the chicks died. In two of these broods both parents attacked both chicks on the same occasions. In the other family, both adults pecked the runt only. After the death of the younger chicks (presumably by sibling rivalry), parental hostility ceased except in one family where one adult continued pecking and shaking the surviving chick even while carrying it. In none of the observed pairs did the parents deny any chick access to food.

In July 2001 J J Vlug watched a pair of Red-necked Grebes with one small chick on Rantzauer Teich, northern Germany. Initially, the chick was carried on the back of one of its parents. It was not being fed and later, after it was thrown into the water, both parents repeatedly pecked it severely. The chick swam away and disappeared.

Although adult Red-necked Grebes may occasionally kill their own small young, which are unlikely to prosper, it is never directly observed, and it is sure that sibling rivalry is a more serious threat to the smallest and weakest chicks (see below).

Ebbutt (1986) described a parent Great Crested Grebe killing its own small chick. He observed a family with four chicks at Les Grangettes on Lac L man (Lake Geneva), Switzerland: "Each parent carried two chicks, half hidden on its back. From time to time, both adults stretched and flapped their wings, making the chicks swim around with them. ... Suddenly, one of the adults seized a chick swimming in front of it and shook it, then threw it into the water and struck it savagely on the head. Was it a "slowcoach", or had it been "disobedient"? In any case, it seemed to me to be smaller than its brothers and sisters. It tried desperately to climb on to the old nest, but the adult continued to attack it until it lay motionless on the water, quite dead. During this time, the other adult grebe had stayed apart with the three remaining chicks."

Sibling Rivalry

Sibling rivalry is probably responsible for many chick losses (Wobus 1964, De Smet 1983, Ohanjanian 1986, Kloskowski 2003a) (see 16.5.12 for more details). It seems that asynchronous hatching and its consequence, the advantage for survival being placed on the first-hatched young, is one of the adaptations to cope with food scarcity.

During the back-brooding period, the benefits of size and strength given to the first-hatched young are enhanced by the establishment of a dominance hierarchy within the brood. In this period, the parents do not interfere in sibling competition, and it is suggested that they allow biased food distribution and consequently even brood reduction (Kloskowski 2001a). The larger chicks may obtain most food and gain initial access onto their parent's back by pecking and chasing the smaller siblings (De Smet 1983, Ohanjanian 1986, Kloskowski 2003a). The subordinates never retaliate and may eventually die. After 1-2 hours of convulsive head shaking, the runts are too weak to keep the head above the water surface. The parents attempt to feed the dying chicks even when these are unable to reach the parent's bill. However, the parents show no preference for them and transfer the prey to other chicks when approached (Kloskowski 2003a).

In the fish-ponds of South-East Poland, the chicks of the largest broods had a higher probability of survival until fledging than the one-chick-broods. The food scarcity in these ponds possibly results in partial clutch abandonment as well as chick mortality thereafter in the same families (Kloskowski 2003a).

12.6 Entanglement of Chicks in Vegetation

For the first few days of life young grebes are weak swimmers, so feeble that on open water after they have tried to escape by diving several times it is an easy matter to capture them by hand. At this stage some become entangled in floating algae or submerged vegetation and have not the strength to extricate themselves (Munro 1941).

12.7 Body Parasites and Diseases

Parasites of birds come in a bewildering array of forms, ranging from relatively large organisms such as ticks, fleas, blood-sucking flies, mosquitoes, parasitic worms (helminths), mites, lice, and leeches (see 12.7.1 and 12.7.3), to microscopic species of viruses, bacteria, fungi,

and protozoa (see 12.7.4). These latter sometimes qualify as pathogens that cause what we typically call a "disease", a clinically abnormal state that may kill or at least compromise an animal's performance. Fortunately, only a relatively small fraction of microscopic organisms cause disease. Those that do, however, can be particularly devastating to bird populations (see 12.7.4). In many cases pathogens are transmitted through the blood or other fluids by vectors such as mosquitoes or ticks (Koenig 2016).

12.7.1 Parasitic Worms (Helminths)

The aquatic existence of Podicipedidae and the wide range of prey taken by individuals and species of grebes are reflected in the extensive range of helminths (parasitic worms) infecting the birds: 113 species of flukes (digenetic trematodes or digenes Digenea; of the groups of trematodes Trematoda, members of only one, the infraclass Digenea, are known to parasitize grebes), 86 of tapeworms (cestodes), 13 of spiny-headed worms (acanthocephalans), and 37 of roundworms (nematodes), most of which have aquatic life cycles (Storer 2000b).

Storer (2000b) wrote: "Grebes, which may seldom, if ever, come on land, are ideal hosts for parasitic worms with aquatic intermediate hosts. Grebes feed almost exclusively on aquatic animals, and the eggs of the parasites are excreted by the grebes directly into the water where they or their larvae can infect intermediate hosts. It is not surprising, therefore, that grebes carry a heavy load of tapeworms. It is not unusual to find large numbers of several species of this group of parasites in the intestines of a single bird... The diversity of internal parasites is increased in the grebes that breed in fresh-water habitats and winter on salt water, because each of these habitats has its own contingent of parasites and their intermediate hosts not found in the other. The long association between these parasites and grebes is reflected in the large proportion of the genera and species of these worms that specialize in grebes. Grebes' habit of picking up land-based insects from the surface of the water or from emergent vegetation may subject them incidentally to parasites with land-based life cycles. This may increase the parasite load of the grebes but is, of course, a dead end in the life cycle of the involved parasite."

One family, one subfamily (each with the exception of a single species), several genera, and 104 species of helminths are considered Podicipedidae specialists, as

are most of the species of ectoparasites. Of the well-studied species of grebe helminths specialists, almost all have been found in more than one grebe species and many more in more than one grebe genus. This is believed related to the fact that even grebes adapted for taking particular kinds of prey will usually take many other kinds. Thus, where several species of grebes are sympatric, there is a considerable overlap in diet and consequently, overlap in the intermediate host ingested (Storer 2000b).

Grebes have greater numbers of genera and species of parasites than divers (loons). Those shared by grebes and divers are mainly generalists. This agrees with the unrelatedness of the two groups. Several factors appear to have contributed to the differences in the two parasite faunas. Most divers spend the breeding season on bodies of oligotrophic water, which have fewer species and numbers of potential prey than the eutrophic waters where most grebes nest. Much of the difference can also be attributed to the greater number of genera (7 in grebes *versus* 1 in divers) and species (22 *versus* 5) in the two groups of the birds, and the wider distribution (nearly cosmopolitan in the grebes *versus* holarctic in the divers). The difference is also consistent with the grebes' greater evolutionary age and degree of parasite host specificity. Other factors affecting the differences in the two helminth faunas are a presumed marine origin for the divers in contrast with a fresh-water one for the grebes. Furthermore, the smaller size of grebes for which a greater number of prey species of optimal size is presumably available, and grebes' greater diversity in bill form and foot proportions which are associated with specializations for taking a greater variety of prey, may be involved (Storer 2002).

The maximum number of parasite species reported for any grebe is 123 for the Little Grebe. A total of 113 named species are reported for the Red-necked Grebe. The recorded endoparasites of *Podiceps grisegena* are 107 species of helminths (parasitic worms): 36 species of flukes Digenea or digenetic trematodes, 41 species of tapeworms Cestoda, 9 species of spiny-headed worms Acanthocephala, and 21 species of roundworms Nematoda. The 6 species of external parasites of the Red-necked Grebe belong to the leeches Hirudinea (1 species), mites Acarina (2 species), and lice Phthiraptera (3 species) (Storer 2000b).

Stock and Holmes (1987) identified and counted all parasitic worms of 96 birds belonging to four species of

grebes taken from lakes in Alberta. Among them were 33 infected Red-necked Grebes. The mean number of intestinal helminths per Red-necked Grebe was 3,116 (the range of worms per bird was 326–10,459): 1,217 individual flukes Digenea (Trematoda), 1,849 Cestoda, 8 Acanthocephala and 42 Nematoda.

There is little direct evidence that parasites (and pathogens, see 12.7.4) limit grebe numbers. In part this is because parasites are difficult to study, and in part because they usually operate in conjunction with starvation and other stress factors such as toxic chemicals to cause mortality and poor breeding performance (Birkhead *et al.* 2014). However, the large number of intestinal helminths per bird makes it likely that they will have a negative impact on the health of the grebes.

Munro (1941) writing about grebes in British Columbia, stated: "Each autumn in the Okanagan, and elsewhere also, numbers of Holboell's Grebe and Western Grebe are found dead, or in a dying condition. In the case of the first-named the subjects are chiefly young of the year; in the second both young and adults are affected. In some years this condition reaches almost epidemic proportions. Specimens are emaciated and the visceral tract is bile-stained; there is no food in the digestive tract and the stomach contains a quantity of feathers greatly in excess of the amount usually found in healthy birds and impacted into a hard bolus which also is stained green with bile. It seems doubtful that these hard lumps of feathers could be digested or could permit the passage of food and this condition may be a factor contributing to the death of the grebe. Sick birds are listless and usually remain close to shore; if pursued they dive but are incapable of remaining under water for long. Segmented tapeworms were found in the intestines of all the sick birds which had been collected for examination but none was present in other specimens that had been found dead, which suggests that the parasites leave the dying host. In other specimens examined the lower part of the tibiotarsus was swollen to double the normal size from the presence of a mass of wire-like nematodes. The precise nature of the malady has not been determined but it is assumed to be the result of excessive infestation by internal parasites."

12.7.2 Helminths, Feather-eating and Pellet-casting

Red-necked Grebes and other Podicipedidae eat large quantities of their own feathers (see 14.8 for more de-

tails). Several hypotheses have been put forward to account for the feather eating habit and pellet-casting in causal or functional terms. Piersma and Van Eerden (1989) stated that the paucity of endoparasites in the upper part of the alimentary tract of grebes compared to species not producing pellets but with an overlapping diet, suggests that regularly emptying the stomach by pellet-casting may not only remove the hard remains of fish or chitin but also the various stages of ingested helminths or other prospective endoparasites.

12.7.3 External Parasites

Six species of external parasites are found in *Podiceps grisegena*. They belong to the leeches Hirudinea (1 species), mites Acarina (2 species), and lice Phthiraptera (3 species) (Storer 2000b).

Leeches Hirudinea of Grebes

Members of one genus of parasitic leeches, *Theromyzon*, called “duck leeches”, parasitize a variety of water birds, including *Podiceps grisegena* and other grebes. These leeches are said to be attracted by heat and by the odour of the oil-gland secretion, which the birds spread on their feathers in the process of preening. Once on the bird, the leeches move forward, following the lie of the feathers, to the head where, most frequently, they attach themselves in the nasal passages or, more rarely, around the eyes. In the latter case, there is a tendency for both adult and young leeches to attach themselves under the nictitating membrane and for young, also to attach themselves under the eyelids. In both sites, they are safe from removal by the hosts’ scratching. Leeches in the nasal passages are also safe from this scratching, but small leeches sometimes are ejected by the birds’ sneezing. Leeches entering through the nares may penetrate further into the body (trachea, lungs). Other uncommon places of attachment include the mouth, legs, feet, breast and cloaca. Parasitism by leeches is known to result in blindness or death of waterfowl, especially the young (Storer 2000b).

From the very few records, it might be thought that leeches rarely feed on grebes, but the study of Gallimore (1964, cited in Storer 2000b) shows that where a species of *Theromyzon* is common, all local species of grebe may be subject to attack by these parasites. On the Red-necked Grebe he found *Theromyzon* “*trizonare*”.

Stout and Nuechterlein (1999) wrote that leeches in nostrils appeared to cause some breathing difficulty in Red-

necked Grebes being handled for banding. Near Yellowknife, Northwest Territories, one juvenile Red-necked Grebe was found weak and debilitated, apparently as a result of leech infestation. The bird was caught by hand and had leeches under its wings, on its cloaca and legs, and in its eye (Fournier cited in Stout and Nuechterlein 1999).

Mites Acarina of Grebes

Although mites are perhaps the most widespread of parasitic arthropods, the number of species known from Podicipedidae is small and limited to forms inhabiting the nostrils and feathers. This is presumably a result of grebes’ extremely aquatic habits and limited physical contact with other birds or places frequented by other birds on land. Because feather mites often occur in very high population density, it is unlikely that most groups of external, feather-inhabiting mites are in any way detrimental to their hosts (Storer 2000b).

Lice Phthiraptera of Grebes

Lice are external parasites of warm-blooded animals. The lice of grebes are very small insects, the largest reaching a length of c. 10 mm. Their mouthparts are adapted for chewing. All the lice of birds feed to some extent on feathers. According to Storer (2000b) they are rarely a pest on healthy wild birds, although they may become a problem on ailing ones. Kloskowski *et al.* (2016) visually examined Red-necked Grebes for the presence of amblyceran chewing lice during the 2000-2015 breeding seasons in eastern Poland. Only one louse species, *Pseudomenopon dolium*, was recorded. Amblyceran prevalence was low; four young birds (2.7%) were found infested out of 147 banded individuals (66 adults and 81 chicks). However, all infested Red-necked Grebes bore heavy parasite loads. Negative consequences of infestation for physiological condition were indicated by low haemoglobin and total protein values when compared with same-age non-infested birds (Kloskowski *et al.* 2016).

The lice of grebes are few in number of species. The reason for this is probably not that grebes are water birds, because petrels, gulls, auks, and most other waterbirds are infested with many species. Instead, the reason appears to be related to the nest platforms built by the birds themselves. Each nest is separated by water from the next one, is vigorously defended, and thus is readily accessible to few other birds (Storer 2000b).

12.7.4 Bacterial and Viral Diseases

Two of three autopsied Red-necked Grebe chicks from Astotin Lake, Alberta, were found to have a septicaemic disease; *Staphylococcus* bacteria were isolated from cultures of the heart and liver of the birds. Diseases of this type can be fatal, but the mortality rates from *Staphylococcus* bacteria are unknown (Kevan 1970).

Other bacterial diseases including avian cholera and botulism annually kill thousands of waterfowl in North America, among them Red-necked, Slavonian and Black-necked Grebes (Jehl 1996, Canadian Cooperative Wildlife Health Centre 2005).

It seems likely that viral diseases are important causes of illness and death in Red-necked Grebes. However, almost nothing is known about these diseases. Lebarbenchon *et al.* (2015) sequenced six type-A low pathogenic influenza viruses from 14 North American Red-necked Grebes. The grebe viruses were closely related to North American duck viruses. The genetic and temporal subtype consistency between the duck and grebe isolates suggest spillover events, potentially enhanced by feather eating.

A large loss from a single epizootic occurred at the Salton Sea, California, in 1992, when an estimated 155,000 birds, primarily Black-necked Grebes, died from an undiagnosed cause. Reoccurrences of that unknown malady have continued to kill substantial numbers of Black-necked Grebes throughout the 1990s (Friend 2002).

13. Movements

Throughout its range the Red-necked Grebe shows a complete, short- to medium-distance migration, typically between the inland freshwater breeding areas and the marine wintering areas. The migratory routes are more east-west than north-south in direction (Fjeldså 2004). The birds often migrate in small flocks. The autumn movements include a moult migration, in which many birds move to moult sites to undergo a simultaneous (flightless) wing moult before proceeding to the wintering areas. All the known moulting areas are en route to the wintering areas, or on the wintering grounds. An especially noteworthy feature of the North American migration patterns is the autumn migration corridor through Lake Superior. The origin and number

of summering birds are enigmatic (Vlug 1996, Stout and Nuechterlein 1999).

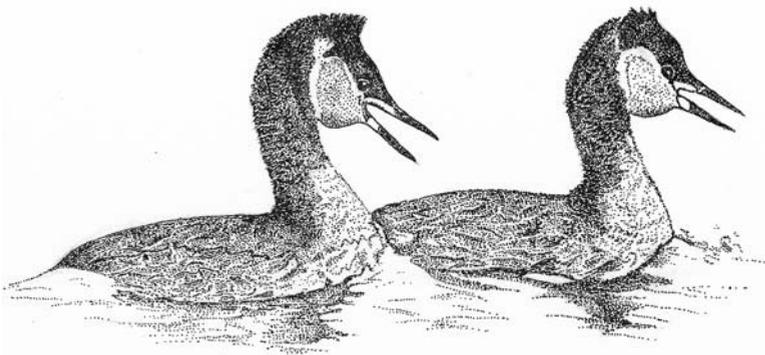
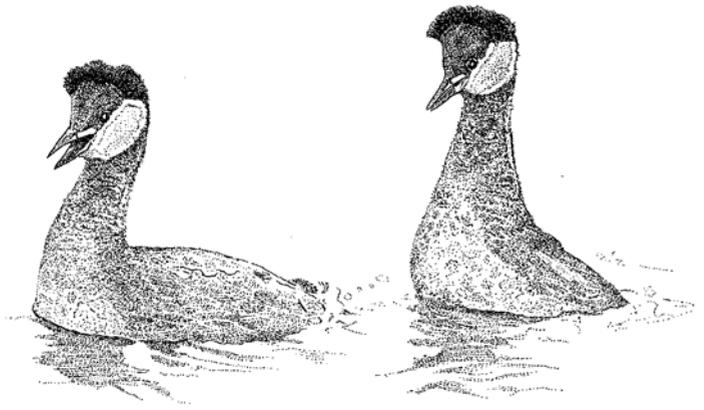
13.1 Timing and Arrival on the Breeding Waters

13.1.1 Timing and Arrival on the Breeding Waters of the Population in Europe-West Asia

Before the dispersal to the breeding lakes in northern Germany and Denmark, the birds are often gregarious along the coast of the Baltic Sea, e.g. off the island of Fehmarn: on 8 April 1989 180 (F Spletzer), on 25 April 2012 70 (C Engelhardt, ornitho.de), on 24 March 2016 100 (B Koop), and on 6 May 2017 120 birds (a number of them were possibly transients) (M Rieck, J J Vlug), along the Baltic Sea coast of Usedom, Mecklenburg-Western Pomerania: on 26 April 1983 120 individuals (Müller 1985 erroneously reported c. 1,200 birds) (Sellin and Schirmeister 2010), and near Hyllekrog, Lolland, Denmark: on 25 April 2012 196 birds (Christensen 2012). In these, usually loose, assemblages the birds often call loudly, show courtship behaviour and agonistic displays, and it must be assumed that the beginning of the pair formation occurs on the wintering grounds just before and during the spring migration, especially in the aggregations (Folkestad 1978, Stout and Nuechterlein 1999, Vlug 2002a) (see 13.7).

Throughout the range of the nominate race *grisegena*, the breeding waters are normally reoccupied from late March to early May (Cramp *et al.* 1977). The first arrivals on the European breeding waters are usually in March/April, related to the latitude and the severity of the winter (Vlug 2002a). In mild winters, the first Red-necked Grebes regularly arrive in Schleswig-Holstein, northern Germany, in February, after normal winters in late March and after cold winters in early April (Scholl 1974). In Europe, the grebes usually appear on the breeding lakes when these are completely free from ice, and often much later (Wobus 1964, Kuročkin 1985).

In southern areas, the birds enter their nesting grounds on average much earlier than in northern areas. Red-necked Grebes reach their breeding waters in southern Sweden in March, in central Sweden in April and in northern Sweden in May (Larsen and Wirdheim 1994). Red-necked Grebes observed along the seacoast in May, are probably on their way to the northern breeding areas; for example, on 11 May 1985 250 birds near Holmsund



(Västerbotten), North Kvarken, Gulf of Bothnia (Risberg 1990).

In the southern parts of European Russia and the Ukraine, Red-necked Grebes reappear from mid- and late March to mid-April (Kuročkin 1985, Buchko *et al.* 1995). In Estonia, the birds arrive in late April and May (Jogi 1970, *cited in* Kuročkin 1985). In the southern part of the Murmansk Region, the grebes reach the breeding waters from 14 May – 9 June (on average 24 May) (Bianki *et al.* 1993, *cited in* Bakkal *et al.* 2002).

After the arrival of the first birds, the reoccupation of the German breeding sites by the majority usually takes 2-3 weeks, at most up to 4-5 weeks (Wobus 1964, Scholl 1974). As a rule, the breeding waters in Brandenburg and Schleswig-Holstein are occupied by most grebes by mid-April (Scholl 1974, Schmidt 1983); however, several birds arrive as late as the first half of May (Scholl 1974, J J VlUG).

It seems that on average the arrival in western Asia is somewhat later than in Central Europe. In the lakes of the Barabinskaya Step', near Novosibirsk, the birds reappear in late April, and there is a strong migration until mid-May (Kuročkin 1985). The Red-necked Grebes in Kazakhstan appear on the breeding lakes from late March to early May (Gavrilov and Gavrilov 2005, Wassink and Oreel 2007). The first birds reach the breeding lakes of Naurzum, North Kazakhstan, between 13 and 23 April (Gordienko 1981). In the delta of the River Ili (Ile), in the south-east of Kazakhstan, they arrive in early springs in late March, sometimes even in early March, but usually *c.* 10 April (Dolgushin 1960).

13.1.2 Timing and Arrival on the Breeding Waters of the Population in East Asia

In eastern Asia, the grebes usually arrive early in the south, on Lake Khanka (*c.* 45° N) from late March (Kozlova 1947, *cited in* Wobus 1964) until the second half of April (Kuročkin 1985). They often appear in northern areas much later, on Kamchatka (*c.* 55° N) in late April and in May, and in the basin of the Anadyr (*c.* 65° N) in the last third of May (Dement'ev and Gladkov 1951/1969, Kuročkin 1985). The birds begin to arrive at the breeding lakes in Hokkaido from April onwards (Brazil 1991). In the Tokachi district of this island, the number of birds observed peak in the second half of May (Fujino *et al.* 2006).

13.1.3 Timing and Arrival on the Breeding Waters of the Population in North America

In North America, the species winters primarily on marine waters along the Atlantic and Pacific coasts and, to a limited extent, on the Great Lakes (Stout and Nuechterlein 1999). The birds wintering along the Atlantic coast occupy the eastern portion of the breeding range, and those from the Pacific coast the western portion. Band recoveries and contaminant data in eggs suggest that the breeding ranges of the two wintering populations diverge somewhere in western Saskatchewan (Forsyth *et al.* 1994, Stout and Nuechterlein 1999). The birds move from the Atlantic and Pacific coasts to the breeding areas and typically arrive on the breeding lakes in spring shortly before the complete break-up of the ice, even when large areas of floating ice remain (from late April to mid-May) (Stout and Nuechterlein 1999). Numbers may increase to a peak in the first week of June (Riske 1976, see below). In North America, like everywhere else, the grebes enter their nesting grounds on average much earlier in southern than in northern areas.

Eastern Migrants

The migratory routes of the Atlantic birds in spring appear to be similar to those used in autumn (see 13.3.3), but greater numbers are observed on Lake Ontario, and the diurnal passage through Lake Superior is much less pronounced. Lake Ontario appears to be especially important as a spring stopover area, with large build-ups of migrant flocks in several areas (Stout and Nuechterlein 1999). Large spring diurnal flights along northern Lake Ontario at Oshawa, Ontario, were discovered in 1997 with up to 881 birds in 1.5 hours on 21 April (Hoar, *cited in* Stout and Nuechterlein 1999).

The birds begin to assemble for the spring migration in March and April, when large flocks are observed along the northern Atlantic coast. Migratory flocks are recorded inland to the southern Great Lakes region from late March to May; peak numbers are seen in March in Pennsylvania and in late April farther north. The grebes migrate through the western Great Lakes region from early April to May; the peak passage is in late April and early May. Migrants are recorded in northern Lake Huron and Lake Superior as late as early June. From the Great Lakes, they continue to travel in a north-westerly direction through late April and into May bringing them to the larger lakes in the breeding range, and from there dispersal takes place to the nesting lakes, the most remote

of which are reached early in June (Palmer 1962, Stout and Nuechterlein 1999, McWilliams and Brauning 2000, Sandilands 2005).

Migrants usually reach southern Manitoba in mid-April and peak around the end of the month. Large concentrations are frequently recorded at Oak Hammock Marsh (maximum 530 or more on 23 April 1988), Seven Sisters dam (maxima 890 on 28 April 1995 and 800 or more on 27 April 2001), and elsewhere along the Winnipeg River. These birds typically rest for just one day, arriving and departing overnight; their final destination could be anywhere in western Canada. Smaller numbers of migrants continue to be seen throughout May (De Smet 2003). Detailed studies of the species at Turtle Mountain Provincial Park showed a similar chronology; in 1981, for example, the first birds arrived on 18 April, and about 50% returned within 10 days. Arrival progressed steadily until 10 May, at which time about 90% of the eventual nesting population were on territory, yet influx of breeding pairs continued until late May and early June (De Smet 1983).

Western Migrants

The spring migration of the Pacific birds in British Columbia may begin as early as late February and early March in the southern areas of the province, depending on open water in the interior, but peaks in the latter half of April. The main movement through the Chilcotin-Cariboo occurs during the second and third weeks of April and in the Peace Lowlands during the first half of May (Campbell *et al.* 1990).

The Red-necked Grebe in Alberta arrives on the breeding grounds in the last two weeks of April (Semenchuk 1992). The first arrivals in central Alberta are in late April and early May. On Pine Lake, central Alberta, during 1971-73, following the break-up of the ice, the numbers of *grisegena* increased to a peak in the first week of June and thereafter remained relatively constant till mid-July. After the end of May, new arrivals that were presumably transients could be identified by their rather furtive behaviour and the fact that they remained in tightly massed rafts usually centrally on the broadest expanse(s) of water. During the summer months, additions to the Pine Lake population could have come from nearby pot-holes, the resident *grisegena* of which had experienced recurring nest losses or suffered the loss of a mate (Riske 1976).

The first birds usually reach southern Yukon in the first week of May (earliest 29 April 1995), and the numbers of migrants peak in the middle of the month, with groups of 30-100 birds occasionally seen. In central Yukon, the first birds, and the highest numbers, are seen in the third week of May (earliest 16 May 1996). There is only one spring record in northern Yukon, from Old Crow Flats on 30-31 May 1976 (Sinclair *et al.* 2003). The main migration through the interior of Alaska is in mid-May (Kessel, *cited in* Stout and Nuechterlein 1999).

13.2 Summering

13.2.1 Summering of Young Birds and Failed Breeders

An unknown number of Red-necked Grebes do not move to the breeding waters, or visit these only for a short time, and spend the summer on water bodies, often large and unsuitable for breeding. It is frequently assumed that these summering (non-breeding) Red-necked Grebes are young birds which are physiologically incapable of breeding. However, second calendar year birds attain the nuptial plumage and are usually sexually mature. There are records of Red-necked Grebes breeding successfully at this age. However, the majority of these young birds do not breed and spend the summer away from the breeding waters (see for more details 11.1). Later in the season, the number of summering individuals probably increases by birds that have been prevented from breeding, or failed to do so, and left the breeding-grounds early. Red-necked Grebes that have been prevented from breeding, failed and non-breeding birds begin to moult earlier than those with chicks (Vlug 1996, 2002a). There is a record of a non-breeding Red-necked Grebe in Switzerland which had already shed his remiges in the beginning of May (Winkler 1987).

13.2.2 Summering of the Population in Europe-West Asia

Larger numbers of summering Red-necked Grebes are recorded in the Grevelingen, an estuary in The Netherlands (up to 18 birds in June, to 15 in July and to 21 in August 1989) (Ouweneel 1990). Probably birds in June along the Baltic Seacoast of Mecklenburg-Western Pomerania, Germany, are summering individuals, e.g. concentrations of 68 Red-necked Grebes on 21 June 1984, and 78 on 4 June 1985 (Müller 1986, 1987).

On 21 June 1988 80 (summering?) birds were seen along the coast of the Black Sea near Shabla, Bulgaria (Jaschhof 1990).

In July 2003 2,240 Red-necked Grebes (summering birds, failed breeders or birds that have been prevented from breeding?) were counted on the Aralskoye More (Aral Sea) (Erokhov 2004, cited in Gavrillov and Gavrillov 2005).

Single individuals or, less often, pairs summer in many countries outside the regular breeding range of the species, sometimes in suitable breeding habitats, e.g. in Great Britain and Ireland (Toms 2002, Brown and Grice 2005, Parkin and Knox 2010), The Netherlands (SOVON 1987, Walhout and Twisk 1998, Bijlsma *et al.* 2001, Boele *et al.* 2014, 2015), Belgium (Voet and Maes 1981, Maes and Voet 1988, Bultinck 1989), Nordrhein-Westfalen (North Rhine-Westphalia) (Sudmann 2013), Baden-Württemberg (Hölzinger *et al.* 2011), Bayern (Bavaria) (Bandorf 1982), Switzerland (Walser and Barthel 1994, Winkler 1999, Mauuary *et al.* 2007, Schuster *et al.* 2014), Austria (Dvorak *et al.* 1993) and France (Dubois *et al.* 2008). Their total number is low. On occasion, summering birds have been reported displaying, copulating or building nesting platforms. The establishment of a breeding pair or small nesting population outside the regular breeding range may be heralded by displaying summering birds.

13.2.3 Summering of the Population in East Asia

There is almost no information about summering of the species in East Asia. On 17 July 2009 H Niesen observed more than 50 (summering?) Red-necked Grebes in nuptial plumage in the Kronotskiy (Kronotskiï) Zaliv, along the Pacific Coast of the Kamchatka Peninsula.

13.2.4 Summering of the Population in North America

Small numbers of supposed non-breeders are scattered along the coast of British Columbia in summer, e.g. 13 Red-necked Grebes on 29 June 1975 in the Esquimalt Lagoon, and 20 birds on 19 July 1971 near Victoria (Campbell *et al.* 1990).

13.3 Timing of Departure from the Breeding Waters, Routes and Moulting Migration

13.3.1 Timing of Departure from the Breeding Waters, Routes and Moulting Migration of the Population in Europe-West Asia

Europe

Red-necked Grebes in Central Europe that have been prevented from breeding and failed breeders (birds which lost their clutch or young) depart from the breeding sites as early as the second half of June and July (Wobus 1964, Köcher and Kopsch 1979, Zimmermann 1987, Vlug 1996). These birds begin the postnuptial moult and moult migration earlier than those Red-necked Grebes with young. On average, 31% of the adult birds in Schleswig-Holstein had left the breeding waters by early summer (17 June-7 July) ($n = 2,997$ adults). However, on bodies of water where only one fifth or less of the breeding pairs had succeeded, on average 62% of the adults had left by then (Vlug 1996). Across the Central European range, the majority of the Red-necked Grebes (including the successful breeders) have vacated the breeding waters by mid-August (Wobus 1964, Scholl 1974).

Before leaving, failed breeders, especially on the island of Fehmarn, Schleswig-Holstein (Germany), may flock on the breeding waters in the first half of July (up to c. 70 adult birds in one group). Sometimes, adults with young or birds which have a partner on the nest, join these flocks which are often called, confusingly, “non-breeder groups” (J J Vlug) (see Fig. 35).

Adult Red-necked Grebes usually leave the breeding waters before their young (Wobus 1964, Scholl 1974, Vlug 1996). For example, at a water body near Flemhude, Schleswig-Holstein, some 30 pairs nested in the summer of 2005 and raised 32 chicks. On 16 July, 21 large young were seen and only one adult (T Runge, J J Vlug).

Mostly the adults depart singly, i.e. not together with the partner, and frequently, one member of a pair abandons its mate and dependent young to moult elsewhere (Scholl 1974, Vlug 1996, Kloskowski 2003b) (see 16.5.16 for more details).

Many birds from the northern part of the breeding range in Europe migrate due west, across the Scandinavian mountain chain, to winter in the wide archipelagos of central Western Norway, as far north as the Arctic Circle (Fjeldså 2004). It appears that the majority of the Red-necked Grebes from southern Finland, the Baltic States, southern Sweden, Denmark, Poland and Germany, and perhaps with some from European Russia, migrate to the Baltic Sea, the Danish Belts, the North Sea and the English Channel (Cramp *et al.* 1977, Fjeldså 2004, Brown



Fig. 35: Failed breeders, especially on the island of Fehmarn, Schleswig-Holstein (Germany), may flock on the breeding waters in the first half of July. Photo: H Niesen (pond near Westermarkelsdorf, Fehmarn, Schleswig-Holstein, 1.7. 2017)

Fig. 35: Tiere, die ihre Gelege oder Jungen verloren haben, insbesondere an Brutgewässern auf Fehmarn, können in der ersten Julihälfte Trupps bilden.

and Grice 2005; ring recoveries in Konter and Konter 2006, Bairlein *et al.* 2014). A small number of birds winter on the Swiss and southern Bavarian lakes. These wintering Red-necked Grebes are possibly breeding birds of Central and West Europe: an adult Red-necked Grebe ringed in May in The Netherlands was recovered in January in the next year in Switzerland, and a bird ringed in Switzerland in December was shot down in June in the next year in Hungary (Maumary *et al.* 2007).

Probably, a great number of the birds from the Ukraine, Romania, Bulgaria and Turkey migrate to the Black and east Mediterranean (Adriatic and Aegean) Seas (AEWA 1999). It is likely that the main winter areas of the Red-necked Grebes breeding in the southern parts of European Russia (e.g. in the basin of the Volga, and the deltas of the Don and Kuban rivers) and in Georgia, are the Black and Caspian Seas. A juvenile bird ringed in July near Odessa at the coast of the Black Sea and found in southern Bavaria in October (distance 1,433 km) suggests contact between the NW European and the Black Sea/Mediterranean flyway (Konter and Konter 2006, Bairlein *et al.* 2014).

The simultaneous (flightless) wing moult in Europe usually takes place in tidal waters, on or near the wintering grounds (Folkestad 1978, Vlug 1996). In the Baltic Sea, near the island of Sjælland (Zealand), Denmark, two moulting sites have been identified in August and September, estimated to hold up to 1,500 birds. Most birds occurred as single individuals or small flocks of up to 11 birds (Pihl 1995), i.e. much smaller flocks than the moulting groups of Great Crested Grebes (Vlug 1983). In late July, August and early September, concentrations of up to 160 Red-necked Grebes are recorded along the coast of Mecklenburg-Western Pomerania. It is assumed that much larger numbers occur here in the moulting period (Vlug 1996). A record of 1,850 non-breeding visitors (average of the period 1980-93) in shallow subtidal areas of the eastern German Bight, North Sea (Rasmussen *et al.* 2000) suggests moult-gatherings. On the wintering grounds along the coasts of Norway, at least some of the adults undertake their wing moult during autumn (Folkestad 1978). Red-necked Grebes summering in the Grevelingen, an estuary in The Netherlands (up to c. 20 birds), moult their wings here (Ouweneel 1990). Small numbers of Red-necked Grebes undergo a post-breeding

moult on Swiss lakes (Winkler 1999, Maumary *et al.* 2007), on breeding sites in Denmark (Pihl 1995) and Schleswig-Holstein (in 1999 38 grebes on ponds near Lebrade and 24 on a pond near Kühren; in 2009 50 birds on ponds between Plön and Selent) (Koop, *cited in* VlUG 2000, Koop 2012). The sites where the majority of the European Red-necked Grebes moult are still unknown.

West Asia

In Kazakhstan migration occurs from mid-June to early November (Wassink and Oreel 2007). In the Barabinskaya Step' (Baraba Steppe), near Novosibirsk, and Naurzum, North Kazakhstan, the birds begin to abandon the breeding lakes in July and go to other water bodies in the area where they moult. From the second half of August the grebes depart to the wintering areas (Kuročkin 1985).

The breeding birds from western Siberia and western Kazakhstan possibly migrate to the Aral, Caspian and Black Seas (Kuročkin 1985, Wetlands International 2006). A few birds ringed near Omsk were recovered on the west coast of the Caspian Sea (Kuročkin 1985), and Patrikeev (2004) stated that a few banding recoveries indicate that Red-necked Grebes wintering on the coast of the Caspian Sea in Azerbaijan nest in West Siberia.

Apparently, a number of Red-necked Grebes from eastern Kazakhstan (and western Siberia?) winter on Lake Issyk-Kul, Kyrgyzstan (Januševič *et al.* 1959, *cited in* Kuročkin 1985).

The population nesting in the Balkhash-Alakol' area in South-East Kazakhstan and Kyrgyzstan (Oz. Sonkel) has a small wintering population in north-eastern Afghanistan (Kabul area), northern and central Pakistan and an increasing one in north-western India (see 10.2.1). The breeding birds of Oz. Sonkel stay here until the entire lake freezes in late November (Kydraliev and Sultanbaeva 1977, *cited in* Kuročkin 1985).

13.3.2 Timing of Departure from the Breeding Waters, Routes and Moult Migration of the Population in East Asia

There is almost no information about the timing of the departure and moult migration of the species in East Asia. The Red-necked Grebe in Hokkaido remains on its breeding grounds well into September, and young have been observed still being fed on breeding lakes in early

September. The birds depart in October, and by early October some can already be seen along the Hokkaido coasts (Brazil 1991).

Red-necked Grebes breeding in East Asia migrate to marine waters and winter along the coasts from eastern Kamchatka in the north to the northern parts of the South China Sea in the south. A young bird ringed at the Lower Amur was shot in March of the next year on the island of Hokkaido (Kuročkin 1985).

13.3.3 Timing of Departure from the Breeding Waters, Routes and Moult Migration of the Population in North America

Across the North American range, the adults depart from the breeding lakes as early as July. Most breeding lakes are vacated by mid-September (Stout and Nuechterlein 1999, Stout and Cooke 2003). However, authors often give different data.

The autumn movement in southern British Columbia begins in late August but occurs mostly from late September to early October (Campbell *et al.* 1990). Munro (1941) stated that the breeding populations in this province leave their nesting lakes early in September. For example, at Swan Lake, Okanagan, some 30 pairs nested in the summer of 1936, and the majority had left by the end of August. On 13 September and for the two weeks following only one bird was seen. The main migration of young through the Okanagan takes place in October (Munro 1941).

In September, Red-necked Grebes in Alberta flock in considerable numbers on large lakes, often in the company of other grebes and loons. Most birds have left the province by mid-October or early November (Semenchuk 1992). The birds usually leave northern Yukon by late August (latest 1 September 1975). There are few autumn records from central Yukon (latest 24 September 1996). In the south, numbers decrease gradually from late June to late October, after which the birds are rarely seen (latest 18 November 1995) (Sinclair *et al.* 2003). Near Yellowknife, Northwest Territories, 29 known nesting adults under regular observation in 1998 and 1999 left their breeding ponds between mid-July and late August (Stout and Cooke 2003).

The earliest Red-necked Grebes to leave the breeding waters may be birds that had been unsuccessful nesters as

well as members of those pairs whose young had already reached about half-size (4-5 weeks of age) (Riske 1976) (cf. 13.3.1). Riske (1976) stated that in the poor *griseogena* reproduction year of 1973, a large proportion of adults left Pine Lake, central Alberta, during July, presumably because of a lack of attachment to young. The unprecedented early appearance on 5 August 1973 of Red-necked Grebes at Victoria and Cordova Bay, British Columbia (Crowell and Nehls 1974, cited in Riske 1976), may have been related to the decrease in numbers of young produced on water bodies in central Alberta (Riske 1976).

The adults depart from the breeding lakes up to 4 weeks before their young (Riske 1976, Stout and Nuechterlein 1999) and mostly they depart singly, i.e. not together with their partner (De Smet 1983). Frequently, one member of a pair abandons its mate and still dependent young (see 16.5.16).

As already mentioned (see 13.1.3), North American Red-necked Grebes winter primarily on marine waters along the Atlantic and Pacific coasts and, to a limited extent, on the Great Lakes (Stout and Nuechterlein 1999). Band recoveries and contaminant data in eggs suggest that the breeding ranges of the Atlantic- and Pacific-wintering populations diverge somewhere in western Saskatchewan (Forsyth *et al.* 1994, Stout and Nuechterlein 1999) (see also 13.1.3).

The migratory routes are more east-west than north-south. The species is a rare migrant in the central United States south of the breeding range. It is very rare from Nevada, Utah, Colorado, Nebraska, and Missouri south to southern California interior, Arizona, New Mexico, and the Gulf Coast states (Stout and Nuechterlein 1999).

Eastern Migrants

The main autumn migration route for Red-necked Grebes in eastern North America is via the Great Lakes, especially Lake Superior, Lake Huron, and Lake Ontario. Smaller numbers move through the Lakes Michigan and Erie, the St. Lawrence River, and inland areas south and east of the Great Lakes (Stout and Nuechterlein 1999). On Lake Superior and northern Lake Huron, the vast majority of the migrants pass from mid-August to mid-September. The major diurnal flights occur on Lake Superior (Stout and Nuechterlein 1999).

Stout (1995) studied the autumn (fall) migration of Red-necked Grebes in the Great Lakes region from 1990 to 1994. She stated that the autumn migration of most eastern-wintering grebes apparently begins with nocturnal flights from the breeding lakes to western Lake Superior. There is no evidence that the grebes conduct overland migration by day. The flights from the breeding lakes to Lake Superior could be accomplished in one to several nights depending on the location of the breeding lakes. Stout (1995) observed the first autumn migrants on eastern Lake Superior on 31 July 1992 and 30 July 1993.

Upon reaching western Lake Superior, the Red-necked Grebes apparently waited for appropriate weather conditions and then began a diurnal flight migration to the eastern end of the Lake (Whitefish Point). Locations of stopover areas on western Lake Superior are unknown. Some grebes may have begun migrating from the breeding or staging lakes west of Lake Superior during the night and continued migrating across Lake Superior on the following day. However, when migration across Lake Superior was delayed by several days of unfavourable weather, the migration volume at Whitefish Point Bird Observatory near Paradise, Michigan, on the next favourable day was increased greatly, indicating that a build-up of grebes occurred somewhere west of the Keweenaw Peninsula. When the weather conditions at Whitefish Point changed from unfavourable to favourable during the day (such as after a cold front passage), migrating grebes appeared almost immediately. This suggests that they lingered somewhere nearby on Lake Superior waiting for good migration weather. Once the Red-necked Grebes began flying across Lake Superior, they probably completed the 400-600 km flight in one day if the weather conditions were good.

Diurnal passage also occurs past Thunder Cape Bird Observatory, near Thunder Bay, Lake Superior, Ontario. During August-November 1992 at this observatory, a total of 1,136 migrating Red-necked Grebes were counted during daily 6-hour counts with peak flights of 150 grebes on 3 and 12 September. As at Whitefish Point, the migration was about 80% complete by mid-September (Shepherd 1993, cited in Stout 1995).

The majority of the Red-necked Grebes migrating through Lake Superior appear to follow a path that takes them past points along the Michigan shoreline from the Keweenaw Peninsula to Whitefish Point. Peak Red-

necked Grebe flights at Whitefish Point occurred during August and September, with the largest daily flights usually occurring in late August or early September (Stout 1995). Seasonal totals of up to 18,739 diurnally migrating Red-necked Grebes were counted in August-November at Whitefish Point Bird Observatory (Stout 1995, Stout and Nuechterlein 1999).

After passing Whitefish Point, the Red-necked Grebes flew southeast to the extreme eastern end of Lake Superior, past Point Iroquois near Brimley. Observations in this area showed that the diurnally migrating grebes did not continue flying from Lake Superior through the St. Mary's River to Lake Huron, but instead reacted as if they had reached a land barrier. When the grebes approached the area where the water narrows, and the St. Mary's River begins, they turned around and flew back to one of at least two main stopover areas, often circling many times before settling on the water. Stout (1995) never observed migrating Red-necked Grebes flying down the St. Mary's River by day. Since the river is interrupted in Sault Sainte Marie by a system of locks and shallow, rocky rapids, it is unlikely that the grebes travel through the St. Mary's River by swimming. Circumstantial evidence suggested that the grebes resumed their migratory journey to Lake Huron at night. On several occasions, Stout (1995) observed flocks of resting grebes at the two known staging areas until dark. At dawn on the following day, nearly all of the grebes observed on the previous evening were gone.

In the waters of northern Lake Huron, two distinct groups of Great Lakes migratory grebes became apparent (Stout 1995). The aerial and ground surveys of Manitoulin Island showed that some of the grebes migrating through Lake Superior stopped at various bays and shoreline areas around Manitoulin Island to undergo the autumn (wing) moult (group 1). Other grebes continued past Manitoulin Island in diurnal flights (group 2). The moulting grebes (group 1) remained in specific sites around the island throughout the moulting period. On 8 December 1994, Red-necked Grebes were still present in large numbers at locations along the north-central shore of Manitoulin Island. They were possibly the same birds which moulted around the island during August through October (Stout 1995). In 1994, flocks of grebes lingered in the bays around Manitoulin Island at least through early January 1995 (Nicholson, *cited in* Stout 1995). From 20 August to 10 September 1994, Stout

(1995) observed diurnal migrants (group 2) from the west end of Manitoulin Island at the Mississagi Strait and along the north shore of the island near Janet Head. The numbers at the Mississagi Strait were small in comparison to the Whitefish Point (Lake Superior) counts (147 grebes counted during 10 hours of observation, 26-29 August 1994). The migratory grebes were in alternate (nuptial) plumage and did not appear to intermingle with the moulters (group 1) at any moult site (Stout 1995).

The exact migratory route east of northern Lake Huron is unclear, but probably includes overland flights across southern Ontario, Quebec, and the north-eastern part of the United States. Lake Ontario and the St. Lawrence River may be used more extensively in the autumn migration than is currently documented. However, records of (moulting) concentrations in September of up to 3,000 individuals in the north-central part of Lake Ontario (Gunn 1951) have not been noted in recent decades. Peak numbers on Lake Ontario and the St. Lawrence River are recorded in October and early November. Along southern Lake Erie, most migrants appear in late October and November, sometimes lingering until early January. The earliest migrants reach the Atlantic Ocean in late August, but most birds arrive in October and November. The apparent time gap between the peak migration through the upper Great Lakes and the build-up of numbers at the Atlantic wintering sites likely is due to the timing and location of the flightless moult (Stout and Nuechterlein 1999).

Important moult sites at the coast of the Atlantic Ocean are found in the Gulf of St. Lawrence (Stout and Nuechterlein 1999). At Chaleur Bay (Quebec and New Brunswick), on 30 September 1974, Canadian Wildlife Service biologists examined 195 oiled Red-necked Grebes, and all were in wing moult. Surveys at the Gulf of St. Lawrence from 19 to 23 September 1994 found 136 Red-necked Grebes at Chaleur Bay, 136 at Baie Verte (Nova Scotia/New Brunswick); and 52 at other locations. At each site, individuals in wing moult were detected (Stout and Cooke 2003).

As already outlined, moult sites are not only found in marine habitats, but also in some large inland-lakes. Freshwater wing-moult locations were found in northern Lake Huron (Stout 1995, see above). From 20 August to 6 October 1994, 1,105 Red-necked Grebes were found at 16 locations around the shore of Manitoulin Island,

Ontario (see above). By early October 1994, the Manitoulin moulters were in the late stages of moult, with the wing moult largely complete and the body plumage approaching the full winter dress. On 15 September 1995, 1,248 Red-necked Grebes were counted at six of the Manitoulin sites (the total at these six sites in 1994 was 726). Wing-flapping grebes seen from the shore were in wing moult. The birds were found in sheltered areas (Stout 1995, Stout and Cooke 2003). As stated above, in the moulting period, large concentrations were seen near Port Britain, Lake Ontario (estimated at more than 3,000 birds on 6 September 1945) (Gunn 1951).

Western Migrants

The Pacific-wintering grebes migrate overland and along the coast, staging at larger lakes and reservoirs en route (Stout and Nuechterlein 1999).

An important moulting site is the Boundary Bay, Pacific Ocean. Red-necked Grebes arrive in this bay, near Vancouver in British Columbia, in August and September, and most depart in October (Stout and Cooke 2003). Other moult sites for Pacific-wintering birds remain undocumented (Stout and Nuechterlein 1999). At three locations in the Boundary Bay, a total of 1,689 Red-necked Grebes was counted on 24 September 1997. In 1998, counts at these three locations were 7 September – 883, 10 September – 1,670 (two of three locations), 22 September – 2,229, 6 October – 1,325, and 10 October – 333. The grebes were undergoing body moult, and some birds were in wing moult or regrowth. For example, on 10 September 1998, ten of 14 birds seen wing-flapping had noticeably incompletely grown remiges (Stout and Cooke 2003).

Probably, a number of grebes in the western part of North America undergo their wing moult on some large freshwater lakes (*cf.* Lake Huron, see above). In September, Red-necked Grebes assemble in large numbers on some large lakes in Alberta. Mingling with Western Grebes *Aechmophorus occidentalis* and Great Northern Divers (Common Loons) *Gavia immer*, they form (moult-) aggregations that may run into the thousands (Salt and Salt 1976, Semenchuk 1992). Salt and Salt (1976) stated: “For days they exercise their wings, taking short practice flights from one part of the lake to another. Then late one evening around mid-October they patter along the surface until air-borne, and on short, rapidly-beating wings that look too weak to carry them

through the night they disappear into the twilight. Only a few individuals remain with us until late October or early November.”

13.4 Timing Arrival at and Departure from the Wintering Areas

13.4.1 Timing Arrival at and Departure from the Wintering Areas of the Population in Europe-West Asia

Red-necked Grebes are present at the coastal waters of Europe chiefly from late September/October to March/ April (in northern Europe to mid-May) (Vlug 2002a).

The main autumn migration period along the Atlantic coasts of Norway is from late September to November. The first birds reach the wintering grounds during the last days of August; these early arriving grebes are (almost) always adults. The main spring migration is from late April until mid-May (Folkestad 1978). The autumn migration to the winter quarters in the Baltic Sea peaks in October, while the spring migration takes place from March to the beginning of May (Durinck *et al.* 1994).

At Blåvandshuk near Esbjerg along the North Sea coast of Denmark, the birds are mainly seen during the autumn migration between mid-October and mid-December (Jakobsen 1988). Along the North Sea coast of The Netherlands, Red-necked Grebes are scarce, but regular observed from the second half of October to April, mainly between November and March. A northward migration is noted in April (Camphuysen and Van Dijk 1983, Camphuysen and Leopold 1994).

Small numbers of individuals are present in British waters typically from September to March, with most birds along the east coast in sheltered localities and a smaller number on larger inland waters in south and central England (Toms 2002). Brown and Grice (2005) stated: “Red-necked Grebes tend to arrive in England from late July onwards, though numbers remain small until October. Passage along eastern coasts is usually noted at this time, the 19 birds passing Sheringham, Norfolk on 4-6 October 1992 being typical of autumn passage. A return is also evident in spring, principally between late March and early May. It is in mid- to late winter, especially between December and February, that numbers tend to peak (...).”

The autumn passage in France is visible from August to December and has its maximum in November. At several

places in northern (for example at Cape Griz-Nez, Pas de Calais) and eastern France, the grebes are already seen from the end of July. The spring migration is noticed by a larger number of observations along the coasts of La Manche (English Channel) in early February and by the disappearance of the wintering birds from the freshwater lakes. A few birds stay until April (Dubois *et al.* 2008).

In the Swiss lakes, the first Red-necked Grebes, usually adult birds, arrive in early/mid-July or August. They come there to undergo their wing moult. There is a regular passage and arrival of wintering birds from the second half of August onwards. The migration and arrivals are the strongest in November. The departure of the wintering birds begins by mid-February, peaks in March-April and largely ends by late April (Zbinden-Schmalz 1978, Leuzinger 1983, G eroudet 1987, G onner 1999, Winkler 1999, Maumary *et al.* 2007).

On the wintering grounds of the southern parts of the Caspian Sea, the Sea of Azov and the Black Sea, Red-necked Grebes appear in September and stay until late March/early April (Kuro kin 1985).

13.4.2 *Timing Arrival at and Departure from the Wintering Areas of the Population in East Asia*

Along the sea coasts of southern Primorskiy Krai, the grebes arrive in early September and stay until mid-October, some until November or December. The first reappear in late March, in early April they become numerous, and then their numbers decline, but a number stay until early May; a few remain even until late May (Panov 1973, *cited in* Kuro kin 1985). The Red-necked Grebe is a fairly common winter visitor arriving in October and early November in Japanese coastal waters from Honshu south to Kyushu. Although it can be found in reasonable numbers also in Hokkaido at this season too, it rarely occurs in anything other than very small numbers. The two earliest "winter" records are both from Suruga Bay, Shizuoka-ken (Honshu), and both in August. Wintering birds may remain as late as early May, but most move north again during March and April (Brazil 1991).

13.4.3 *Timing Arrival at and Departure from the Wintering Areas of the Population in North America*

Eastern Migrants

In North America, the earliest migrants reach the Atlantic coast in late August, but most birds arrive in October and

November. As already mentioned above (13.3.3), the apparent time gap between the peak migration through the upper Great Lakes and the build-up of numbers at the Atlantic wintering sites likely is due to the timing and location of the flightless moult. The birds may gradually move south along the Atlantic coast as the winter progresses. The beginning of the staging for the spring migration is in March and April, when large flocks are observed along the northern Atlantic coast (Stout and Nuechterlein 1999).

Western Migrants

The autumn arrivals to the Pacific coast of Alaska begin in mid- to late August and continue to late October (Isleib and Kessel 1973, *cited in* Stout and Nuechterlein 1999). The autumn movements in British Columbia begin in late August but occur mostly from late September to early October. A few observations of (migrating or moulting) Red-necked Grebes from the coast are: Tofino 5 September 1974 160, Island View Beach 20 September 1982 200, Blackie Spit 23 September 1984 200, and Island View Beach 5 October 1980 95 Red-necked Grebes (Campbell *et al.* 1990). Boundary Bay, at the Pacific coast of British Columbia, is inhabited by moulting Red-necked Grebes from late August to early October (Stout and Nuechterlein 1999). The birds arrive on the Oregon coast in late August and October (Gilligan *et al.* 1994, *cited in* Stout and Nuechterlein 1999), and on the northern California coast from early September, but they do not reach southern California until mid-October (Small 1994, *cited in* Stout and Nuechterlein 1999).

In spring, the departures from the Pacific coasts are generally related to latitude. The birds depart from the northern California coast by late April (Small 1994, *cited in* Stout and Nuechterlein 1999). Along the Oregon coast, migrating birds are observed in late March and April (Gilligan *et al.* 1994, *cited in* Stout and Nuechterlein 1999). Spring migration in British Columbia may begin as early as late February and early March in southern areas, but peaks in the latter half of April. Examples of observations from the coast are: Departure Bay 13 March 1930 250, Campbell River 29 March 1975 156 at the estuary, Central Saanich 10 April 1983 175, Cowichan Bay 16 April 1968 187, Menzies Bay 29 April 1966 300, and Tofino 1 May 1974 150 Red-necked Grebes (Campbell *et al.* 1990). The peak migration through the northern Gulf of Alaska coast and the Prince William Sound, Alaska, is from late April to mid-May (Isleib and Kessel 1973, *cited in* Stout and Nuechterlein 1999).

13.5 Migratory Behaviour

Red-necked Grebes migrate primarily at night, whether they move between local water bodies or over longer distances. In the pre-migratory period, the birds become restless at dusk, moving around over the lake surface, sometimes in dense rafts. The migration starts soon after it gets dark and normally ends before dawn (Salt and Salt 1976, Stout and Nuechterlein 1999, Fjeldså 2004).

The overland movements are strictly by nocturnal flights, but Red-necked Grebes sometimes continue their migration by day, flying or swimming. Extensive diurnal movements may occur along ocean and sea coastlines and over other large water bodies (Stout and Nuechterlein 1999, Vlug 2002a, Fjeldså 2004). Some diurnal flights are recorded along the North Sea coast of The Netherlands (Camphuysen and Van Dijk 1983). The autumn flights of Red-necked Grebes through Lake Superior appear to be the most extensive diurnal migration of grebes ever reported (see 13.3.3). Each autumn, between 9,000 and 19,000 Red-necked Grebes have been observed flying past Whitefish Point, Michigan, during daylight hours. During these diurnal flights, the birds moved past Whitefish Point singly or in small flocks that ranged from 2 to 74 individuals. Most grebes remained between 750 and 2,000 meters offshore and flew at heights of about 0.5-50 meters above the water (Stout 1995).

When grebes reach coastlines, they may swim in the direction of migration rather than fly. Diurnal swimming migration seems not exceptional but is difficult to observe. This type of migration would presumably be more time consuming than flying migration but would allow grebes to forage while en route and take advantage of areas where food is abundant (Stout 1995). In the Åland Channel, near the island of Vaddö (Sweden), diurnal migrating birds followed the coast at a distance of usually 50-200 meters, swimming (and also diving for food) at an average pace of some 2 km/hour (Andersson 1954).

13.6 Spacing, Flock Size and Aggregations Outside the Breeding Season, in the Moulting Period and During Migration

13.6.1 Gregariousness Outside the Breeding Season in *P. g. grisegena* and *P. g. holboellii*

Outside the breeding season, the birds of the nominate race *grisegena* are most frequently solitary or in twos, or

in small, usually loose, assemblages, e.g. in spring before dispersal to the breeding lakes and in late summer before and during the wing moult (Cramp *et al.* 1977, Vlug 1996, 2002a, Fjeldså 2004). Cramp *et al.* (1977) consider the nominate race to be the least gregarious of the west Palearctic grebes. However, Blomdahl *et al.* (2007) write: “(The) Red-necked Grebe is the grebe most likely to occur in flocks, with groups of up to ten birds being far from unusual and up to 50 birds having been counted at sites where the species regularly passes on migration. Such flocks are often dense and difficult to count and there is always the chance of another grebe species being present among them. (The) Red-necked Grebe can, more often than its congeners, be seen joining flocks of ducks (mergansers and eiders in particular).”

In North-America, groups of several hundred Red-necked Grebes (subspecies *holboellii*) are a regular occurrence at some moulting and migratory staging areas (Campbell *et al.* 1990, Stout and Nuechterlein 1999, Vlug 2002a). Campbell *et al.* (1990) write that *Podiceps grisegena* in British Columbia is gregarious but rarely associates with other species of grebes. The authors state that large flocks of more than hundred birds are common on the coast in autumn and winter and may be seen occasionally throughout the province in spring migration (Campbell *et al.* 1990).

13.6.2 Spacing of Moulting Birds

In late July, August, and early September, concentrations of up to 160 (moulting) Red-necked Grebes are recorded along the coast of the Baltic Sea in Mecklenburg-Vorpommern (Mecklenburg-western Pomerania) (Vlug 1996). Unfortunately, there are no detailed records on individual spacing of the birds in these concentrations. More is known about the spacing of moulting Red-necked Grebes in the Baltic Sea near the island of Sjælland (Zealand), Denmark. These birds occur as single individuals or in small flocks of up to 11 birds (Pihl 1995).

Although the simultaneous (flightless) wing moult in Europe usually takes place in tidal waters, there are some records of flocks of moulting birds on inland lakes. On July 13, 1991, Vlug (1996) saw 85 adult Red-necked Grebes on the Mehnert-Teich, a pond on the island of Fehmarn, Schleswig-Holstein; 67 of the birds were together in a dense (pre-moult) flock.

In North-America, large concentrations in the moulting period were seen near Port Britain, Lake Ontario, by Reeve (*cited in* Gunn 1951). Gunn (1951) wrote: "The greatest number Mr. Reeve has ever observed was on September 6, 1945, when the lake in front of his property was literally black with Red-necked Grebes, their numbers being conservatively estimated at upwards of 3,000."

As already stated (see 13.3.3), the birds flock in considerable numbers on some large lakes in Alberta in September, often in the company of other grebes and divers, forming (moult-) aggregations that may run into the thousands (Salt and Salt 1976, Semenchuk 1992).

Approximately 1,300 Red-necked Grebes completed their autumn moult at various bays and shoreline areas around Manitoulin Island, Lake Huron, in 1994. The moulting birds were present as single individuals and in loose flocks of 2-40 birds per flock (Stout 1995).

13.6.3 Spacing During Migration (*see also* 15.3.1)

Red-necked Grebes of the nominate subspecies *griseogena* migrate singly or in small parties (Cramp *et al.* 1977). During migration along the Norwegian coasts, the birds are fairly social, and move in flocks of 10-20 birds (Folkestad 1978).

In Europe, the concentrations during the migration are usually small, and records of flocks of more than 100 birds are rare (*see* 13.1.1).

In North America parties of several hundred are a regular occurrence at some staging areas, e.g. Cape Cod, north-east USA, where over 2,000 birds may gather on spring migration (Llimona and Del Hoyo 1992).

Large concentrations are frequently recorded in Manitoba, e.g. at Oak Hammock Marsh (maximum 530 or more on 23 April 1988), and Seven Sisters dam (maximum 890 on 28 April 1995 and 800 or more on 27 April 2001) (De Smet 2003).

From 1990 to 1994 7,000-15,000 diurnally migrating Red-necked Grebes were counted each autumn at Whitefish Point, Lake Superior. During their diurnal flights, the birds there moved singly or in small flocks that ranged from 2-74 individuals. In the major migration period at Whitefish Point (August through Septem-

ber), solitary birds and flocks of 2-6 grebes were most frequent (median flock size = 3) (Stout 1995).

13.6.4 Spacing During Foraging Outside the Breeding Season

Red-necked Grebes usually feed singly, but at wintering sites in Europe and British Columbia, some Red-necked Grebes form commensal feeding associations with scoters *Melanitta* (Byrkjedal *et al.* 1997, Stout and Nuechterlein 1999, Byrkjedal 2000).

13.7 Pair Formation and Migration

Because courtship occurs on the wintering grounds, mainly just before the spring migration and at the migratory staging points, it must be assumed that many pairs begin to establish a bond before and during the spring migration, especially in the spring aggregations, and as late as the arrival at the breeding sites for the remainder of the birds (Folkestad 1978, Stout and Nuechterlein 1999, Vlug 2002a; *cf.* Stedman 2000 for *Podiceps auritus*) (*see* 15.3.2).

13.8 Weather and Migration, Causes of Death During Migration and in Winter (these topics are also treated in 12.2.4)

13.8.1 Weather Conditions and Migration

Thanks to the work of Stout (1995) it is known that weather conditions greatly influence the diurnal flights. The peak of the diurnal flights during autumn migration at Whitefish Point, Lake Superior, Michigan, is associated with the recent passage of cold fronts and approaching high-pressure systems, i.e. conditions characterized by north-westerly winds, low but rising barometric pressure, falling temperatures, decreasing precipitation, and increasing visibility (Stout 1995, Stout and Nuechterlein 1999).

The influence of the weather on nocturnal migration is largely unknown, apart from instances of grebes being grounded during bad weather.

At wintering locations subject to occasional freeze-over, grebes may become involved in "hard weather migrations". During these movements, the grebes move from normal wintering areas to other areas where they are not usually found. During severe winter weather (gales and

cold temperatures) over north-western Europe, Red-necked Grebes have staged influxes into Great Britain and The Netherlands. Similar winter influxes of Red-necked and Slavonian (Horned) Grebes have occurred over the eastern United States during severe cold which led to freezing up of the Great Lakes and other inland waters. These movements seem to result more from icing of wintering waters than from cold temperatures or storms themselves, although storms may play a direct role in influencing the direction of the movements (Stout 1995). Snow- and ice-storms, rain, and fog can cause nocturnal migrants to become disorientated and force them to land on glistening wet or icy pavement, where they become grounded and unable to fly. These groundings make the influxes very noticeable.

13.8.2 Influxes and Grounded Red-necked Grebes in Europe

A comparatively small number of Red-necked Grebes winter in Great Britain, but occasional influxes occur on the east coast in hard weather, as in 1865, 1891, 1895, 1922, 1937 and 1979 (Witherby 1937, Witherby *et al.* 1947, Chandler 1981, 1986).

During the rush of February and March 1865 no less than 35 Red-necked Grebes were brought into Norwich market alone, the majority shot between 18 and 28 February (Bannerman 1959).

The invasions of 1937 and 1979 were discussed by Chandler (1986): “The influxes occurred during easterly winds when the birds appeared suddenly in late January or February, having originated probably from the western Baltic and the Continental North Sea coast. In 1979, the birds were forced to move west by the onset of cold weather on 14 February. Within 3-4 days Red-necked Grebes had appeared at ice-free waters throughout England; the influx continued for 2 weeks, the overall numbers of birds involved being about 500. Their arrival coincided with a similar widespread appearance of Red-breasted Mergansers *Mergus serrator* on inland waters.”

It is obvious that the birds may fall victim to the bad weather conditions, and so it is not amazing that at least some of them die. By far the greatest number of dead Red-necked Grebes in the invasion of 1979 was found between 19 and 25 February, the week in which the greatest numbers were present in Britain. In two or three instances, birds were reported to have had empty stom-

achs apart from a small quantity of water-weed: since the species normally feeds on animal matter, this points to starvation as the most likely cause of death (Chandler 1981).

The influx of 1979 was also recorded in The Netherlands. In February more than 100 dead Red-necked Grebes were found at the Dutch beaches of the North Sea (SOVON 1987).

Observations of stranded Red-necked Grebes in Europe are rare. Two birds found on rain-wet streets in Luxembourg during the migration period are reported by Lorgé *et al.* (2004): one *grisegena* was found on 14 August 2000 near Trintange, and another one, a juvenile, on 30 August 2002 near Leudelange.

Remarkable is the observation of a juvenile Red-necked Grebe that flew into a tent at a camping site on the island of Texel, The Netherlands, on the night of 9 August 1971 (Dijkse 1996).

13.8.3 Influxes and Grounded Red-necked Grebes in North America

Stout (1995) stated: “Some evidence suggests that Red-necked Grebes which molt on the Great Lakes also remain there to winter. Freeze over of the Great Lakes is a relatively rare event (occurring about once every 20-30 years), but presents an obvious risk for grebes wintering on the Great Lakes. However, wintering on the Great Lakes could have advantages. Migration distances for Great Lakes molters are shorter than those of grebes which winter on the coast (savings of 480-1,000 km each way). Grebes remaining on the Great Lakes can also avoid the hazards of late fall migration such as severe weather (...).”

In contrast to Europe, the number of reports on stranded Red-necked Grebes in eastern North America, especially by icing of the Great Lakes, is large. Snyder (1930) wrote that on the night of December 12, 1929, during a heavy sleet storm which glazed the pavements and snow-covered landscape of the Toronto region, an extensive flight of Red-necked Grebes took place. These birds were probably passing over southern Ontario from upper Lake Huron and Georgian Bay to Lake Ontario, Lake Erie and southward. Upon striking the storm area of the lower Great Lakes some of them came to grief, either permanently or temporarily, while others apparently

made the open waters of the lakes. A total of 37 birds were picked up in Toronto. The majority of the grebes were found alive on the streets. Snyder (1930) commented: "It would seem evident from the number of birds picked up alive and uninjured in Toronto that the birds came to rest on the city streets voluntarily. Only two were reported as being found in "back yards". Such circumstances give rise to the theory that the Grebes, travelling in a loose company, over a wide area, were perhaps attracted by the lights of the city and from their elevation mistook the icy pavements below for water. Having alighted they were unable to take wing because of their well-known handicap on solid surfaces."

Another Red-necked Grebe invasion occurred in 1934 (Bull 1974, Kaufman 1994). In this flight, many of the grebes died. In his work "Birds of New York State", Bull (1974) stated: "During the great winter irruption of late February 1934, when a severe freeze closed the Great Lakes, large numbers of Red-necked Grebes were reported both dead and alive along the coast of Long Island. On Feb. 22, while visiting the Montauk area, Breslau counted 225 dead – frozen carcasses – chiefly on the ocean beaches. He estimated at least another 150 alive, but in much weakened condition, including 14 waddling about on the main street of Montauk village. On the same day at Long Beach (Nassau Co.), Sedwitz saw 50 alive; also eight dead there on March 18."

During late February and early March 1963, 26 stranded Red-necked Grebes were reported in Ontario. The majority (18) were alive when found (De Vos and Allin 1964). The authors wondered whether it would be plausible that the grebes were displaced by drifting ice or were moving from one lake to the next and unable to find open water.

With the harsh weather of the winter 1993-94 in eastern North America, the Great Lakes were frozen over almost completely, forcing out many waterbirds that ordinarily winter there. Almost certainly as a result of this, an unprecedented invasion of Red-necked Grebes moved east to the Atlantic Coast and south into the interior of the east and Midwest during February. The push of Red-necked Grebes was preceded in January by a southward flight of Slavonian Grebes, undoubtedly vacating the Great Lakes as the winter got worse. But the Red-necked Grebes appear to have held on as long as possible, so when they finally did leave the Great Lakes, they did it

all together in large numbers. Birders in the North encountered these birds mainly as failed migrants: at least six were picked up dead or grounded in New England during February; in southern Ontario, dozens of Red-necked and Slavonian Grebes were found grounded on roads in late January and early February. The total Hudson-Delaware region tally came to at least 850 Red-necked Grebes, and most appeared healthy (Kaufman 1994). Stout (1995) stated, that in February 1994 the widespread invasion of grebes occurred in an area extending from interior New Hampshire, New York, southern Ontario, and southern Michigan south to North Carolina and west to Missouri, and that during this period, over 2,210 Red-necked Grebes were counted in this region, where observers usually record fewer than 100 each winter. Brinkley *et al.* (cited in Kaufman 1994) pointed out that hundreds of grebes made stops on the Finger Lakes in upstate New York during this invasion (February 1994), whereas in 1934 (see above) those lakes froze over completely. Perhaps such stopovers in 1994 allowed more birds to get to the coast before becoming exhausted.

13.8.4 Bad Weather in the Wintering Areas and Food Shortage (these topics are treated in more detail in 12.2.4 and 12.2.5)

Even adult Podicipedidae are affected by storms and frost periods in winter. Piersma (1988b) estimated that a healthy *grisegena* with average winter reserve levels can (only) survive a period of about eleven days without food in midwinter, and so it is likely that severe winters are an important factor influencing the numbers of the birds.

Not much is really known about the relation between food and weather. During the 1979 winter invasion in Great Britain, starvation by bad weather conditions was the most likely cause of death in at least some of the Red-necked Grebes found dead (see 13.8.2).

14. Food, Food Habits, Geographic Variation in Diet and Interspecific Competition

14.1 Main Foods Taken

P. grisegena grisegena mostly feeds on aquatic insects and their larvae, molluscs, crustaceans, annelids, amphibians and small fish (Vlug 1993, 2002a, Kloskowski 2004, 2011, Vlug 2011).

14.2 Microhabitat for Foraging

At the breeding waters, the nominate race typically forages in shallow areas with much floating and submerged vegetation, in small pools in reed marshes, and in areas of water with many small islands of emergent vegetation. It takes its prey anywhere from just above the water surface to the bottom (Wobus 1964, Vlуг 1993).

At the breeding lakes in North America, *P. griseogena holboellii* normally forages in shallow, open water zones (often within marshy areas) and areas of scattered emergent vegetation, where aquatic vegetation does not impede swimming and diving (Stout and Nuechterlein 1999). Begin and Handford (1987) stated that on many of the larger and deeper western Canadian lakes, Western and Red-necked Grebes co-occur. The latter seldom stray far from the shore and forage primarily within the shallow territorial waters. Western Grebes, on the other hand, leave their colonies soon after hatching to forage pelagically in deeper waters.

In marine waters, the nominate subspecies frequents shallow areas with a depth of 3-20 m and a mixture of soft and hard, partly vegetated (Kelp *Laminaria*) bottom (Folkestad 1978, Durinck *et al.* 1994, Pihl 1995, Byrkjedal *et al.* 1997). Fjelds  (2004) reported that it prefers to feed in sub-tidal locations down to 15 m depth with sand- and gravel-bottomed areas with scattered rocks and patches of seaweed. Red-necked Grebes are widespread throughout the southern Baltic Sea in winter and visit coastal as well as offshore areas. Although they occur in deeper waters, 81% of the recorded birds in this area are observed in waters up to 15 m depth. Fish, especially gobies Gobiidae, dominate their diet here (Sonntag 2009).

14.3 Food Capture and Consumption

14.3.1 Food Capture in Red-necked and Other grebes

Red-necked Grebes and other Podicipedidae often catch active prey, and have to rely on their vision when feeding, which will usually restrict them to feed in shallow and fairly clear water. Although Podicipedidae have large olfactory bulbs, which might help them to locate places with good food supplies, olfaction would hardly be useful to guide the capture of active prey (Fjelds  2004).

Podicipedidae feed mainly by diving but are able to vary their feeding techniques and strategies according to where

and how each prey type is most easily found and handled. Under the water surface, Red-necked Grebes catch many, relatively slow moving, nektonic animals, which usually live among the submerged vegetation and submerged parts of reeds. Very frequently, to a greater extent than most other Podicipedidae, they pluck items off the bottom and off the underwater plants. The species, especially the nominate race, depends much more on gleaning invertebrates from the bottom (benthos) and aquatic plants than taking fish. The birds may dive in shallow water and probe with the bill along the edge of the boulders on the lake bottom to catch prey such as small sculpins Cottidae or crayfish. Sometimes they probe with only the tip of the bill under water (Munro 1941, Onno 1966, Borodulina 1976, Ouweneel 1985, Vlуг 1993).

Podicipedidae capture their prey by grasping it with a quick snap of the mandibles, and normally swallow their food under water, as quickly as possible, but bring larger items or items that are difficult to handle to the surface (see Fig. 36). The birds swallow their prey whole, often killing it first by pinching or shaking it in the bill (Stout and Nuechterlein 1999, Fjelds  2004).

Red-necked Grebes of the nominate race spend more time on food capture than the other European grebes, a consequence of their relatively large body and specialization in small prey (Onno, *cited in* Wobus 1964). Wintering Red-necked Grebes in the North Sea that are solitary feeders, take fish more often than do conspecifics that feed together with scoters and specialize in polychaetes (bristle worms, annelid worms). The first spend less time in feeding and more time in comfort activities (preening). Energetically, one fish prey may be equal to 25 to 325 polychaetes (Byrkjedal *et al.* 1997).

14.3.2 Feeding Techniques: Pursuers and Searchers, Leg and Jaw Anatomy

Red-necked Grebes are, as other grebes, specialized foot-propelled diving birds, and they obtain their food mainly by diving. The feet are placed laterally at the rear end of the body, where they can be rotated freely. The skeleton of Podicipedidae is dense, which means that they sit low on the water. The joints of the tibiotarsus and toes are extremely flexible. Flexibility, together with the position of the lobed feet far aft, confers great manoeuvrability while swimming under water. Although several other diving birds can achieve higher top speeds under water, they can scarcely measure up to the Podicipedidae when it comes

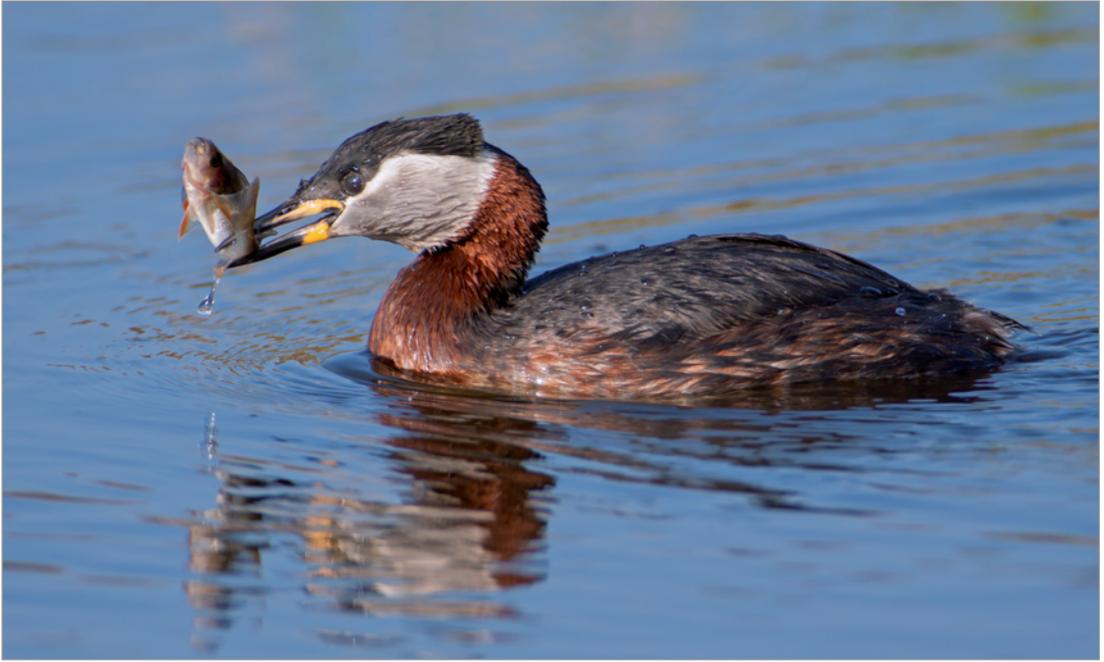


Fig. 36: Red-necked Grebe swimming with prey (probably Rudd *Scardinius erythrophthalmus*). Photo: T Runge (Schleswig-Holstein)

Fig. 36: *Rothalstaucher schwimmend mit Beute (wahrscheinlich Rotfeder Scardinius erythrophthalmus)*.

to manoeuvrability (Storer 1960, Llimona and Del Hoyo 1992, Fjeldså 2004).

The grebe species differ from each other in leg and jaw morphology, and, connected with this, in their feeding techniques; they belong either to the pursuers or to the searchers. Great Crested, Western and Clark's Grebes are usually pursuers. They dive in water clear of dense vegetation and actively chase agile prey, especially fish. Black-necked, Silvery and Hooded Grebes, on the other hand, are searchers, since they normally do not actively pursue their prey, but simply pick small slow-moving prey (emerging midges, amphipods, and corixid bugs) from the vast supply that is found in some wetlands. While capable of spurting 2 m/second in emergency, they mostly feed in a stationary position: descending right down with a clumsy jump and emerging after 10-15 seconds almost in the same spot. When feeding in dense vegetation, movements on the surface indicate that they usually stay within 1-2 m² (Fjeldså 2004).

It is not easy to assign the Red-necked Grebe to one of these feeding types. The species, especially *P. grisegena grisegena*, seems a searcher rather than a pursuer. As

stated above, it frequently gleans invertebrates from submerged plants, and picks prey from the bottom of ponds and lakes (Onno 1966, Vlug 1993). Fjeldså (1982a) reported: "Red-necked Grebes have strong jaw muscles, which in many respects resemble the unspecialized and probably primitive states shown by Golden Grebes *Rollandia* spp. (...). However, they approach their congeners *Podiceps occipitalis* (Silvery Grebe, JJV) and *taczanowskii* (Junin Flightless Grebe, JJV) (...) by showing some adaptations for foliage-gleaning, viz. moderate divergence of the insertion angles of the adductors and a relatively small pseudotemporal muscle with a short power arm. This means that the bird cannot fully contract the mandibular adductors without backward sliding of the mandible. Although Red-necked Grebes are certainly not so specialized as the two above-mentioned congeners, the conditional phrases are certainly narrower than in *Rollandia*."

14.3.3 Diving Capabilities and Fish Diet

The nominate race of the Red-necked Grebe, notwithstanding its large size, has a diet very similar to that of the Slavonian Grebe and differs clearly from the food re-

quirements of the largely piscivorous Great Crested Grebe (Fjelds  1973a). Especially in the breeding ponds, it usually feeds mainly on aquatic macroinvertebrates and, to a lesser extent, fish. Casual observations may give the impression that Red-necked Grebes often eat fish. However, grebes normally swallow small prey underwater, which means that the significance of little prey items in the diet are greatly underestimated.

Nehring (1894, cited in Hennicke 1903) found no fish remains in numerous stomachs of Red-necked Grebes, and Eckstein (1907, cited in Madsen 1957) found fish only in 3 of 13 stomachs. Fish remains were recorded in just one of 45 stomachs from Estonia (Onno 1960). Smogorzhevskii (1959) counted 710 prey items in 12 birds from breeding waters in Ukraine, of which not more than 2 items were fish. Gordienko and Zolotareva (1977) analysed 60 stomachs from birds on their breeding waters, the Naurzum Lakes, in North Kazakhstan. They found fish debris only in 4 stomachs. Of all the prey items found in the 60 grebes, not more than 0.03% was fish.

However, the nominate subspecies sometimes relies heavily on small fish and fry (Wobus 1964, Vlug 1993). In fish ponds in South-East Poland, Kloskowski (2011) found that young-of-the-year (0+) Carp *Cyprinus carpio* are an essential food source for young Red-necked Grebes. Large quantities of Ten-spined Stickleback *Pungitius pungitius* are frequently taken in breeding waters (Wagner 1997, Vlug 2002a). When Red-necked Grebes feed from large lakes and in coastal waters, fish may be an important food item. In the southern Baltic Sea, fish dominated the diet of the Red-necked Grebe and accounted for 85.2% of all prey items. Gobies Gobiidae occurred most frequently and were the dominant fish species, not only in numerical abundance, but also in the total consumed fish biomass (Sonntag 2009). Red-necked Grebes which make food-flights from the breeding sites to the Baltic Sea frequently feed their larger young with relatively large fish such as Butterfish *Pholis gunnellus*, Sand Goby *Pomatoschistus (Gobius) minutus*, Common Goby *P. microps*, sand lances or sand eels *Ammodytidae* and Snakeblenny *Lumpenus lampraeformis* (Vlug 1993, 2009) (see Fig. 37 and 38).

P. g. grisegena is unable to dive as well as the Great Crested Grebe for larger (faster) fish. Fish taken by Red-necked Grebes are usually less than 15 cm, in general 2-7 cm long (Witherby *et al.* 1947, Madsen 1957, Wobus

1964, Markuze 1965, Davis and Vinicombe 1980, Piersma 1988b, Vlug 1993). Great Crested Grebes also take many relatively small fish (Geiger 1957, Simmons 1974, B ttiker 1985). However, this highly piscivorous bird takes on average larger prey than *grisegena*. It is able to catch and swallow fish that are 20 cm (Dace *Leuciscus leuciscus*), 21.5 cm (Roach *Rutilus rutilus*), 27 cm (Pike *Esox lucius*), over 30 cm (Eel *Anguilla anguilla*) and c. 40 cm long (Pike) (Geiger 1957, B ttiker 1985, Felten 2013). This means that the daily needs of a Great Crested Grebe (c. 200 g) may sometimes be met through a single successful dive (Fjelds  2004).

Piersma (1988b) analysed the stomach and oesophagus contents of 18 Red-necked and 6 Slavonian Grebes. The birds had drowned in gill nets while foraging in winter in Lake IJsselmeer, The Netherlands. Both species fed exclusively on fish. Smelt *Osmerus eperlanus* was the most important prey for both grebes and was almost the only prey species of the Slavonian Grebe, though the diet of the Red-necked Grebe was a little more varied. Fish taken by Red-necked and Slavonian Grebes were 2-12 cm long. Both species took more, smaller Smelt than expected from the food supply that is present in the habitat. However, the relatively large-billed Red-necked Grebes took, on average, even smaller Smelts (mean 5.99 cm) than the small-billed Slavonian Grebes (mean 6.53 cm). Slavonian Grebes may be the more speedy and agile species under water. On the basis of a comparison of limb morphology of *P. grisegena* and *auritus*, Onno (1966) also concluded that the Slavonian Grebe is the superior diver. Perhaps this is why, in the samples of Piersma (1988b), Slavonian Grebes were slightly fatter and contained more fish than Red-necked Grebes. Food selection in grebes may be determined more by agility than bill dimensions (the bill of the Red-necked Grebe is almost twice as large as that of the Slavonian Grebe) (Piersma 1988b). Another example is perhaps the largest of the grebes, the Great Grebe *Podiceps major*; although this bird has a bill length (exposed culmen to the feather edge) of 72-85 mm, it takes fish up to 10.5 cm long, but mostly of a length between 2 and 5 cm! It seems that ecological segregation in many cases involves functional systems other than the bill (Piersma 1988b, Llimona and Del Hoyo 1992, Fjelds  2004).

The fish caught by Red-necked Grebes in the Baltic Sea often live at the bottom and frequently hide in burrows in the substrate, in crevices in rock or amongst seagrass,



Fig. 37: Red-necked Grebe flying with prey from the Baltic Sea to the breeding water. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 37: Rothalstaucher fliegend mit Beute aus der Ostsee zum Brutgewässer.



Fig. 38: Red-necked Grebe swimming with prey caught in the Baltic Sea. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 38: Rothalstaucher schwimmend mit Beute, gefangen in der Ostsee.

or adhere to rocks. The birds possibly find these fish by systematically searching the bottom of the sea, exactly in the same way in which they systematically search for the larvae of aquatic insects, molluscs and crustaceans at submerged plants and the bottom of the breeding pond (Vlug 2009).

In winter, larger (faster) fishes are attainable as prey, as the decrease in water temperature leads to a reduction in the maximum swimming speed of fish. Wintering Red-necked Grebes in lakes with great transparency sometimes pursue these larger fish, which live closer to bottom, at greater depth (up to 42 m or more in Lake Starnberg, Southern Bavaria) (Müller 1989, Müller *et al.* 1989, 1990).

It is asserted that *Podiceps grisegena holboellii* of North America is more piscivorous than the nominate race (Cramp *et al.* 1977, Fjeldså 2004). However, although it consumes many fish when available, the fish are usually relatively small-bodied, and it also regularly nests on fishless waters. Nuechterlein *et al.* (2003) reported that the adult Red-necked Grebes on Lake Osakis, Minnesota, spend little time feeding, requiring only 15-30 minutes to catch several 10-15 cm fish. On Armstrong Lake in Alberta, *holboellii* consumes small-bodied fishes (Fathead Minnow *Pimephales promelas* and Brook Stickleback *Culaea inconstans* between *c.* 50 and 65 mm), along with many aquatic and terrestrial invertebrates; and at Duck Lake and an adjacent marsh, British Columbia, the adult birds usually feed their larger young (until 7 weeks old) with fish smaller than 100 mm (Yellow Perch *Perca flavescens*, Pumpkinseed Sunfish *Lepomis gibbosus* and Largemouth Bass *Micropterus salmoides*) (Ohanjanian 1989, Stout and Nuechterlein 1999, Paszkowski *et al.* 2004, McParland *et al.* 2010) (see 14.4.6 and 14.5).

14.3.4 Diving Times and Diving Depth

When diving, the nominate subspecies may be submerged for up to a minute and longer (130 seconds) (Madsen 1957, Müller *et al.* 1989). Onno (1960) reported a maximum of 46 seconds and Géroutet (1965) an average of 53 seconds (range 17-74 seconds).

However, feeding dives of less than *c.* 30 seconds seem to be normal (Madsen 1957). Many sources indicate dives of relatively short mean duration, for example 18.4 seconds (Dewar 1924, *cited in* Simmons 1970a) and 20 seconds (Ingram and Salmon 1941, *cited in* Simmons

1970a). Between 31 January and 7 March 1968, Hancock and Bacon (1970) timed 155 feeding dives, and 40 intervals between dives, of a Red-necked Grebe on the west water at New Theale gravel pits, Berkshire, England. They found a mean duration of a dive of 25.0 seconds (range 8.2-40.9), and a mean interval between dives of 19.4 seconds (range 0.5-45.0). In Northern Caucasia, 530 feeding dives in winter averaged 27.28 seconds (range 5.2-50.4 seconds), and 117 in the breeding period 15.16 seconds (range 4.0-32.2 seconds) (Ryazanova 2002).

Variations in the mean duration of the feeding dives seem chiefly correlated with the depths of water in which the birds are diving. Because Red-necked Grebes prefer to live and feed in richly vegetated, and shallow wetlands, their diving times are often of relatively short duration. Simmons (1970a) timed 189 feeding dives by Red-necked Grebes: 59 on the Danish island of Sjælland (Zealand) between 7 and 18 June 1967 and 130 in Somerset, England, on 26 and 30 September 1969. The Danish records were of various birds on one small shallow breeding pond and of a male and female on another. The depth of water in both ponds was probably at least 180 cm. The Somerset records all involved a single, transient, juvenile diving off the north shore of Cheddar Reservoir, in water up to 370 cm deep. The Somerset grebe was making significantly longer mean dives (29.3 seconds, range 16-42) than the Danish birds (mean 24.8 seconds, range 14-34). Simmons (1970a) concluded that the depth of water is probably the most important single factor determining the mean duration of a long series of dives.

This conclusion is corroborated by the work of Epprecht (1982), and Müller *et al.* (1989). Epprecht (1982) measured diving times of wintering Red-necked Grebes in Zürichsee (Lake Zurich), Switzerland. In water with a maximum depth of *c.* 8 m the diving times were between 10 and 39 seconds (*n* = 18 dives), in water between *c.* 8 and 15 m the maximum time was around 65 seconds (*n* = 28 dives), and at greater depth (16-19 m) the diving times ranged from 71 to 93 seconds (*n* = 12 dives). Thus, the deeper the water, the longer the diving times.

Müller *et al.* (1989) timed 44 dives of wintering Red-necked Grebes in the very deep Lake Starnberg, Southern Bavaria (mean depth 53.2 m, maximum depth 127.8 m). The dives averaged 94 seconds (range 40-130 seconds), the longest durations (maximum 130 seconds) being in

deeper parts of the lake, the shortest (minimum 40 seconds) in shallow parts (Müller *et al.* 1989).

Cramp *et al.* (1977) suggest that the diving times of the larger race *holboellii* ("up to 1 minute") are longer than those of the nominate race ("generally less than 30 seconds"). Saunders (*cited in* Bent 1919) watched a pair of *holboellii* and wrote: "I timed them to see how long they stayed under, and, after several observations of both birds, found the time to be almost uniformly 55 seconds in every case. The time was so exact that I could tell when a bird dove just when to expect it to reappear." Palmer (1962) stated that, judging from various reports, the duration of dive is often about 1 minute.

A Red-necked Grebe, foraging in deep water off southern Vancouver Island, British Columbia, had a mean dive duration of 134 seconds ($n = 21$ dives, $SD = \pm 32.9$) (Clowater 1998). According to Stout and Nuechterlein (1999) the range of dive durations of this bird was 23-171 seconds. These records of feeding dives more than 2 min. long in marine areas suggest deep diving.

14.3.5 Types of Feeding Dives (*see also* 15.1.3)

Red-necked Grebes use two types of feeding dives (Davis and Vinicombe 1980, Simmons 1980, Stout and Nuechterlein 1999). In the "smooth" or "level dive", the birds submerge in a smooth manner typical of Great Crested and Western Grebes. Simmons (1977) wrote about the level dive in *Podiceps cristatus*: "It typically surface-dives, submerging from a stationary position, first sinking lower in the water while depressing its contour feathers (including crest and tippets) to reduce buoyancy by pressing out surplus air from its plumage, and then smoothly disappearing bill-first with a rapid forward and downward swing of the neck, body following. Normally, this submergence causes little turbulence on the water; as the bird still holds its legs forward as it disappears, they are obviously not used to give propulsion until it is under the surface." Nuechterlein (1981a) described the level dives in Western Grebes as follows: "Level dives are the most common: the grebe sleeks its head and neck feathers, then propels itself smoothly forward beneath the water in a seemingly effortless, head-first motion. Neither the breast feathers nor the tarsi emerge from the water (...), and the bird submerges with scarcely a ripple."

In the "springing dive" there is an initial leap well clear of the surface, entering at an acute angle, rather like a Shag *Phalacrocorax aristotelis* (Davis and Vinicombe 1980). Nuechterlein (1981a) stated: "In springing dives (of Western Grebes, JJV), the grebe cocks its head backwards, after sleeking its feathers, then springs up out of the water while arching neck and body so as to enter the water more vertically. In its most exaggerated form, the entire body, including the feet and tarsi, emerge from the water as the head disappears under the surface (...)."

The type of feeding dive used seems to depend to some extent on the depth of the water, but also on the location of its usual capture (at the bottom or in the intermediate water layer), and on weather conditions (wind, wave action) (Davis and Vinicombe 1980, Simmons 1980, Stout and Nuechterlein 1999). Nuechterlein (1981a) suspected that the Western Grebe goes deeper in springing dives than in level dives. The Slavonian Grebe uses the more violent springing dive in rough seas or when diving into the swell on coasts. Smooth dives of Red-necked Grebes may predominate in breeding-waters (shallow water, in general slight wave action) and springing dives in winter lakes and at sea (deep water, often large wave action) (Vlug 2002a). It is likely that the two types of feeding dive grade into one another (Storer 1969, Nuechterlein 1981a).

14.3.6 Less Common Methods of Capturing Food

During the feeding periods, Red-necked Grebes sometimes show some surface feeding. In the time of mass emergence of midges, they feed like Black-necked Grebes by picking midges from the surface (B Koop, J J Vlug).

Red-necked Grebes and other Podicipedidae occasionally hunt from the water surface for invertebrates and small fish by peering under water, neck-dipping, up-ending, and plunging to re-appear tail-first (Wobus 1964, Fjeldså 1973a, Simmons 1977, Stout and Nuechterlein 1999, Fjeldså 2004). Simmons (1977) described this behaviour extensively in one of his studies on Great Crested Grebes. The method is especially used in shallow water or amongst submerged vegetation such as bistort *Polygonum* and crowfoot *Ranunculus*. Firstly, the bird peers by looking under water with part of its head submerged, up to just beyond the level of the eyes. Peering thus, it often pushes the head and bill forwards and brings them back with a continuous nodding action (shovelling), usually while moving forward (swim-peer-

ing). It may also, while peering, sweeping the head laterally from one side to the other. While prey may occasionally be caught while peering, this is usually only a method of detecting prey; sooner or later, the surface hunting grebe sights food beneath it and actively tries to secure it, first neck-dipping by entirely submerging the head and most or all of the neck. If the prey still lies beyond reach, the grebe next starts up-ending by submerging most of its body as well, maintaining it in an almost vertical position in the water by vigorous paddling of the feet and with only the tail-end visible. If necessary, it will then submerge further so as partly or wholly disappear, “screwing” itself down briefly by kicking movements of the feet usually to re-appear tail-first with a bob at the same spot, unlike when really surface-diving (Simmons 1977). In normal surface-diving the birds usually dive without apparent preliminary searching.

Insects are also taken from the emergent vegetation, and sometimes low-flying insects are snatched from the air.

14.3.7 Prey Handling

Fjeldså (2004) wrote: “The primary prey types of grebes are invertebrates, as the birds use rapid interaction between pincer-like bill-tips and a smooth, fleshy tongue (quite unlike the spiny tongue of loons). Only secondarily did some species specialize on a fish diet. This is evident if we consider the evolutionary relationships of grebes: the specialized fish-eating grebes (Great, Great Crested and Swan Grebes, and three single-lake endemics) all represent terminal branches on the phylogenetic tree (...).” Although the Red-necked Grebe is narrowly related to the Great Crested Grebe, it is much less piscivorous than the latter. It captures its prey (larger invertebrates and smaller vertebrates) by grasping it with a quick snap of the mandibles (Stout and Nuechterlein 1999). The bird usually swallows its prey underwater, whole, and as quickly as possible, but brings larger items, or those that are difficult to handle, to the surface.

The diameter of fish-prey is an important variable in deciding whether it can be ingested. Fish are manoeuvred and swallowed head first. Fish are killed either by crushing their head with the beak or by severe shaking, though sometimes they are swallowed alive. If fish are too big for swallowing, they are abandoned in the end. The bird occasionally drops large or spiny prey back into the water and recaptures it with a quick dive (Wobus 1964, Cramp *et al.* 1977, Stout and Nuechterlein 1999).

Spiny prey, such as North American ictalurid catfish, is dangerous to Red-necked Grebes and other gape-limited predators. Forbes (1989) studied the feeding behaviour of five piscivorous birds at Duck Lake and Corn Creek Marsh in British Columbia. In these shallow (less than 2 m) eutrophic systems three species of fish, Yellow Perch *Perca flavescens*, Pumpkinseed *Lepomis gibbosus*, and Black Bullhead *Ictalurus (Ameiurus) melas*, the latter an ictalurid catfish, occur in abundance. He discovered that locking spines are not an effective defence against predators such as Ospreys *Pandion haliaetus* which do not swallow prey whole, but instead dismember them. However, the handling times of Red-necked, Western and Pied-billed Grebes and Great Blue Herons *Ardea herodias* were longer for bullheads than for other prey of comparable mass. In Duck Lake, Red-necked Grebes did not eat Black Bullheads, and in Corn Creek Marsh only 14% of their fish diet consisted of this prey (and 86% of Yellow Perch). Although handling costs were higher, Pied-billed Grebes took bullheads more often than Red-necked or Western Grebes. This is consistent with differences in morphology. With their stout bills and heavy jaw musculature, Pied-bills are better able to manipulate, tear, and crush large prey than are slender billed forms such as Red-necked and Western Grebes.

Birds can acquire skills to handle prey with spines. In a study in British Columbia, approximately 20% of the Three-spined Stickleback *Gasterosteus aculeatus* escaped from adult Red-necked Grebes, while subadult and inexperienced grebes had about 80% manipulation failure (Reimchen 1988).

14.3.8 Diurnal and Nocturnal Feeding

The diurnal feeding of Red-necked Grebes normally decreases during midday and in the afternoon (Wobus 1964). The extent of nocturnal feeding is unknown, but it is highly possible that at least some feeding takes place during clear nights, because the species is quite active at dusk and dawn, and its calling may even be most intense during moonlit nights and during the light summer nights in northern parts of the world.

14.3.9 Food Capture and Vision

In his book “The Grebes”, Fjeldså (2004) gives information on the vision of Podicipedidae: “The very intense colour of grebes’ eyes (...) is caused, in addition to iris colour, by an extremely constricted pupil fringed by a

vermiculated white line (...). The constricted pupil suggests that the retina is pre-adapted to the low light levels encountered underwater. Similarly intense eyes with a "pinhole pupil" can also be seen in penguins, loons, and some cormorants. The pupil dilates to a large circular aperture underwater, judging from photos of diving grebes (...). Although grebes mainly feed in full daylight, some species (especially White-tufted Grebes) are crepuscular feeders (active in twilight, JJV), possibly taking advantage of the fact that the fish leave their hiding places at twilight and move up towards the surface. Although it may be very dark underwater (because of the total reflection of light, when the angle of incoming light to the water surface is small), the prey may be spotted from below, against the light surface"

Fjeldså (2004) continues: "The eyes of diving birds must also be adapted to function in the dense aquatic medium. This is not so critical for birds that dabble, filter-feed at the surface, or for plunge divers spotting their prey from above water. However, need for acuity is certainly strong for those that search underwater for hidden prey and sometimes pursue very active prey. The problem is that a typical terrestrial eye will be very long-sighted (hypertrophic) in water, and a specialized aquatic eye will be short-sighted (myopic) in air."

Earlier speculations that the transparent nictitating membrane of diving ducks, alcids, loons, and grebes, or a layer of air trapped between this membrane and the cornea, could function like the goggles of human divers have been rejected. The thin and uniform thickness of the nictitating membrane (0.2-0.3 mm), which assumes the shape of the cornea when drawn over it, does not contribute to accommodation (...). So it is because of extreme accommodative ability that these birds manage to focus underwater. In this connection it is worth noting that pursuit-diving birds tend to have a very thick cornea. Accommodation is achieved by two groups of striated muscles acting on the curvature of the cornea and on the lens shape, which becomes more rounded with the anterior part bulging out into the pupil. Birds have, in general, a higher accommodative power than mammals, and in diving birds this amounts to 50-80 diopters, which is 5-10 times higher than in humans."

Each cone in the retina of a bird contains an oil droplet. The droplets are placed so that light passes through before reaching the visual pigment. The oil droplets are

thought to be essential for colour vision and for reducing chromatic aberration. It is believed that there is an association between relative abundances of the various types of oil droplets in bird retinas and the birds' foraging habits and habitat. Begin and Handford (1987) studied the retinal oil droplets in the five Canadian grebe species. If Western, Red-necked, Black-necked, and Slavonian Grebes retinas are adapted primarily to coastal marine conditions, then one would expect them all to approach the oil droplet constitution of the Shag *Phalacrocorax aristotelis* or Razorbill *Alca torda*, since these are both marine pursuit divers, possibly operating under lowered light. However, these two species have about 20% red and orange droplets, while all of the grebes in the study of Begin and Handford (1987) had between 30 and 40%; the grebes compare better with many terrestrial species than with other underwater marine predators (e.g. the American Coot *Fulica americana* has about 45% red and orange droplets).

Begin and Handford (1987) were especially interested in the comparison of Red-necked and Western Grebes. Western Grebes feed primarily pelagically, both on breeding lakes and in their marine winter habitat. They probably employ the attack from below technique and are (year-round) strongly counter shaded, as are their chicks; they also show features of cranial anatomy and behaviour suggesting an upward strike at prey. Since the visual task would be to discriminate dark targets silhouetted against a bright back-ground, i.e., enhancing contrast, we may expect a retina similar to that of aerial or crepuscular hunters, that is, one relatively low in red- and orange-coloured droplets and high in colourless droplets. Red-necked Grebes, on the other hand, forage primarily at or near the bottom in well-lit shallow water and face a visual task very similar to that of terrestrial birds and so may be expected to show high levels of red and orange droplets. However, the study of Begin and Handford (1987) failed to show clear species differences in droplet proportions.

14.3.10 Commensal Feeding Associations

Red-necked Grebes typically forage alone. However, at wintering sites, commensal feeding associations with scoters have been recorded. In Norway and Denmark, they form associations with Velvet Scoters *Melanitta fusca*, and in British Columbia with the very abundant Surf Scoter *M. perspicillata* and with the less abundant Velvet (White-winged) Scoter (Folkestad 1978, Pihl

1995, Byrkjedal *et al.* 1997, Stout and Nuechterlein 1999, Byrkjedal 2000). Also in the moulting period (of *grisegena*), an association between the Red-necked Grebe and *Melanitta fusca* was observed in Danish and Norwegian marine waters (Pihl 1995).

Byrkjedal *et al.* (1997) investigated the feeding associations between the Red-necked Grebes and Velvet Scoters wintering along the coast of southwest Norway: “The study was made on the coast of Jaeren, a stretch of about 60 km of shallow water exposed to the North Sea with patches of sandy bottom partly colonized with Kelp *Laminaria* making up about a quarter of the coast. About 10,000 waterfowl of 20 species spend the winter there, amongst them 50 to 100 Red-necked Grebes (...)” The grebes were found to feed either solitarily or in close association with other waterbirds. Among the available waterfowl, Velvet Scoters were strongly preferred as partners by the Red-necked Grebes. On a stretch of coast observed in mid-November, 18 Red-necked Grebes were seen in association with other birds; 16 of these grebes (89%) were with Velvet Scoters, although this duck made up only 30% of the waterfowl. The remaining two Red-necked Grebes associated with Slavonian Grebes.

Grebes associating with scoters synchronized their activities with those of the scoters: when a scoter stopped feeding so did the grebe, but instead of seeking a new scoter which was actively feeding, the grebe continued its association with the original scoter. Grebes kept close to their chosen scoter, both while they were feeding and when not feeding. In feeding associations, the grebe dived a few seconds after the scoter it accompanied. Scoters were never seen to attack or show hostility toward the grebes or to try to avoid them.

The Velvet Scoters fed on sandy bottoms, where they dug for burrowing organisms, mainly sea urchins *Echinocardium flavescens*, but also on animals such as crabs *Carcinus* and *Portunus*, and flounders (flatfish species). The Red-necked Grebes were never seen attempting to steal prey or pick morsels from the prey brought to the surface by the scoters for handling. It is most likely that the grebes fed on organisms made available but not preyed upon by the scoters. Errant polychaetes (annelid worms) are a likely group of prey. They had a notably high abundance in the bottom samples, emerged actively out of the substrate when the latter was probed with a knife (presumably not dissimilar to the

feeding action of scoters), and polychaetes have been found to be important food of wintering Red-necked Grebes in Danish waters (Fjeldså 1982a). Also, small fish like gobies Gobiidae and Bullheads *Cottus* (*Myoxocephalus scorpius* (sculpins Cottidae), which often lay still on the bottom until closely approached, and sand lances (sand eels) *Ammodytes*, which regularly lie buried in the sand, may be disturbed by the scoters. Observations on grebes showed that they surfaced with *Ammodytes* in a few cases after having dived along with scoters.

Solitary grebes showed a food-searching behaviour similar to that of divers *Gavia*. Unlike grebes following scoters, they often peered under the sea surface while swimming. They dived less often than did grebes associated with scoters, stayed a shorter time under water, covered a much larger horizontal distance under water and swam a greater distance between dives. The solitary grebes brought fish (sand lances Ammodytidae, herring-like fish Clupeidae, Sea Stickleback *Spinachia spinachia* and sculpins Cottidae) to the surface significantly more often than did grebes associated with scoters. Energetically, one fish prey may be equal to 25 to 325 polychaetes. This may explain why solitary grebes spent less time in feeding and more time in comfort activities (preening) than did scoter-associated grebes.

The association appears to be a route whereby naive first-year birds can more easily obtain prey. Byrkjedal *et al.* (1997) wrote: “Why should grebes associate with scoters? Presumably scoters make prey so easily available that they constitute an attractive food resource to the grebes even though the most commonly available prey, polychaetes, may be nutritionally less favourable. The birds associating with scoters are often birds of the year. These birds may have fed on insects in freshwater localities (Wobus 1964) before they reach the sea for the first time in their life. Polychaetes may be more similar to the prey they are used to, besides being easier to capture than more agile fish. The association of grebes with scoters diminishes over the winter: presumably the grebes gradually become more skilled at capturing fast-moving prey, enabling them to adopt the more demanding but energetically favourable pursuit of diving for fish.”

14.3.11 Juvenile Red-necked Grebes Learn Adult Foraging Skills

Juvenile birds differ from conspecific adults in their diet and methods of prey capture and prey handling. Juve-

nile-adult differences in foraging result from immaturity of the beak, skeleton-muscular and neurological systems and the time required to learn foraging skills. Juvenile birds appear to be under strong selection to reach adult form and function as rapidly as possible (Marchetti and Price 1989). Undoubtedly, first-year Red-necked Grebes are no exception, but not much is known about the feeding techniques of young grebes.

As stated above (see 14.3.10), the commensal feeding association at wintering areas between Red-necked Grebes and scoters appears to be the method in which inexperienced first-year birds can more simply secure food. The skills needed to dive for more nutritious but agile fish are probably gradually acquired through the winter as more grebes adopt solitary feeding (Byrkjedal *et al.* 1997).

Red-necked Grebes can acquire skills to handle prey with spines. In a study in British Columbia, approximately 20% of the Three-spined Stickleback *Gasterosteus aculeatus* escaped from adult Red-necked Grebes, while subadult and inexperienced grebes had about 80% manipulation failure (Reimchen 1988) (see 14.3.7).

14.3.12 Food Flights

Red-necked Grebes rarely fly outside the migration period, and typically do not fly to foraging areas. Usually, they swim on the breeding water, with young accompanying the foraging adult, either brooded on the back of the other parent, or, when 2-3 weeks of age, swimming alongside. However, birds nesting on lagoons and other shallow wetlands separated from the Baltic Sea by a barrier beach or dyke make food flights to the adjacent sea. This especially occurs in northern Germany and Denmark. The Baltic Sea offers the birds abundant food but no breeding sites; thus, they have to use the lagoons as nesting grounds.

The adult grebes obtain (almost) all their own food from the sea and not from the lagoon, but the chicks are partly fed with prey from the breeding water and partly with fish from the Baltic Sea. The amount of food that is flown in gets larger as the young grow.

The old grebes foraging at sea obtain their food in shallow water (presumably with a depth between 1.5 and 10 m), especially in seagrass meadows *Zostera marina*. They catch relatively large fish, fly with these fish in their bills

over the barrier beach or dyke to the breeding water. Upon landing, they present the prey to their young, who remain in the breeding water until they are capable of flight. The young frequently receive Butterfish *Pholis gunnellus* (up to a length of 15 cm), gobies Gobiidae, and sand lances or sand eels Ammodytidae (Nielsen and Tofft 1987, Vlug 1993, 2009).

As adult Red-necked Grebes on lagoons and other shallow wetlands near the Baltic Sea not (or only to a very small extent) depend on the food supply of the breeding-waters, they can achieve extremely high population densities here (up to 13.3 breeding pairs/ha). Nowhere in the whole breeding range of the Red-necked Grebe have such high densities ever been recorded (Vlug 1993, 2009; R K Berndt, B Koop, J J Vlug) (see 11.3.1 for more details).

Reproductive rates of *griseogena* on a lagoon near Hohenfelde (14 breeding pairs in 2008) averaged higher than the overall mean of lagoons in Schleswig-Holstein. This high reproduction of the grebes is possibly caused by a relatively favourable food situation for the chicks. In Hohenfelde large meadows of submerged vegetation are found, especially Spiked Water Milfoil *Myriophyllum spicatum*, with a corresponding richness of prey for the grebe chicks which therefore are less dependent on fish from the Baltic Sea. This is in stark contrast to the situation in the majority of the lagoons on the island of Fehmarn, where prey items are scarce. The first ten days or so the chicks are completely dependent on the food found in the breeding water. The adults begin to fly fish back from the Baltic Sea when the young are in their second week, and because of poverty of food in the breeding wetland most of the food for the young has to be caught at sea. Because Red-necked Grebes have a high wing-loading, food flights are energetically costly, and their frequency is not high, and it is likely that many chicks on the island of Fehmarn die of starvation. The adults bring relatively large food items to their young, but this does not seem to compensate for the low feeding frequency. However, the large Baltic Sea offers the adult birds predictable conditions and a great deal of food, and so long-life expectancies of the old grebes are high. Probably, Red-necked Grebes breeding on lagoons follow the strategy of living a long life with a high life-time reproduction rather than trying to have high annual productivity with a greater chance of dying at a relatively young age (Vlug 1993, 2005, 2009).

In addition to the energy costs of food flights, there is another disadvantage of these flights. Older chicks make continuous attempts to steal fish from incoming adults who are not their parents. The fish is quickly grabbed from the adult's bill as it lands and swallowed. This kleptoparasitism is especially striking in the Grüner Brink, a lagoon on the island of Fehmarn, where food is scarce.

Although food flights in Red-necked Grebes are common near the Baltic Sea, they are not widespread (they are more widespread in Great Crested Grebes, see for example Lunau 1933, Leys, Marbus and De Wilde 1969, Vlug 1983, 2005, and Kjeldsen 2008). In North America food flights are recorded only at Creston in British Columbia (Ohanjanian 1986, 1989). A number of birds here nested in Bulrush (or Cattail) *Typha latifolia* in a marsh behind a man-made dyke, and other grebes nested on accumulations of Spiked Water Milfoil *Myriophyllum spicatum* on an adjacent lake (Duck Lake). The birds that nested in the marsh ("fliers") obtained a part of their chicks' diet locally, and another part from Duck Lake: they flew up to 2.5 km to the lake to forage for their young and themselves. Red-necked Grebes that nested on the lake ("swimmers") obtained all their chicks' prey from the lake.

The "fliers" foraged in the same areas of the lake as did the "swimmers"; however, there were significant differences between them in the size of prey they selected for similarly-aged young. The "fliers" took no small fish (≤ 50 mm) from the lake, whereas the "swimmers" did. The "fliers" fed small fish (and invertebrates) to their young, it is true, but these were obtained locally, behind the dyke, not flown in. In addition, whereas both groups took more medium (51-75 mm) than large fish (76-100 mm) from Duck Lake, the "fliers" took many more large fish than did the "swimmers" (40.5% versus 17.9%). Because food flights are energetically costly, it seems that the "fliers" try to compensate for the loss of energy by taking larger, more profitable prey than the "swimmers" (central place foraging theory).

Chicks were fed both invertebrates (primarily larvae of dragonflies and damselflies Odonata) and fish. The importance of odonates decreased as the chicks aged. Parents behind the dyke began to fly fish back from Duck Lake when the young were in their second week. The proportion of the diet that was flown in increased as the

chicks grew. Yellow Perch *Perca flavescens* was the preferred prey species.

The grebes nested behind the dyke because the habitat quality was superior, with greater protection from wind and wave damage, more stable water levels, lack of perches for aerial predators, and low human disturbance. The clutch size behind the dyke (mean = 3.25 eggs) was smaller than in Duck Lake (mean = 4.07). Ohanjanian (1986) attributed this to the greater energetic demands on laying females who must fly to forage for themselves throughout the pre-laying and laying periods, but it seems more plausible that by reducing the clutch size (and so the number of chicks), the adults decreased the extra costs of reproduction (flying to forage for the chicks) and increased their own life expectancies. Nevertheless, the hatching success (the percentage of complete clutches which hatched at least one young) behind the dyke was significantly greater than on Duck lake and young hatched about one month earlier (Ohanjanian 1986).

14.4 Diet

14.4.1 Dietary Studies in Podicipedidae

Although their oesophagus has no crop which might contain unfermented food, grebes are well suited for dietary studies because of their feather-eating habits. The swallowed feathers break down in the stomach, to form a greenish, felt-like spongy material that may fill up half the stomach volume, and also forms a plug in the pyloric exit. This feather debris retains indigestible roughage for a considerable time. So, every collected grebe provides a good deal of information, unlike in other birds, where many collected individuals will have empty stomachs. However, whole prey is rather exceptional and careful microscopic examination is needed as it is necessary to identify and count the large numbers of tiny fragments, such as well-chitinized mandibles or centres of etched fish otoliths (Fjeldsø 1973a, 2004).

14.4.2 Overlapping Diets

Although several grebe species are specialists, all are opportunists and may take prey in which they do not specialize when such prey is particularly abundant, or their speciality is rare or unavailable. Thus, where several species of grebes are sympatric, there is a considerable overlap in diet (Storer 2000b).

14.4.3 Plant Material in Stomachs

Red-necked Grebes and other Podicipedidae feed on living animals. However, frequently plant material, such as Pondweed *Potamogeton*, Stonewort *Chara fragilis*, and seagrass *Ruppia* and *Zostera*, is found in the stomachs of *grisegena* (e.g. Wetmore 1924, Madon 1931, Madsen 1957, Kiss and Sterbetz 1973, Oleĭnikov *et al.* 1973, and Gordienko and Zolotareva 1977). The few fragments of unfermented plant material found in grebe stomachs in no way suggest that plants are part of their normal diet. Some waterweeds or filamentous algae are taken accidentally with animal food, or they come from the digestive tracts of the prey (Storer 2000b, Fjelds  2004).

Madsen (1957) investigated stomachs of 25 Red-necked Grebes from Danish marine or brackish-water localities. He stated: "Traces of brown algae and sea-grasses (*Ruppia*, *Zostera*, *Potamogeton*) are found in about half the stomachs, probably always as an accidental content. In a single stomach there were several, a few cm long, pieces of sea-grass, but in the same stomach were remains of many fishes, and the vegetable matter thus was undoubtedly swallowed by accident along with the fishes. Five stomachs, of birds from Fakse Bay, K ge Bay, Kalundborg, and Sams , contained one or two seeds, *Potamogeton*, *Ruppia*, *Zannichellia*, and an undeterminable one. One stomach content also included a few fruiting bodies of Musk-grass (*Chara*)." He also analysed 5 *grisegena* stomachs from Danish fresh-water localities: "Some vegetative growth was present in the stomach content of the bird from Kirke V rl se, no doubt taken accidentally in the gathering of the many fishes, insects, and snails taken in the meal."

14.4.4 Staple Diet of the Nominate Subspecies

The staple diet of *Podiceps grisegena grisegena* in the breeding waters consists of aquatic insects and their larvae (such as dragonflies and water-beetles), molluscs (freshwater snails), crustaceans, amphibians, small fish and fry (Naumann 1838, Hennicke 1903, Curry-Lindahl 1959, Wobus 1964, Vlug 1993, 2002a, Kloskowski 2011). Probably, annelids (leeches Hirudinea) are also an important food item at some breeding sites (Vlug 2002a).

14.4.5 Diet Composition of the Nominate Subspecies

Of 34 stomachs from different parts of Europe and from different times of the year, 28 stomachs contained insects and 8 contained fish (Madon 1931).

The diet of 12 Red-necked Grebes from breeding waters in Ukraine (710 prey items) consisted almost exclusively of molluscs (127 river snails *Viviparus viviparus*), insects and their larvae (521 prey items, mainly 110 caddis flies Trichoptera, 34 leaf beetles Chrysomelidae, 62 scavenger beetles Hydrophilidae, 121 diving beetles Dytiscidae, 49 backswimmers *Notonecta glauca*, and 133 saucer bugs *Naucoris/Ilyocoris cimicoides*) and crustaceans (37 water slaters/hog-lice *Asellus aquaticus* and 20 tadpole shrimps *Triops/Apus*). Not more than 2 of the 710 prey items were fish, and 1 item was a tadpole (Smogorzhevskii 1959).

Invertebrates dominated the contents of 73 stomachs from breeding waters (fish ponds) in the Volga delta (92-100% by numbers and 71-97% by weight), mainly tadpole shrimps *Triops (Apus)*, larvae of scavenger beetles Hydrophilidae, diving beetles Dytiscidae and dragonflies Anisoptera. Waterbugs Hemiptera (saucer bugs *Naucoris*, Long-bodied Water Scorpions *Ranatra linearis* and backswimmers Notonectidae) are also consumed by the birds. Large quantities of imagos (imagines) of diving beetles Dytiscidae are especially found in the diet of young Red-necked Grebes at the end of the summer. Leaf beetles Chrysomelidae, true weevils (snout beetles) Curculionidae, medium-sized and small imagos of scavenger beetles Hydrophilidae are food of Red-necked Grebes, but by weight they are not important. Small Marsh Frogs *Rana ridibunda (Pelophylax ridibundus)* and their tadpoles are always found in the diet of *grisegena*. Although their numbers are not large, these amphibians are an essential part of the food by weight. From June fish regularly occur in the stomachs, but their numbers are not large. Most consumed fish are young Carp with a length of 2-7 cm, and less frequently Pike-perch *Sander (Stizostedion) luciperca* of 2.5-3 cm length (Markuze 1965).

A total of 60 stomachs of adult Red-necked Grebes from western Anterior Caucasus (breeding period) contained a few fish (2.0-2.5% by weight). Aquatic insects and their larvae predominated. The stomachs contained many scavenger beetles *Hydrous/Hydrophilus*, diving beetles *Dytiscus* and *Cybister*, water boatmen *Corixa*, long-bodied water scorpions *Ranatra* and saucer bugs *Naucoris/Ilyocoris*, dragonflies *Gomphus* and *Anax*, and plumed gnats *Chironomus/Tendipes* (Oleĭnikov *et al.* 1973).

The stomach-contents of eight Red-necked Grebes from Hungary (period March-September) were dominated by

larvae and imagos of aquatic insects, such as Tisza Mayflies *Palingenia longicauda*, plumed gnats *Chironomus*, crawling water beetles *Haliplus*, Great Diving Beetles *Dytiscus marginalis*, and Great Silver Diving Beetles *Hydrous (Hydrophilus) piceus*. Frogs also belonged to the diet. Fish remains were rare and only three fish of the carp family Cyprinidae were found. They had a length of 5-8 cm (Kiss and Sterbetz 1973).

Borodulina (1976) studied the summer diet of *grisegena* from the river forelands of the Dniester (Ukraine) and the Kuban (North Caucasus region), and from Lake Kurgal'dzhino (North Kazakhstan). He investigated the stomachs of 31 birds (20 adults and 11 young). The most important food items were aquatic insects. In 71% of the 31 stomachs he found saucer bugs *Naucoris*, in 58% larvae of scavenger beetles Hydrophilidae, and in 52% larvae of diving beetles Dytiscidae. In 39% of the stomachs larvae of dragonflies Anisoptera were present. Water Spiders *Argyroneta aquatica* were discovered in 32% of the birds. In no more than 10% of the stomachs fish were found.

Gordienko and Zolotareva (1977) analysed 60 stomachs from birds on breeding waters in North Kazakhstan: 78.3% of the prey items were imagos of water-beetles Dytiscidae and Hydrophilidae, and 13.3% larvae of caddis flies Trichoptera. The remaining prey items were mainly larvae of plumed gnats Chironomidae (1.9%), imagos of water bugs Hemiptera (3.8%), and freshwater shrimps Amphipoda (1.8%). Only 0.03% of the prey items were fish. The diet varied with the seasons. In spring (April-May) 70% of the prey items consisted of diving and scavenger beetles, and 17 % of larvae of caddis flies. In summer the larvae of caddis flies (53%) and water bugs (20.6%) predominated, and the number of spiders Araneae and larvae of dragonflies grew. In autumn water bugs (76.5%) and amphipods (freshwater shrimps) (15.3%) were in the majority (Gordienko and Zolotareva 1977).

The nominate subspecies sometimes relies heavily on small fish (e.g. Ten-spined Stickleback *Pungitius pungitius*), fry and amphibians (Wobus 1964, Wagner 1997, Vlug 2002a). In fish ponds in South-East Poland, Kloskowski (2011) found that young-of-the-year (0+) Carp *Cyprinus carpio* are an essential food source for young Red-necked Grebes. Amphibian larvae were the principal alternative prey to fish, followed by macroinvertebrates (parental feeding observations). Kloskowski

and Trembaczowski (2015) obtained alimentary tracts from 11 adult Red-necked Grebes. Altogether, 832 prey items were identified (53.38 g by dry weight). Leaf beetles Donaciinae were present in all guts and were the most frequently recorded prey item. These beetles belong to the family Chrysomelidae. Their larvae live attached to the roots or stems of aquatic plants, and the adults are often found on the floating or emergent leaves of the same plants. In the guts of grebes living in fishless ponds leaf beetles constituted 42% of the total dry weight, and in fish-stocked ponds 23%. In the fishless ponds large diving beetles Dytiscidae (> 30 mm) (21% of the dry weight) and amphibians (0.3% of the food items, but 16% of the dry weight) were also important prey. In the fish-stocked ponds Carp *Cyprinus carpio* (up to 12.5 cm) were the major food and made up 59% of the dry weight (but only 0.6% of the food items).

When feeding from large lakes and in coastal waters, especially in winter, fish may predominate (Wobus 1964, Müller *et al.* 1989, 1990, Vlug 1993, 2002a, 2009). Madsen (1957) analysed stomachs of 30 Danish Red-necked Grebes, 25 from marine or brackish water areas and 5 from fresh-water localities. The birds were mainly collected from October to January, only one being from April. Fish were the principal food, taken from very small to about 15 cm long (25 cm in the case of a *Nerophis*, a long, thin, and snake-like pipefish Syngnathidae). In the marine habitats, gobies *Gobius*, small cod *Gadus* and sticklebacks *Gasterosteus* and *Spinachia* probably accounted for about half the food or slightly more; other fish species constitute about a quarter of the food. The rest of the diet in marine habitats was primarily crustaceans such as shrimps and prawns Crangonidae and Palaemonidae, but polychaetes and molluscs were also included.

In fresh water habitats the food of 5 Danish birds (October to January) consisted mainly of sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius*. Aquatic insects and their larvae (such as beetles, water bugs and caddis fly larvae) supply a similar part of the diet as do crustaceans in marine habitats (Madsen 1957).

The diet of 18 Red-necked Grebes drowned in gill nets in winter, in Lake IJsselmeer (freshwater), The Netherlands, consisted exclusively of fish (2-12 cm long), especially Smelt *Osmerus eperlanus* (61.3% by mass), Perch *Perca fluviatilis* (18.0%) and Ruffe *Gymnocephalus cernua* (12.3%) (Piersma 1988b).

Stomach contents of *grisegena* from a Danish coastal wintering area near Samsø, Kattegat, were analysed by Fjeldså (1982a). They differed greatly from the winter diets described by Madsen (1957) and Piersma (1988b). The diet of 87 birds (4,054 prey items) was dominated by polychaete (bristle) worms (3,730 items, mainly *Nereis*, *Nephtys*, and *Lepidonotus*), crustaceans (139 isopods *Idothea*), cephalopods (105 squids *Aloteuthis subulata*) and some fish (47 items, mainly 39 Three-spined Sticklebacks *Gasterosteus aculeatus*). No attempts were made to calculate the mass composition of the diet, but squids probably predominated, followed by scaleworms *Lepidonotus* and big King Ragworms (Sandworms) *Nereis (Alitta) virens*.

Sonntag (2009) studied the feeding selection by analysing the stomach contents of 23 Red-necked Grebes accidentally caught and drowned in set nets in the Pommersche Bucht (Pomeranian Bight) in the eastern part of the southern Baltic Sea. Fish dominated the diet and accounted for 85.2% of all prey items ($n = 6,257$ items). Polychaete worms were the second most frequent prey category, comprising 14.5% of all the items. Bottom living Gobies Gobiidae occurred most frequently and were the dominant species (in numerical abundance) and accounted for 97.2% of all fishes consumed in Red-necked Grebes ($n = 5,333$ fish items). Gobies also dominated the diet with respect to total consumed fish biomass (90.3% of the total). The majority of the gobies were Common Gobies *Pomatoschistus (Gobius) microps* and Sand Gobies *Pomatoschistus (Gobius) minutus*. Another 2.7% of the fish biomass consisted of Three-spined Stickleback *Gasterosteus aculeatus* and 5.6% of Ruffe *Gymnocephalus cernua*.

Sellin and Schirmeister (2010) mention the results of an analysis of the stomachs of 10 Red-necked Grebes drowned in nets in the Oderbucht (Oder Bight), Baltic Sea, in winter and spring. The results correspond with the study of Sonntag (2009): 78% of the prey items consisted of fish, and 21% of polychaete worms. Almost all fish (96% of the fish items) were gobies. *Pomatoschistus microps* and *P. minutus* accounted for 90% of the fish biomass.

The young of Red-necked Grebes which undertake food flights from the breeding waters to the Baltic Sea receive many fish, such as Butterfish *Pholis gunnellus* (up to a length of 15 cm) and gobies (Nielsen and Tofft 1987, VlUG 1993, 2009) (see 14.3.12).

14.4.6 Diet Composition of *Podiceps grisegena holboellii*

The staple diet of *Podiceps grisegena holboellii* in the breeding waters consists of a wide variety of aquatic invertebrates, fish (usually small-bodied individuals) and occasionally amphibians.

Bent (1919) wrote the following on the food of North American Red-necked Grebes: "Holboell's grebe feeds to some extent on small fish or minnows which it obtains by diving, but its food consists largely of other things and it can live perfectly well in lakes where there are no fish at all. In the lakes of Manitoba it lives largely on crawfish, amblystomæ (*Amblystoma* is a synonym of *Ambystoma* = mole salamanders, JJV), and aquatic insects; its bill of fare also includes various aquatic worms, insects, and their larvæ, small crustaceans, fresh water mollusks, tadpoles, and some vegetable substances. An adult bird caught on the ice near my home was fed on small live shiners which it ate readily."

In the interior of British Columbia, in summer, small fishes (Redside Shiners *Richardsonius balteatus* and small sculpins Cottidae) and crustaceans (crayfish *Potamobius klamathensis*) are sought where these are available. Many lakes in British Columbia inhabited by Red-necked Grebes lack a fish population and on such waters the larvae and nymphs of aquatic insects are the chief food (dragonflies and damselflies, corixids, *Dytiscus*, and *Haliphys*) (Munro 1941).

Kevan (1970) analysed the stomachs of 11 Red-necked Grebe chicks found dead on Astotin Lake, Alberta. Their diets consisted of leeches Hirudinea, water insects and their larvae (dragonflies Anisoptera, damselflies Zygoptera, water boatmen Corixidae, diving beetles Dytiscidae and larvae of caddis flies Trichoptera). She found only one fish species, namely the Brook Stickleback *Culaea inconstans*.

Riske (1976) stated, that on potholes and small lakes in Alberta *holboellii* feeds largely on arthropods, although the food items are larger than in *Podiceps nigricollis* and *P. auritus*, e.g. adult dytiscids are selected in preference to corixids, chironomids, haliplids (small water beetles), and damselfly larvae. An analysis of 85 Red-necked Grebe stomachs showed that on larger lakes in Alberta (where fishes were recovered) 20% of the stomachs of adults and 38% of the stomachs of young birds contained fish remains (Gallimore, cited in Riske 1976). On

Pine Lake, Riske (1976) often saw birds carrying and swallowing freshly caught Yellow Perch *Perca flavescens*. Of fishes eaten at Lake Wabamung, perch were most often taken, some up to 18 cm in length. Brook Stickleback *Culaea inconstans* formed an important part of the food of young *holboellii* on Big Island Lake, Alberta, during July and August (Gallimore, cited in Riske 1976).

On Armstrong Lake in Alberta, *holboellii* consumes small-bodied fishes (Brook Stickleback *Culaea inconstans* and Fathead Minnow *Pimephales promelas*), along with many aquatic and terrestrial invertebrates (dragon- and damselflies Odonata and beetles Coleoptera such as diving beetles Dytiscidae). On fishless lakes, aquatic insects, crustaceans Crustacea, and leeches Hirudinea provide the primary food (Stout and Nuechterlein 1999, Paszkowski *et al.* 2004, McParland *et al.* 2010).

In the stomach contents from 6 Red-necked Grebes (5 adults and 1 juvenile) taken from a nesting lake with fish in North Alberta, fish contributed 21.6-91.7% (mean 54.6 ± 26.3 SD), insects 8.3-77.8% (mean $41.3\% \pm 24.8$ SD) of stomach contents by dry weight, excluding feathers. Amphipods contributed 20.8% of stomach contents in one individual. Stomach contents from 2 adults taken from a nesting lake without fish in North Alberta consisted entirely of insects, with aquatic beetles being the predominant food item (69.5 and 99.8% of stomach contents by dry weight, excluding feathers) (Klatt, cited in Stout and Nuechterlein 1999).

Red-necked Grebes in prairie wetlands of southern Manitoba (where fish are usually absent) catch and swallow large (> 10 cm) Tiger Salamanders *Ambystoma tigrinum* (a species of mole salamander) (Osnas 2003).

Kindopp (2006) investigated the habitat use of breeding grebes and ducks on 75 wetlands near Yellowknife, North West Territories, Canada. In all but one wetland, there was no evidence of the presence of fish. Forty-six percent of the studied wetlands were used consistently by Red-necked Grebe broods. The total number of Red-necked Grebe broods was positively correlated with an abundance of freshwater shrimps Amphipoda, seed shrimps Ostracoda and caddis flies Trichoptera.

Nechaev (1991) found in four stomachs of *holboellii* from Sakhalin (breeding period) terrestrial beetles Coleoptera: *Plateumaris sericea* (a leaf beetle Chrysomelidae), *Selatosomus rugosus* (a click beetle Elateridae),

longhorn beetles Cerambycidae and scarab beetles Scarabaeidae. He also discovered Hemiptera (spittle bugs Aphrophoridae), cleaner shrimps Hyppolytidae, and the remnants of one species of fish (Ten-spined Stickleback *Pungitius pungitius*).

Podiceps grisegena holboellii, like the nominate race, takes more fish when feeding from large lakes and coast, especially in winter. Wetmore (1924) studied the food of 46 North American Red-necked Grebes. Stomachs from the months of September, October, and November were best represented, while for the summer season there was very little material. Fish constituted the most important single item in the food of *holboellii*, as in 36 stomachs it made 55.5% of the total food items (in 10 stomachs feathers alone composed the contents). Fish remains occurred in 23 stomachs, or half the total number examined, and made the sole food items in 14. Two birds taken on Barkley Sound, Vancouver Island, British Columbia, during the winter season had eaten several Alaska (Three-spined) Sticklebacks *Gasterosteus caphractus (aculeatus)*. One *holboellii* taken at Nahant, Massachusetts, in April, had eaten a Grubby (a small sculpin) *Myoxocephalus aeneus*, while three others secured near Shelter Island, New York, in February and March had eaten, respectively, 2, 14, and 18 fishes of the same species. Another had taken an American Eel *Anguilla chrysypa (rostrata)* and a top minnow of the genus *Fundulus*.

Wetmore (1924) found crustaceans in 9 stomachs, making up one-fifth (20%) of the total food items. Crustaceans taken by Red-necked Grebes included Mud Shrimps (Mud Lobsters) *Upogebia affinis*, Common Shrimps *Crago vulgaris*, Common American Prawns *Palaemonetes vulgaris*, crayfish *Cambarus* and *Potamobius*. Insects formed 21.5% of the food items and occurred in 13 stomachs. They comprised larvae of caddis flies, adult and larval diving beetles, a whirligig beetle Gyrinidae, adult dragonflies, water boatmen, and backswimmers. Scavenger beetles were encountered once. Other food from the group of insects consisted of remains of flies Muscidae, wasps, ants, and other Hymenoptera, a stink bug Pentatomidae, scarab beetles Scarabaeidae, ground beetles Carabidae, and billbugs Calandridae.

Munro (1941) wrote that on the sea, fish are seasonal foods of importance. Large numbers of Red-necked

Grebes in company usually with other species of waterfowl follow the Pacific Herring *Clupea pallasii* during the spawning period in the spring when these fish are in relatively shallow water. Pilchards *Sardinops caerulea* are also part of the diet of *holboellii*. In the summer of 1940 a migration of young Pilchards into Georgia Strait, British Columbia, took place and in the winter following they congregated in such sheltered waters as Finlayson Arm at the head of Saanich Inlet where, over a period of several months, great numbers died. The unusual abundance of food provided by dying and thus easily captured fish attracted many gulls and other birds amongst which Red-necked Grebes were prominent on March 29, 1941. Munro (1941) discovered that Three-spined Sticklebacks *Gasterosteus aculeatus* belonged to the food of *holboellii* too: two birds taken in Barkley Sound, British Columbia, had eaten these fish.

Adult *Podiceps grisegena holboellii* undertaking food-flights from their breeding marsh behind a dyke to Duck Lake (British Columbia) give their young many relative large fish (the same is the case with birds of the nominate race undertaking food-flights, see 14.3.12). The Red-necked Grebe chicks in the marsh were fed both invertebrates (primarily larvae of dragonflies Anisoptera and damselflies Zygoptera) and fish. The contribution of fish increased as the chicks grew. The fish flown from Duck Lake to the marsh and fed to the young birds was usually Yellow Perch *Perca flavescens*, but the grebes broadened their flown-in diet to include more Pumpkinseed Sunfish *Lepomis gibbosus* and Largemouth Bass *Micropterus salmoides* following a year-class failure of perch (Ohanjanian 1986, 1989).

14.4.7 Helminth-eating

Helminths are parasitic worms of grebes. The habit of eating their own helminths and feeding them to their young is a peculiar habit of grebes. Simmons (1975a) observed Great Crested Grebes eating helminths, almost certainly tapeworms Cestoda. These were extracted from the bird's own cloaca or obtained from the water after defecation. Chicks obtained them (directly or indirectly) from the parents and adult birds, at least occasionally, from the mate. Young Great Crested Grebes also show interest in their own helminths.

There is one record of helminth-eating in Red-necked Grebes. Simmons (1975a) saw, on 30 September 1969, a transient juvenile at Cheddar Reservoir (Avon, England).

It extracted a helminth from its cloaca during a preening session. The worm resembled a length of vermicelli; the bird "played" with it, flicking it away and retrieving it, and had twice to crash-dive away from Black-headed Gulls hovering overhead before eventually swallowing it.

Simmons (1975a) believes that the grebes do get nutriment from the ingested tapeworms because they seem usually to break up the helminth before swallowing it. Certainly, there can be no doubt that the birds show great interest in the tapeworms as potential food and appear to relish them.

14.5 Geographic Variation in Diet and Competition with Great Crested and Western Grebes

According to Fjeldså (1982a, 1983), geographic variation in the diet of the Red-necked Grebe is probably caused by selection due to the presence or absence of Great Crested Grebes, that is by character displacement or character (competitive) release (see also 9.1.5). Character displacement refers to the phenomenon where differences among similar species (here *Podiceps grisegena* and *P. cristatus*) whose distributions overlap geographically are accentuated in regions where the species co-occur but are minimized or lost where the species' distributions do not overlap. Character (competitive) release, defined as the expansion of an ecological niche in the absence of a competitor, is essentially the mirror image of character displacement.

The two species are well separated ecologically, when breeding sympatrically (Vlug 1993). Red-necked Grebes, breeding sympatrically with Great Crested Grebes, may mainly feed by foliage-gleaning, picking prey items from the bottom and capturing relatively slow moving, nektonic animals (Fjeldså 1982a, Vlug 1993). In the far north of Europe (Finland and Russia), where Great Crested Grebes are absent, Red-necked Grebes (*Podiceps grisegena* "schioleri") have a long and slender bill. The development of their jaw muscles approaches that of *holboellii* (Fjeldså 1982a, 1983). These northern birds specialize (in winter) on squid and fish (Fjeldså 1982a).

P. g. holboellii, which breeds in eastern Siberia and North America, where Great Crested Grebes are absent, is much bigger and longer-billed than the nominate and "schioleri". This matches the Great Crested Grebe in some anatomical details, while an increased *Musculus protractor quadrati et pterygoidei* may be a paradaptation to the

expanded *pseudotemporalis* muscle of the Great Crested Grebe (“Those aspects of a feature that are dependent upon, resulting from, or under the control of chance-based evolutionary mechanisms may be termed *paradaptive*...”, Bock 1967, cited in Cracraft 1972). The anatomy should enable a quick opening of the bill and a firm, strong grip, probably, according to Fjeldså, advantageous for fish-eating (Fjeldså 1982a, Fjeldså 1983).

However, it is doubtful whether *holboellii* is really an ecological counterpart of the highly piscivorous Great Crested Grebe, as Fjeldså (1983) suggests. Although *holboellii* consumes many fish when available, it also regularly nests on fishless waters. The breeding waters of Great Crested Grebes, by contrast, are never fishless (J J Vlug). On lakes with fish *holboellii* eats a mixed diet of fish and a wide range of macroinvertebrates. On fishless lakes, aquatic insects, crustaceans, and leeches provide the primary food (Stout and Nuechterlein 1999, Paszkowski *et al.* 2004, McParland *et al.* 2010) (see 14.4.6). Moreover, food selection may be determined more by agility of the bird than by its bill dimensions (Onno 1966, Piersma 1988b) (see 14.3.3).

Although it is known that *holboellii* usually consumes small-bodied fish, no details are available on the typical prey sizes taken by adult birds. It can be expected that *holboellii* is able to catch larger fish than the smaller nominate race. Of fishes eaten at Lake Wabamum, Alberta, Yellow Perch *Perca flavescens* were most often taken, some up to 18 cm in length (Riske 1976). The largest fish consumed by a Red-necked Grebe that Forbes (1989) observed was a 19 cm Yellow Perch which would correspond to a girth of 11 cm.

Probably *holboellii* is more of a generalist than the nominate race and has a larger range of prey size (from relatively small invertebrates to larger fish). The study in Alberta of Paszkowski *et al.* (2004) seems to confirm this. They stated that a Red-necked Grebe from a lake that lacks small-bodied fish species had eaten a 141 mm Yellow Perch, as well as numerous invertebrates. In Armstrong Lake, where small-bodied fish species were present, the birds ate Fathead Minnows and Brook Sticklebacks (*c.* 50-65 mm), along with a wide range of aquatic and terrestrial invertebrates. In contrast, gut analysis of two Red-necked Grebes indicated that the birds from fishless Gilbert Lake primarily ate aquatic arthropods (Paszkowski *et al.* 2004).

Some authors assume that Red-necked and Western Grebes *Aechmophorus occidentalis* are food competitors. This is clearly not the case. Western Grebes are fish specialists, foraging on extensive areas of open water of large lakes. They (and the closely-related Clark’s Grebes) are unique among grebes in possessing a mechanism in the neck that permits them to thrust forward the head like a spear (Storer and Nuechterlein 1992). As described above, food choice and foraging habitat of Red-necked Grebes differ from those of *Aechmophorus*. Macroinvertebrates are an important component of the diet of *holboellii*, and such invertebrate prey is most abundant and diverse in structurally complex littoral habitats. Therefore, the more varied diet of Red-necked Grebes links them more closely to the littoral food web than the highly piscivorous Western Grebes (Newbrey *et al.* 2012). Thus, both species are separated in their ecology and no serious competitors.

14.6 Competition Between Red-necked Grebes and Fish

Common Carp *Cyprinus carpio* and other Cyprinidae, especially the old, large specimens, compete directly for food with Red-necked Grebes. These fish can also impede indirectly the development of prey for Red-necked Grebes (macroinvertebrates and small vertebrates such as tadpoles) (see 9.1.5 for more details).

Diet composition studies show that invertebrates preferred by Red-necked Grebes and other waterfowl are often also preferred by common, and usually abundant fish species such as Carp *Cyprinus carpio*, Crucian Carp *Carassius carassius*, Roach *Rutilus rutilus*, Common Bream *Abramis brama*, Tench *Tinca tinca* and Perch *Perca fluviatilis* (Eriksson 1979, Steffens 1980, Eadie and Keast 1982, Giles *et al.* 1990, Vlug 1993, Wagner 1997, Vlug 2011). Dietary analysis of 36 fish stomachs in Lake Tåkern showed that the dominant prey consumed by Tench was water boatman *Corixa*. Other food items of importance were mayflies Ephemeroptera, caddisflies Trichoptera, molluscs Mollusca and plumed gnats Chironomidae. Perch and Roach showed preferences for Ephemeroptera, Trichoptera, and *Corixa* (Wagner and Hansson 1998). Actually, there is a large feeding overlap between breeding Red-necked Grebes and the fish community, indicating that it should be advantageous for Red-necked Grebes to choose breeding habitats with low fish abundance. Fish-removal from lakes increases food for Red-necked Grebes and other waterfowl (Eriksson

1979, Andersson 1982, Giles 1994, Wagner 1997) (see 9.1.5 for more details).

14.7 Daily Intake and Nutrient Reserves

Markuze (1965) found a daily intake of 175 g fish per Red-necked Grebe in June (and 187 g of a mixed diet of fish, tadpoles and aquatic insects) ($n = 10$ captive adult birds of the nominate race). Piersma (1988*b*) calculated that a Red-necked Grebe with a weight of 840 g would require 156 g of fresh fish per day. A Slavonian Grebe (with a weight of 500 g) would require 100 g.

The larger Great Crested Grebe normally consumes *c.* 200 g food a day, and a hungry bird of this species *c.* 260 g (Heinroth and Heinroth 1928). The exact figures may vary with the available food supply, as the energy content of some prey (e.g. herrings *Clupea*) is twice as high as of others (Fjeldså 2004).

Piersma (1988*b*) stated that the total nutrient reserve level of 14 Red-necked Grebes wintering on Lake IJsselmeer, Netherlands, averaged 363 g or 43% of the body mass. He estimated that a healthy Red-necked Grebe with average winter reserve levels wintering on this lake could survive about 11 days without food before starving to death.

The amount of food consumed by Podicipedidae fluctuates. Wiersma *et al.* (1995) showed that food intake in Great Crested Grebes in Lake IJsselmeer, Netherlands, varied considerably during the season, increasing 1.8 fold from October to January. The intake rate was even lower in September than in October, but during this time most adult Great Crested Grebes in Lake IJsselmeer are undergoing their wing moult which involves a strong reduction in diving activity. Responsible for the observed increase in food intake from autumn to mid-winter were changes in the air and water temperature (in mid-winter there is an increase in heat loss in the birds), time spent submerged (the grebes, which have to eat more during the cold months, probably dive more and spend more time submerged), heating up food (the fish eaten by the grebes have the same temperature as the lake water and the birds have to warm up this cold prey), diving depth (this depth is 1.5 times as large in January than in October), and fattening and buoyancy (fresh body mass of adult Great Crested Grebes increased by *c.* 7% from October to January, resulting in higher buoyancies in heavier individuals). These variables can explain a total of 55% of the observed increase in food intake. The re-

maining 45% must be due to higher activity costs (increased feeding and locomotory activity) during the winter as a result of the increased food intake. Undoubtedly, wintering Red-necked Grebes have to contend with similar problems.

14.8 Feather-eating, Pellet Formation and Pellet-casting

Red-necked Grebes and other Podicipedidae eat large quantities of their own feathers, and with this habit they are unique among birds. Intact feathers are not actively pulled out of the plumage, but only ingested after they are shed during moult or loosened during preening. Many feathers are eaten during preening sessions; they are sometimes dabbled in the water, to be moistened and then swallowed (see Fig. 39). The feathers are often picked up off the surface of the water. Parent Red-necked and other grebes will give them to the chicks from the day of hatching, even before these receive their first real feed. The young birds actively beg for them (Wetmore 1924, McAllister 1963, Wobus 1964, Piersma and Van Eerden 1989, Simmons 1989, Stout and Nuechterlein 1999).

Piersma and Van Eerden (1989) noted that 68% of identified stomach feathers of Great Crested Grebes originated from the breast and belly feather tracts. This percentage is larger than would be predicted if feathers were taken in proportion to their abundance on the body. Flank feathers (19%) also occurred in larger numbers than expected, whereas head and neck feathers, scapulars and wing coverts occurred less. Because the feathers eaten are not plucked from the bird but come out naturally in the course of preening, one might expect that there would not be enough flank feathers available. But this is not the case; there is an almost constant moult and growth of flank feathers in grebes. This is a remarkable adaptation, which presumably coevolved with the habit of feather-eating (Piersma 1988*a*, Piersma and Van Eerden 1989, Storer 2000*b*).

The mass of the ingested feathers is found free in the lumen (main chamber) of the stomach where they break down into a greenish felt-like spongy material. This mixes with ingested food and forms a characteristic feather-ball, which can fill the stomach (gizzard bolus). In addition to the feather-ball, a small mass of more or less whole ingested feathers forms a plug or feather-pad in the lower chamber of the stomach (the small pyloric lobe) from which the upper end of the small intestine



Fig. 39: Red-necked Grebe dabbling a feather in the water to moisten it. Photo: T Runge (Schleswig-Holstein)

Fig. 39: Rothalstaucher eine Feder mit Wasser befeuchtend.

opens. This feather-plug blocks the entrance to the intestine. Unlike the feather-plug of the pyloric lobe, the feather-ball of the lumen of the gizzard, whole or in bits (see below), is periodically regurgitated from the stomach together with its contents (pellet-casting or pellet-ejection, see Fig. 40). These pellets include the indigestible and more slowly digested parts of the food: scales, vertebrae and certain other harder bones, otoliths and the like from fish, and chitin from insects (Simmons 1989, Storer 2000b). Pellet-casting seems to take place regularly, mostly by night or very early in the morning, and is often preceded by drinking (Fjeldså 2004) (but drinking is not a necessary precursor of pellet-casting). Jehl (2017) studied casting in Black-necked Grebes (Eared Grebes) caught for banding or rehabilitation by retaining them in a dry box under natural photoperiod and checking periodically for regurgitations. Grebes netted at Mono Lake in September, when they were feeding heavily, cast pellets daily. Jehl detected no particular pattern, except that most were regurgitated after dark in the first 18-20 hours of containment. The gizzard bolus was not disgorged in a single bout, and in several cases, pellets were cast up to 38-41 hours after capture, when observations ended. In one set of observations, five Black-necked Grebes kept for 18-20 hours produced an average

of 6.4 pellets each. In a second set, six grebes kept over two nights (38-41 hours) averaged 7 pellets the first night; and four individuals cast pellets (mean 2.8) into the second day. One Black-necked Grebe cast 14-16 pellets overnight (Jehl 2017).

Several hypotheses have been put forward to account for the feather eating habit and pellet-casting in causal or functional terms (e.g. Buffon 1781, Wetmore 1924, Madon 1926, 1931, Hanzák 1952, Simmons 1955, 1956, Storer 1961, 1969, Simmons 1973, Piersma and Van Eerden 1989, Simmons 1989, Storer 2000b, Fjeldså 2004). It seems clear that the pyloric feather-plug effectively prevents the passage of hard prey parts into the intestines (in this way injury to the intestinal walls from these hard fragments may possibly be avoided), and that fish bones eventually dissolve completely in the stomach. The contents of the intestines are fluid, with no discernable prey remnants (see below) (Storer 2000b, Fjeldså 2004).

Piersma and Van Eerden (1989) observed that there is an inverse relation between the amount of fish debris and the number of ingested feathers. When the diet of Great Crested Grebes consisted of Smelt, which leave little indigestible matter, more feathers were eaten than



Fig. 40: Red-necked Grebe casting a pellet. Photo: T Runge (Schleswig-Holstein)

Fig. 40: Rothalstaucher ein Gewölle auswürgend.

with a diet of Perch and Pike-perch, which leave more fish debris. This suggests, that in the absence of other indigestible matter (fish remains or chitin of arthropods), the feathers contribute substance to the stomach content and enable the formation of pellets that are ejected. Thus, feathers are not necessary for pellet-formation because other matter can take over this function, but they presumably aid in pellet-formation and without them pellets are possibly difficult to cast (McAllister 1963).

A number of observations probably corroborate this theory. Storer (1961) reported that a Slavonian Grebe on Portage Creek in Manitoba coughed up a pellet after feeding on small particles of food taken from masses of green algae. The pellet was presumably most algae. McAllister (1963) saw that a young captive Red-necked and a Black-necked Grebe cast their first pellets on the eighth day while eating fish and no feathers. From then on, they cast regular pellets consisting entirely of undigested fish bones, an oval mass cemented together and coated with mucus. Stout (*cited in* Stout and Nuechterlein 1999) observed two adult Red-necked Grebes casting pellets on fishless lakes in Northwest Territories, Canada.

Fjeldså (2004) stated that the two *Poliiocephalus* species (Hoary-headed Grebe and New Zealand Grebe) do not normally eat feathers and do not drink before ejecting pellets. He found only six feathers in 19 analysed stomachs of Hoary-headed Grebes *Poliiocephalus poliocephalus*. This could possibly be related to specializations for an arthropod diet.

Piersma and Van Eerden (1989) wrote that out of 1,540 examined oesophagi and stomachs of Great Crested Grebes none was obviously infested by endoparasitic helminths (nematodes and trematodes). They examined the digestive tracts of sixteen species of fish-eating waterbirds from Lake IJsselmeer and found that the gastric parasite load was negatively associated with the habit of producing pellets. The paucity of endoparasites in the upper part of the alimentary tract of grebes compared to species not producing pellets but with an overlapping diet, suggests that regularly emptying the stomach may not only remove the hard remains of fish (or chitin) but also the various stages of ingested helminths or other prospective endoparasites. Thus, producing pellets cleans up the stomach and oesophagus. Because Podicipedidae often drink before ejecting a pellet, it is possible that the alimentary tract can only be properly cleaned if

a suitable substrate for pellet formation, either fish (or chitin) debris or ingested feathers, is available, and the compacted remains can be coughed up with the help of a little water.

Storer (2000*b*) remarked that in spite of the pyloric feather-plug, Podicipedidae usually contain very large numbers of intestinal parasites, especially tapeworms Cestodes. How the larval parasites get from the stomach into the intestine is not known. A number of them may get into the intestines at a time when the feather-plug is not in place. The amabilids Amabiliidae, abundantly occurring cestodes in grebes, comprise many forms of almost microscopic size (an adult *Tatria fimbriata* reaches a length of 0.62 mm), which may be able to pass through the pyloric filter (Storer 2000*b*, Fjelds  2004).

Jehl (2017) proposed that grebes originated as surface feeders and adopted feather-eating to enhance the efficiency of feeding on small arthropods or other hard-bodied taxa. Small invertebrates provide nutrition but have a high surface/volume ratio, low yield per individual, and need to be consumed in large quantities. And, they are not easy to digest as shown by the long retention times. This was demonstrated in grebes by Markuze (1965, Fig. 4 at p. 255, and text at pp. 252 and 255), who found that Red-necked Grebes were able to digest *c.* 55% of a Common Carp *Cyprinus carpio* diet but only *c.* 30% of various invertebrates in 3-5 hours and that almost no digestion of invertebrates occurred in the first 2 hours. Jehl (2017) suggested that early grebes addressed the challenge of exploiting abundant but hard-to-digest tiny invertebrates by adopting chemical digestion and eating feathers to retain food in the gizzard until it could be fully liquified. The fact that Podicipedidae present feathers to their chicks before giving them food also supports the primacy of a digestive role for feather-eating.

14.9 Drinking

Red-necked Grebes drink by dipping the bill in the water and then tipping the head back, well above the horizontal, to swallow the water, usually repeating this sequence one or more times. The birds often drink before casting pellets (Simmons 1977, Stout and Nuechterlein 1999).

14.10 Defecation

The birds defecate on the water while they are swimming. The chicks defecate when they are dumped off the

parent's back, or while they are scrambling to get out of the water and try to climb up on to the parent's back (Stout and Nuechterlein 1999). However, for the first four or so days of life only, the young grebe, like a nestling passerine, produces its faecal droppings enclosed in a sac, depositing them on the parent's back (Simmons 1989).

15. Behaviour and Social Pattern

Behaviour is the integrated pattern of movements or other overt responses of animals to internal and external stimuli. Behaviour is the product of the action of the nervous and muscular or other effector systems (Campbell and Lack 1985). Four types of behaviour are here distinguished: locomotion (a variety of movements or methods that animals use to move from one place to another, see 15.1), comfort behaviour (activities that help maintain the feathers, integument or musculoskeletal system and increase the physical comfort of the animal, see 15.2), social behaviour (the behaviour among two or more organisms, typically from the same species, see 15.3) and interspecific behaviour (the behaviour between individuals of different species, see 15.4).

15.1 Locomotion

15.1.1 Terrestrial Movements and Postures

Red-necked Grebes are almost exclusively aquatic and specialized foot-propelled diving birds. The feet are placed laterally at the rear end of the body, where they can be rotated freely in the water. The grebes avoid firm ground but may end up on land by accident, for instance when night-migrating birds land on a wet tarmac road (probably mistaking it for water), or if the nesting sites dry up. Once on land, they move awkwardly. The birds may lie down, shuffling and pushing themselves forwards on the breast by kicking the feet. They may also stand erect on the toes and walk a few staggering steps in nearly upright posture before dropping onto the breast, or they may run, flapping their wings when running to keep their balance (White 1931, Wobus 1964, Stout and Nuechterlein 1999, Fjelds  2004).

Sim (1904) gave a description of the standing position and walking of a Red-necked Grebe captured in Ohio: "Contrary to the common belief in regard to grebes, this individual was never seen to rest upon his heels, though observed untiringly. The ordinary standing position was

with the body somewhat inclined forward, the shoulders humped up, and the tarsi descending forward and outward on a slant – and so entirely free from the ground. The bird could stand for nearly a quarter of a minute or run ten or twelve feet before dropping to his breast. While vigorously preening or jabbing at his feathers he would sway around and sometimes had to take a step or two to regain balance. He seemed to become fatigued after standing for a moment, the strain being felt most, I think, in the toe-joints and in the muscles and tendons which flex the digits; for even with the tarsus sloping back as it did (...) the toes were necessarily pressed upward to an unnatural degree. This conclusion was strengthened by the fact that the toe-joints became much swollen and developed corn-like protuberances. In pattering rapidly along the bird held his body in a semi-erect attitude and it swayed but little, on account of the quickness of the steps; but when walking slowly along he swung noticeably to the side whose leg for the moment supported his weight. He sometimes took food from the floor without first lying down, though he usually assumed the ventropodal position when feeding. When going under chairs and other low articles the bird progressed in short leaps, giving a spring with both legs together and coming down on his breast.”

White (1931) described the terrestrial movements and postures of a North American Red-necked Grebe, which was found in the snow in a field in Warner, New Hampshire: “Out of water my Grebe’s customary position was sitting flat on its belly. ... The feet were usually extended out at right angles, on line with the end of the tail. The neck was held well up most of the time when human beings were present to interest the bird and keep it alert; but at quieter times the neck would lie along the back as far as would go consonant with holding the head up. ... Attempts to walk were humorous: they resulted in a few staggering steps ending in a lurch forward and a bump down on the breast. One time, out on the snow, the bird ran twenty-five feet, flapping the wings; I thought I had lost it, but the effort to rise proved vain. Its efforts to stand were at first abortive; an erect position could be held only momentarily, ending in bumping forward hard on the breast. After a few days, however, it learned to stand erect on the whole length of toes and tarsus, and subsequently this position was frequently assumed and maintained balance satisfactorily. Rarely would it flap its wings when out of water, and the support given to standing erect on the toes was only brief.”

There is a record of a pair of Red-necked Grebes transferring two chicks (3-4 weeks old) from the breeding pond (Silkteich near Lübeck, Schleswig-Holstein) across a barrier beach to a larger water body (Trave, B Koop). Kloskowski and Frączek (2017) discovered that some Red-necked Grebes, breeding on ponds in Poland, moved their flightless young (2-4 weeks old) to other, unconnected ponds. Sometimes adult Slavonian Grebes carry their small young on their backs across land to other pools (Iceland, Fjeldså 1973d).

15.1.2 Flight

The tremendous development of the hind limb musculature in foot-propelled diving birds is often associated with a reduction in the relative size of other structures. Red-necked Grebes and most other Podicipedidae maintain the necessary architecture and minimum of wing musculature for a direct, rapid flight. Grebes, including *Podiceps griseogenus*, are characteristically high wing-loaders – that is the ratio of the wing area to the weight of the bird is low. The wings of the Red-necked Grebe are small and narrow compared with the body. The flight is sustained by rapid wing beats, and the birds show a fast flight (Storer 1960, Wobus 1964, Ohanjanian 1986, Stout 1995, Vlug 2002a, Fjeldså 2004). The air speed of Red-necked Grebes, migrating in “no wind” conditions along Lake Superior, Michigan in autumn averaged 61.5 km/hr. The speed increased significantly using tail winds adjusted for wind vectors as the migration season advanced: 68 km/hr in August, 70.1 km/hr in September, and 78.7 km/hr in October (Binford and Youngman 2010). This fast flight speed is a compensation for the high wing-loading. Blomdahl *et al.* (2007) describe the flight of Red-necked and Great Crested Grebes as straight and even, with fast and shallow wing beats. The birds are not very manoeuvrable, so they are easy victims of larger falcons, and this may be a principal reason why they mainly fly at night (Fjeldså 2004).

A Red-necked Grebe flies with the neck stretched, and the feet outstretched behind the body (see Fig. 41). It usually keeps the head and neck level, but can hang its neck down, albeit never as much as a flying Great Crested Grebe does (see Fig. 42). The body is held completely still in flight, as if it were threaded on an invisible skewer, with the wings working hard to maintain speed. The head and neck are held stable relative to the body, unlike Slavonian Grebes (Blomdahl *et al.* 2007) (see photographs in Line *et al.* 1987, p. 210, in Larsen and Wird-



Fig. 41: Red-necked Grebes starting food flights often circle over the breeding-water, gaining altitude before flying off to the Baltic Sea. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 41: Rothalstaucher kreisen häufig über dem Brutgewässer, um Höhe zu gewinnen, bevor sie zur Nahrungssuche auf die Ostsee fliegen.



Fig. 42: A flying Red-necked Grebe usually keeps the head and neck level, but can hang its neck down. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 42: Im Fluge hält ein Rothalstaucher gewöhnlich Kopf und Hals auf gleicher Höhe mit dem Körper, kann aber seinen Hals auch nach unten hängen lassen.

heim 1994, p. 2, in Blomdahl *et al.* 2007, p. 47, and in Behrens and Cox 2013, pp. 259-61).

The flight is characteristically preceded by a special pre-flight posture, in which the head is held high and the head and neck feathers are “slicked down”. The grebes in this posture swim about “nervously” before taking off. They generally attain flight by a long, foot-assisted take-off along the surface of the water, preferably upwind, before becoming airborne (see Fig. 43). At Creston, British Columbia, a number of Red-necked Grebes make food flights (see below). These birds required a minimum of 50-60 m of open water to taxi for take-off. By timing the length of these runs it was determined that they could not achieve speeds sufficient for take-off in windless conditions until they had taxied for an average of 5.6 ± 0.8 sec. ($n = 60$). Distances flown at Creston were estimated to range from 30 m to about 2.5 km (Ohanjanian 1986). Birds starting food flights in Schleswig-Holstein, Germany (see below), often circle over the breeding-water, gaining altitude before flying off to the sea (Vlug 2002a). But at Creston, the Red-necked Grebes breeding behind a man-made dyke flew directly across the dyke to the foraging areas and rarely circled or altered direction (Ohanjanian 1986).

When preparing to land, the grebe brakes by spreading the wings and gliding, sometimes sliding side to side in the air (see Fig. 44). During landing, the feet are stretched behind the body and trail briefly in the water before the abdomen lands with a splashing glide on the water (Wobus 1964, Stout and Nuechterlein 1999, Vlug 2002a, see photograph in Vlug 2009, p. 21) (see Fig. 45 and 46). Red-necked Grebes that land on the ground are usually doomed since they can not become airborne without a long running take-off along the surface of the water (Vlug 2002a, see 15.1.1). There are rare reports of other grebe species managing to take off on land, e.g. of Slavonian (Horned) Grebes (Rogers 1918) and Pied-billed Grebes (Cuthbert 1954), and so it is possible that Red-necked Grebes in very rare cases are able to take flight from land.

Red-necked Grebes rarely fly outside the migration period, and typically do not fly to foraging areas. However, birds nesting on lagoons and other shallow wetlands separated from the Baltic Sea by a barrier beach or dyke make food flights to the adjacent sea. This occurs especially in northern Germany and Denmark (Nielsen and

Tofft 1987, Vlug 1993, 2009). The adult grebes obtain almost all their own food from the sea and not from the lagoon, but the chicks are partly fed with prey from the breeding water and partly with fish from the Baltic Sea. Although food flights in *Podiceps grisegena* are common near the Baltic Sea, they are not widespread. In North America food flights are recorded only at Creston in British Columbia, where the most suitable nest sites were separated from the main feeding area by a dyke (Ohanjanian 1986, 1989).

Though Red-necked Grebes are generally considered to be poor fliers, they are capable of long distance migration. Outside the migration period sustained flight is rarely observed. The overland migration appears to be almost exclusively nocturnal, so nothing is known about the altitudes at which Red-necked Grebes regularly fly over land, except that they are clearly able to cross mountain ranges. When caught in bad weather, Red-necked Grebes may land on ice or wet roads, apparently mistaking them for bodies of open water (Snyder 1930, De Vos and Allin 1964, Kaufman 1994). The diurnal flights occur low over water, often within several metres of the surface of the water, along ocean and sea coastlines, and over other large water bodies (Camphuysen and Van Dijk 1983, Stout 1995, Stout and Nuechterlein 1999). The autumn flight of Red-necked Grebes through Lake Superior appears to be the most extensive diurnal migration of grebes ever reported. Each autumn, between 9,000 and 19,000 Red-necked Grebes have been observed flying past Whitefish Point, Michigan, during daylight hours (Stout 1995).

15.1.3 Swimming and Diving

Red-necked Grebes and other Podicipedidae are strong foot-propelled divers and swimmers with large lobed feet.

Swimming

On the surface, they swim with alternating strokes of the feet. The three front toes have only a small connecting basal membrane, and instead each toe has an asymmetric and stiff swimming lobe, of which the medial part is the larger and trails behind the toe during the forwards stroke of the feet and stands “beam-on” during the backwards stroke. Because of a special construction of the proximal hinge joint of the toes, they rotate up to 120° as the toes are spread and stretched. They therefore form a large broad paddle when the foot is pushed back. An-



Fig. 43: Red-necked Grebes generally attain flight by a long, foot-assisted take off along the surface of the water. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 43: Das Auffliegen vom Wasser ist normalerweise nur nach langem "Fluglaufen" über die Wasseroberfläche möglich.



Fig. 44: When preparing to land, the grebe brakes by spreading the wings. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 44: Vor der Landung bremst der Taucher, indem er die Flügel ausbreitet.



Fig. 45: During landing, the feet are stretched behind the body and trail briefly in the water. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 45: Während des Landens werden die Füße hinter dem Körper ausgestreckt und schleifen kurz im Wasser.



Fig. 46: The abdomen lands with a splashing glide on the water. Photo: T Runge (Hohenfelde, Schleswig-Holstein)

Fig. 46: Körperende und Bauch gleiten bei der Landung spritzend über die Wasseroberfläche.

other characteristic feature of the feet is the very strong flattening of tarsi and bony elements of the toes. With this construction, maximum power production can be combined with minimal drag during the return stroke, analogous with how primary flight feathers move during flight (Fjeldså 2004). Thus, when the foot moves forwards, it is flattened and, when it pushes back, the toes are turned so that the lobes form a large, broad-bladed paddle.

When swimming unhurriedly, Red-necked and Great Crested Grebes seem to glide effortlessly along with little or no visible action of head or leg to disturb the water, and with the neck held vertically. The body lies rather low in the water, not high like a gull, and the white underparts are usually invisible. Unless engaged in preening or carrying young, for example, grebes tuck their wings well away, tightly pressed to the flanks where they are covered over by the feathers, and against the back so that they do not protrude and break the smooth contour. When swimming quickly, the grebe inclines its neck forward to an angle of about 45 degrees, and at the breast a considerable bow wave originates. The bird may jerk the head a little like Coots *Fulica atra* (“Nickschwimmen” of Wobus 1964). However, if a grebe wants to make real speed from place to place it will dive because it can move much quicker underwater than on the surface (Simmons 1955, Wobus 1964).

Diving

When grebes are swimming about peacefully on the surface, their plumage is loosely puffed out, but when they are about to dive, they press their feathers close in to the body so that the air between them is expelled. Inside the body, connected to the lungs, there are large air sacs which can also be contracted. All this means that the bird's volume or capacity decreases so that it sinks lower in the water. This technique is employed if there is danger in the offing. The bird appears very small and thin. It can sink so low in the water that only the head and a little of the back are visible. The same technique is used when diving for food. Then the bird will dive swiftly and silently down into the water (“smooth” or “level dive”; see below for more details) (Fjeldså 1977a). Because of the position of the feet far aft, and a high ability to rotate the tibiotarsus, grebes can move their feet above, below, or on a level with the body. Underwater, the rear end of the body is held high, and the feet are usually pivoted high above the birds' back and waved constantly with alternating strokes during stationary feeding. However,

both feet are used simultaneously in rapid pursuit. Steering is accomplished on the propulsive strokes with minimal loss of energy. In this way the feet act both as “propellers” and as “rudders”. The wings are only exceptionally opened underwater, during panic or during intense foraging manoeuvres when they pursue fish, which dart about. Top speeds of diving grebes are poorly documented, but records range from 1.2 to 3 m/sec. Divers and penguins achieve higher top speeds, but this is hardly surprising when we consider their much larger size. However, they can hardly match grebes in agility underwater (Fjeldså 2004). The surfacing is passive, without using the feet, the neck held vertically.

Two Diving Techniques (see also 14.3.5)

Red-necked Grebes use two types of feeding dive (Davis and Vinicombe 1980, Simmons 1980). In the “smooth” or “level dive”, *grisegeta* submerges in a smooth manner typical of Great Crested Grebes: submerging from a stationary position, first sinking lower in the water while depressing its contour feathers to reduce buoyancy, and then smoothly disappearing bill first, with a rapid forward and downward swing of the neck, the body following. Neither the breast feathers nor the tarsi emerge from the water. Normally, this submergence causes little turbulence on the water; as the bird still holds its legs forward as it disappears, they are obviously not used to give propulsion until it is under the surface (Simmons 1977). In the “springing dive” of *grisegeta* there is an initial leap well clear of the surface, entering at an acute angle, rather like a Shag *Phalacrocorax aristotelis* (Davis and Vinicombe 1980).

In his work “Life Histories of North American Diving Birds”, Bent (1919) reported on *holboellii*: “It is a strong and rapid swimmer and like all of its tribe a splendid diver. It usually prefers to escape by swimming rapidly away if the enemy is not too near, but, in the latter case, it dives like a flash, so quickly that it is useless to try to shoot one if it is watching. When undisturbed and not hurried it makes a graceful curving plunge, leaving the water entirely and going straight down with its wings closed; probably it can dive to a greater depth in this way than in any other. It can also sink gradually downward until only its head is above water or go swimming off among the reeds with only its bill and eyes showing. When really alarmed it goes under water with astonishing rapidity, so quickly that we cannot see how it is done, but it is probably accomplished by a sudden kick and forward dive”.

The type of feeding dive used (“smooth” or “springing”) seems to depend to some extent on the depth of the water, but also on the nature of the prey (invertebrates or fish), the location of its usual capture (at the bottom or in the intermediate water layer), and on weather conditions (wind, wave action) (Simmons 1980). Nuechterlein (1981a), like Bent (1919), suspects that the grebe goes deeper in “springing dives” than in “smooth (level) dives”. Smooth dives of Red-necked Grebes predominate in shallow breeding-waters (in general slight wave action, usually invertebrate diet) and springing dives in deep winter lakes and at sea (often large wave action, fish diet more important than in the breeding ponds). It is likely that the two types of feeding dive grade into one another (Storer 1969, Simmons 1980, Nuechterlein 1981a).

Simmons (1980) observed an immature Red-necked Grebe at Cheddar Reservoir, Somerset, England, in September 1969. This bird produced a noticeable “double-splash” as it dived: two weak splashes or swirls to the rear as it swung its head down at the start of its action; then two stronger splashes, farther apart, one each side of its posterior flanks, as it went under.

Splash-diving

Splash-diving is rare in Red-necked Grebes, and there are no detailed notes on this behaviour. In splash-diving, the feet are used to give an extra impetus for rapid submergence in emergency, often producing a noticeable splash (Vlug 2002a). Red-necked Grebes may splash-dive on very close range (J J Vlug). Fjeldså (1973c) described it in Slavonian Grebes *Podiceps auritus*: “As judged from observations on less than one metre range, the feet are raised, anterolaterally, above the water surface, and abruptly beaten down to give a loud splash, simultaneous with a forwards thrust of the head. Occasionally the bird may splash without diving. Less frequently both wings and feet are used simultaneously for splashing.”

Diving Capabilities of Red-necked Grebes Compared to Great Crested and Slavonian Grebes

The nominate *P. g. grisegena* is unable to dive as well as the Great Crested Grebe for larger (faster) fish (Vlug 1993). Even the smaller Slavonian Grebe *Podiceps auritus* is better adapted to diving, due to its leg morphology, and can catch comparatively larger and quicker fish than the Red-necked Grebe (Onno 1966, Piersma 1988b).

15.2 Comfort Behaviour

Comfort behaviour is a general term given to behaviour patterns such as bathing, preening, oiling, stretching, and scratching that are typically associated with body care. Since grebes spend most of their entire life in water, plumage maintenance is a very important activity. Grebes spend a lot of time preening and oiling their plumage. This happens during loafing breaks in the feeding activity, and at odd moments during diving pauses and lulls (Fjeldså 2004).

Comfort behaviour of the Red-necked Grebe is closely similar to that of *Podiceps cristatus* and *P. auritus*. The following is based mainly on the excellent work of Simmons (1977), who compared comfort behaviour of Great Crested and Red-necked Grebes (see also Wobus 1964).

15.2.1 Bathing

Red-necked and Great Crested Grebes, with their waterproof plumages, have to use special movements to wet themselves deliberately during bathing, the latter being the first in a functional series of feather care (or “feather-maintenance”) activities.

Surface-bathing

Each bird bathes several times a day, mostly by surface-bathing. When performing at full intensity, the grebe ruffles up its plumage and repeatedly makes vigorous bathing movements on top of the water, including: ducking-and-rubbing (in which the head, neck, and forebody are dipped under water with a “bouncy” action and the wet head is rubbed against the flanks), wing-thrashing (in which the partly open wings are beaten against the water as grebe rises somewhat by treading with its feet) (see photograph in Walser and Barthel 1994, p. 113); wing-scissoring (in which the folded wings are shuffled in the water); and barge-swimming (in which the bird swims slowly along in a bizarre posture with its rear-end sunk and its forebody raised out of the water) (Simmons 1977).

Dive-bathing

Grebes have also a thorough bathe, getting its plumage very wet (but not waterlogged) by dive-bathing and wallowing between intense spells of surface-bathing. When dive-bathing, it makes a series of complete submergences, kick-diving vertically under the water with a quick flip-up of the folded wings, while keeping its con-

tour feathers ruffled up throughout and its wings held loosely (Simmons 1977).

15.2.2 Oiling

After bathing, the grebe oils its feathers. Oiling is functionally associated with bathing: the wetting of the plumage seems to act as much to facilitate the oiling as to clean the feathers, i.e. it is easier to spread preen-oil on damp feathers than on dry. Oiling is done both with the bill, as in ordinary preening (see 15.2.3), and also with the head and even, at times, with the wings. In such aquatic species like grebes, the habit is evidently of particular importance in maintaining the good condition and hence, at least indirectly, the waterproofing of the plumage.

When oiling with the bill, the grebe obtains oil from its preen-gland, situated on the lower back just above the tail-tuft, by turning the head and stretching the neck backwards dorsally, nibbling the feathered orifice of the gland with the bill, stroking the bill across it, and transferring the oil to the plumage by preening. When oiling with the head, it rubs its head on the preen-gland and then progressively over the rest of the accessible areas of its dorsal plumage, using all parts of head with a rubbing and rolling action. Such behaviour also serves to oil the head itself, both directly on the preen-gland and by secondary contact with other parts of the plumage. Particularly characteristic are the oiling thus of the flanks (flank-rubbing), the mantle and mid-back area (back-rubbing), and the mantle while simultaneously rubbing the underside of the lower mandible against the front of the curved neck (jugulum-mantle rubbing). Finally, though most parts of the wings are oiled with the bill or head, the tips of the primaries are at times treated, usually only after a thorough bathe, by being repeatedly rubbed alternately directly on the preen-gland with slow, deliberate wing-twitching movements (Simmons 1977).

15.2.3 Preening

Preening is a form of grooming behaviour performed by birds as part of feather maintenance. The most conspicuous sign of preening is when a grebe rolls over on its side to preen its under parts, exposing its white belly.

After bathing, Red-necked and Great Crested Grebes start preening their plumage, pure preening soon giving over to oiling and then back again gradually. If there has

been no effective bathing, the grebe may leave out the oiling phase; in such cases, it often wets the bill intermittently between preens by dipping it in the water. Much preening is carried out with the bill (true preening or preening with the bill); also, but to a much lesser extent, with the foot as in head-scratching (see below), especially during prolonged bouts of feather care (Simmons 1977).

True preening consists largely of the usual nibbling and drawing bill movements found in most birds. When nibbling, the grebe passes an individual feather through the bill with tiny pecking actions; when drawing, it pulls the feather through the mandibles with a single movement of the head. The grebe also frequently strops its plumage; in this highly characteristic form of true preening, whole areas of feathers, particularly those of the flanks and underparts, are rapidly stroked with a smoothing or flicking action of the closed or part-open bill. Repeated stropping is especially effective in quickly removing surplus water, re-adjusting the plumage after disarrangement, and spreading preen-oil, all in a relatively rough, crude manner, leaving other functions (such as repairing breaks in barbs and barbules) to the more precise nibbling and drawing movements.

While preening with the bill, the grebe assumes a number of distinctive poses. The most characteristic of these is the preening-roll: the bird lies over on its side to a greater or lesser extent while paddling with its submerged foot and sculling on the surface with the other, its conspicuous white underparts exposed, and engages in ventral preening the lower breast, belly, and adjacent areas (“Stochern in den Bauchfedern”, drawing in Wobus 1964, p. 28) (see Fig. 47). While doing so, the Red-necked Grebe may rotate on the water and “spin” round to a much greater extent than does the ventrally-preening Great Crested Grebe. In dorsal preening, the grebe turns its head and neck backwards to preen the mantle, scapulars, wings, mid-back, rump, and tail-tuft areas; in dealing with the under surface of the wing, it lifts the folded wing somewhat (see Fig. 49). In frontal preening (“Knabbern im Brustgefieder”, drawing in Wobus 1964, p. 28), the bill is lowered and the front and sides of the neck and the upper breast above the water-line are dealt with, the bird at times stretching up its neck and sharply tucking the bill to get at the higher parts (high preening). Finally, in lateral preening, the head is again turned back, this time to reach the “edge” and underside of the wing and



Fig. 47: Preening-roll. Photo: T Runge (Schleswig-Holstein)

Fig. 47: Stochern in den Bauchfedern.



Fig. 48: Lateral preening. Photo: T Runge (Schleswig-Holstein)

Fig. 48: Putzen der Federn der Körperseiten.

also the flanks at and just below water-line, the grebe rolling over in the water a little when necessary to do so (Simmons 1977) (see Fig. 48).

15.2.4 Feather-eating, Pellet Formation and Pellet-casting (these topics are discussed in more detail in 14.8)

Red-necked Grebes and other Podicipedidae eat large quantities of their own feathers. Intact feathers are not actively pulled out of the plumage, but only ingested after they are shed during moult or loosened during preening. Many feathers are eaten during preening sessions; they are sometimes dabbled in the water, to be moistened and then swallowed (see Fig. 39). The feathers are often picked up off the surface of the water. Parent Red-necked and other grebes will give them to the chicks from the day of hatching, even before these receive their first real feed. The young birds actively beg for them.

The mass of the ingested feathers is found free in the lumen (main chamber) of the stomach where they break down into a greenish felt-like spongy material. This mixes with ingested food and forms a characteristic feather-ball, which can fill the stomach. This feather-ball

of the lumen, whole or in bits, is periodically regurgitated from the stomach together with its contents (pellet-casting or pellet-ejection, see Fig. 40). Although feathers are not necessary for pellet-formation because other matter can take over this function, they presumably aid in pellet-formation and without them pellets are possibly difficult to cast (McAllister 1963). Pellet-casting seems to take place regularly, probably every other day and mostly by night or very early in the morning and is preceded by drinking (Fjeldså 2004).

Fjeldså (2004) wrote, that three main advantages of pellet ejection have been suggested: “(1) Sharp fish bones are rapidly wrapped up in a felt-like substance (preventing damage to the stomach wall) until they are dissolved. (2) By ejecting pellets, the grebes get rid of all the indigestible roughage that is left after a meal. (3) They can minimize the build-up of gastric parasite populations, which may represent a considerable health hazard (...).”

15.2.5 Shaking-movements

These include the head-shake, foot-shake, body-shake, and wing-flap.



Fig. 49: Dorsal preening. Photo: T Runge (Schleswig-Holstein)

Fig. 49: Putzen der Rückenfedern.

Head-shake

The head-shaking of Red-necked Grebes consists of a marked lateral jerk, which seems often to be a more forceful movement than the standard head-shake of the Great Crested Grebe. It appears largely to replace the throat-touching of Great Crested Grebes (see 15.2.8). Thus, lateral head-shaking in *griseigena* seems to play an even more important role in ridding the bill of surplus water than for the Great Crested Grebe (Simmons 1979).

Foot-shake

In the foot-shake, the leg is extended backwards and waved a few times in order to dry the toes, as prior to stowing the foot away for example (Simmons 1977).

Body-shake

When performing the body-shake, the grebe ruffles up its feathers, especially those of the mantle and scapulars, and slightly lifts the wings; it raises itself by treading water while simultaneously erecting its plumage more fully, and extending and rotating head and neck. Then it subsides to the swimming position while "tightening" its feathers up again. Simmons (1977) calls the whole sequence the rise-and-shake (see Fig. 50).

Wing-flap

When performing the wing-flap (rise-and-flap), the grebe raises itself, treading water, opens its wings fully and beats them deliberately a few times before subsiding (see photograph in Walser and Barthel 1994, p. 110) (see Fig. 51 and 52).

15.2.6 Stretching-movements

These include the leg-and-wing stretch, full-stretch, wing-glide, jaw-stretch and yawn.

Leg-and-wing Stretch

In the leg-and-wing stretch, one leg and then the wing on the same side are extended backwards so that they are, more or less, unflexed; the wing and then the leg are returned to their former positions after a slight pause. In its movement, the wing is stretched downwards over the back beyond the tail-tuft, primary tips clear of or barely touching the water. Sometimes, the leg is extended back on its own without any accompanying wing movement (the leg-stretch); also, following either form of stretch, the foot may be left behind for a while with all its digits spread (the toes-stretch) (Simmons 1977).



Fig. 50: Body-shake (rise-and-shake). Photo: T Runge (Schleswig-Holstein)

Fig. 50: Körperschütteln



Fig. 51: Wing-flap (rise-and-flap). Photo: T Runge (Schleswig-Holstein)

Fig. 51: Flügelschlagen



Fig. 52: Wing-flap (rise-and-flap), detail. Photo: T Runge (Schleswig-Holstein)

Fig. 52: Flügelschlagen, Detail.

Full-stretch

When performing the full-stretch (“*Strecken des ganzen Körpers*” of Wobus 1964), the Red-necked Grebe extends its neck low along and sometimes actually in the water (neck-stretch, see photograph in Walser and Barthel 1994, p. 116); it braces up the chin, the bill pointing upwards, sometimes also tilting the head slowly from side to side. This last movement (head-rotate) is more marked in *grisegena* than in the Great Crested Grebe. At the same time, the bird raises the “elbows” above the back and partly extends the “wrists”, thus lifting and partly opening both wings, rotating them forwards; alternatively, the Red-necked Grebe holds its wings more or less in the same position as in the wing-glide (Simmons 1977, Vlug 2002a) (see drawing in Wobus 1964, p. 29, and photograph in Walser and Barthel 1994, p. 116) (see Figure 53).

Wing-glide

When performing the wing-glide, the Red-necked Grebe extends both wings sideways so that they are at right-angles to the body with their undersurfaces parallel to the water; the bird holds its neck and head in “normal” relaxed position (see photograph in Walser and Barthel 1994, p. 110).

Jaw-stretch and Yawn

Two stretches involve the bill. In the jaw-stretch, both mandibles are opened but the movement of the upper one is greater than that of the lower (see Fig. 54). In the yawn, the bill is also opened but particularly the lower mandible, and the tongue is arched up inside mouth (see photograph in Walser and Barthel 1994, p. 101). There are good reasons to believe that this second bill movement is indeed a true yawn as in man (Simmons 1977).

15.2.7 Head-scratching

When performing a head-scratch, the grebe holds its head downwards and sideways close to the water to meet the foot, without any corresponding movement of wing, and scratches away with the flattened nail of the longest toe. Particularly during a prolonged head-scratch, the other foot is extended sideways and sculled to keep balance (Simmons 1977).

15.2.8 Throat-touching

Simmons (1977) describes throat-touching in Great Crested Grebes. When performing a throat-touch, *Podiceps*

cristatus, after first sometimes elongating its neck vertically, makes a quick, downward, rather formal-looking nod of the head to press the bill tip momentarily on the lower part of the foreneck just above the jugulum and water-line (the jugulum is the lower part of the throat, just above the breast). This movement is common in Great Crested Grebes but is easily overlooked because it happens so rapidly and briefly.

Head-shakes dispel much excess water, and the throat-touch drains any surplus water then remaining from the bill, perhaps that coming partly from within the nostrils or mandibles; this water runs down to collect as a large droplet at the bill tip and is then disposed of against the feathers of the foreneck (Simmons 1977).

The Red-necked Grebe rarely makes throat-touching movements (see Fig. 20). Bill-draining by preening seems to be rather a speciality of *grisegena*. For this species, as mentioned previously (see 15.2.5), lateral head-shaking appears to play an even more important role in ridding the bill of surplus water than for *Podiceps cristatus* (Simmons 1979).

15.2.9 Resting

After completing a bout of feather care, the grebe often rests. The bird adopts either the relax-posture, with the neck arched and drawn back so that the nape comes near to or touches the mantle area, or the full rest-posture (“pork-pie” attitude), with the back of the head lying on the mid-back area and the bill inserted laterally into the side of the neck (see photograph in Walser and Barthel 1994, p. 112) (see Fig. 55). When about to relax or rest fully, the grebe usually shakes one foot, to rid it of surplus water, and then holds it up against the flank (foot-resting), or puts it right away under the closed wing (foot-stowing), slightly raising and then lowering the wing as the foot is “shipped” against the flank and then encasing both foot and wing in the watertight “pocket” formed by the flank feathers. In order to maintain maximum stability on the water while resting, the bill is almost invariably inserted into the neck on the same side of the body as the foot is stowed. The free foot is paddled if necessary, and, at least at times, the grebe even swims along one-footed in the rest-posture (it may well have to do so, for instance, in order to keep its position against the wind or current). Occasionally, both feet are stowed simultaneously, particularly in cold weather (to reduce heat loss) or on very calm days (Simmons 1977).



Fig. 53: Full-stretch. Photo: T Runge (Schleswig-Holstein)

Fig. 53: Strecken des ganzen Körpers.

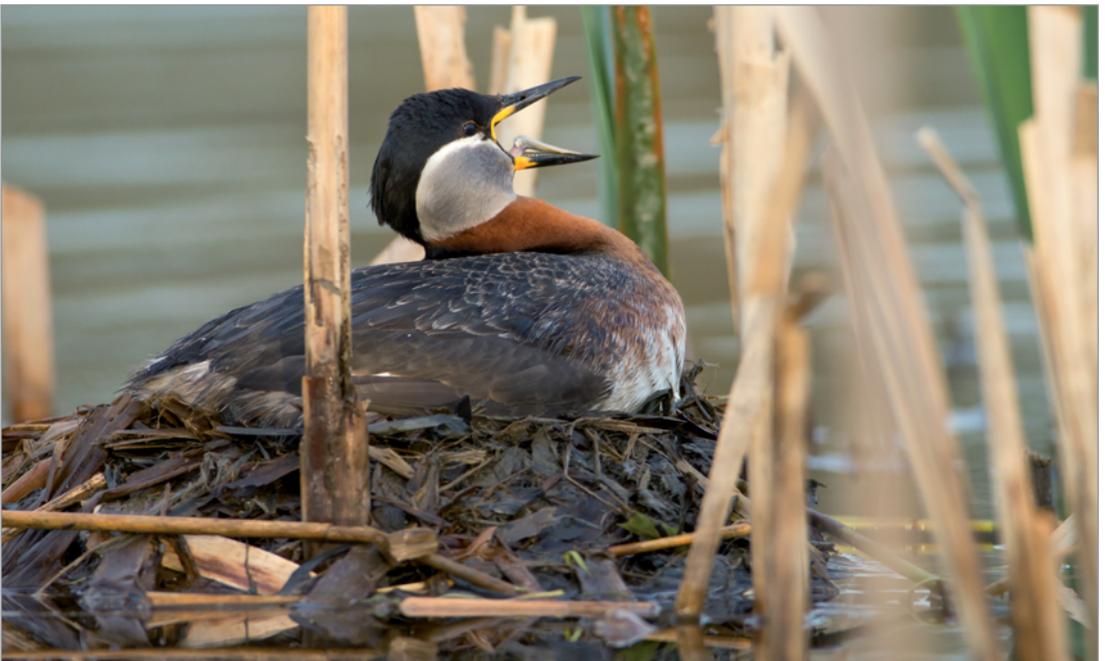


Fig. 54: Jaw-stretch. In the jaw-stretch, the movement of the upper mandible is greater than that of the lower (in the yawn, the bill is also opened but particularly the lower mandible). Photo: T Runge (Schleswig-Holstein)

Fig. 54: Strecken der Kiefer. Im Gegensatz zum Gähnen wird beim Strecken der Kiefer vor allem der Oberschnabel geöffnet.



Fig. 55: Full rest posture. Photo: T Runge (Schleswig-Holstein)

Fig. 55: *Schlafhaltung*.

Sim (1904) described the resting position on firm ground of a Red-necked Grebe captured in Ohio (drawing in Sim 1904, p. 70): “The grebe slept from dark until dawn, and generally for about an hour after a hearty meal. In roosting he ordinarily lay on his keel, his feet projecting behind. As the bird became sleepy the feathers gradually fluffed out and the head settled down upon the back. Soon one foot would be seen to twitch slightly. This twitching and curling up of the toes would increase in violence until, with a preliminary rapid waving movement the foot was tucked under the wing which in turn was quickly covered with the flank feathers. Then the other foot was similarly hidden. Thus, the feet were entirely concealed beneath the wings and feathers, not even the heel-joints showing.”

Sim (1904) continues: “While in this position the bird allowed me to lay back the feathers and then gently raise the wing. The flat, flipper-like foot was found to lie at full length against the warm, down-covered side of the body, the toes reaching nearly to the “arm-pit.” After tucking his feet away one by one, he would draw his head far back and with a peculiar wagging motion, settle it amongst the feathers of the back. With this movement the bill was thrust quite out of sight among the feathers

on either side of the neck, more commonly on the right side.”

15.3 Social Behaviour

Social behaviour is behaviour taking place between members of the same species such as territorial behaviour, agonistic behaviour and courtship.

15.3.1 Spacing

Outside the breeding season, the birds of the nominate race are most frequently solitary or in twos, or in small, usually loose, assemblages, e.g. in spring before dispersal to the breeding lakes and in late summer before and during the wing moult (Cramp *et al.* 1977, Vlug 1996, 2002a, Fjeldså 2004). Cramp *et al.* (1977) consider the nominate race to be the least gregarious of the west Palearctic grebes. However, Blomdahl *et al.* (2007) write: “(The) Red-necked Grebe is the grebe most likely to occur in flocks, with groups of up to ten birds being far from unusual and up to 50 birds having been counted at sites where the species regularly passes on migration. Such flocks are often dense and difficult to count and there is always the chance of another grebe species being present

among them. (The) Red-necked Grebe can, more often than its congeners, be seen joining flocks of ducks (mergansers and eiders in particular).”

In North-America, groups of several hundred Red-necked Grebes (subspecies *holboellii*) are a regular occurrence at some moulting and migratory staging areas (Campbell *et al.* 1990, Stout and Nuechterlein 1999, Vlug 2002a). Campbell *et al.* (1990) write that *Podiceps grisegena* in British Columbia is gregarious but rarely associates with other species of grebes. The authors state that large flocks of more than hundred birds are common on the coast in autumn and winter and may be seen occasionally throughout the province in spring migration (Campbell *et al.* 1990).

Spacing of Moulting Birds (see also 13.6.2)

In late July, August, and early September, concentrations of up to 160 Red-necked Grebes are recorded along the coast of the Baltic Sea in Mecklenburg-Vorpommern (Mecklenburg-West Pomerania) (Vlug 1996). Unfortunately, there are no detailed records on individual spacing of the birds in these concentrations. More is known about the spacing of moulting Red-necked Grebes in the Baltic Sea near the island of Sjælland (Zealand), Denmark. These birds occur as single individuals or in small flocks of up to 11 birds (Pihl 1995).

In North America, large concentrations in the moulting period are recorded. In September, Red-necked Grebes in Alberta “assemble in large numbers on some large lakes in preparation for migration. Mingling with Western Grebes and Common Loons, they form aggregations that may run into the thousands. For days they exercise their wings, taking short practice flights from one part of the lake to another. Then late one evening around mid-October they patter along the surface until airborne, and on short, rapidly-beating wings that look too weak to carry them through the night they disappear into the twilight” (Salt and Salt 1976).

Approximately 1,300 Red-necked Grebes completed their autumn moult at various bays and shoreline areas around Manitoulin Island, Lake Huron, in 1994. The moulting birds were present as single individuals and in loose flocks of 2-40 birds per flock (Stout 1995).

Spacing During Migration

Red-necked Grebes of the nominate subspecies *grisegena* migrate singly or in small parties (Cramp *et al.* 1977).

During migration along the Norwegian coasts, the birds are fairly social, and move in flocks of 10-20 birds (Folkestad 1978).

In Europe, the concentrations during the migration are usually small, and records of flocks of more than 100 birds are rare (see 13.1.1), but in North America parties of several hundred are a regular occurrence at some staging areas (see 13.6.3).

In the major migration period at Whitefish Point, Lake Superior (August through September), solitary birds and flocks of 2-6 grebes were most frequent (median flock size = 3) (Stout 1995) (see 13.6.3).

Spacing During Foraging

Red-necked Grebes usually feed singly, but at wintering sites some Red-necked Grebes form commensal feeding associations with scoters *Melanitta* (Cramp *et al.* 1977, Stout and Nuechterlein 1999).

Breeding Dispersion

The pairs of Red-necked Grebes are typically territorial with well-dispersed nests (see 15.3.4).

15.3.2 Pair Bond, Pair Formation and Similar Roles of the Sexes

Pair Bond and Pair Formation

Some Red-necked Grebes probably establish a pair-bond during winter. There are records of all courtship displays at the wintering areas, and even observations of attempts to build copulation platforms out of seaweed and other floating debris (Stout, *cited in* Vlug 2002a). However, most birds probably pair up during spring migration within large assemblages along the migration route, and as late as the arrival at the breeding waters before serious nesting behaviour begins (Wobus 1964, De Smet 1983; *cf.* Stedman 2000 for *Podiceps auritus*).

Stout and Nuechterlein (1999) wrote that many individuals arrive on their breeding grounds already paired, or pair shortly after arrival, and that the early pair-formation displays are only infrequently observed on the breeding lakes. De Smet (1983) stated that during his study in Turtle Mountain Provincial Park, Manitoba, only c. 15% of the Red-necked Grebes returned unpaired and subsequently mated. Upon returning, the other pairs were unsynchronized in their actions and appeared recently mated. Thus, although the majority of the birds

give the appearance of being paired on arrival at the nesting waters, unsynchronized actions and frequent changes of partners show that a number of these grebes are not definitively paired at this stage (Wobus 1964, VlUG 2002a; cf. McAllister 1958 for *Podiceps nigricollis*).

The pair formation in *Podiceps* species is a long process and begins before establishing true territories and serious nesting behaviour. All *Podiceps* species are very pugnacious after spring arrival. However, since the sexes are alike, close contact is probably necessary for sex recognition. A close approach naturally releases conflicting attack/escape tendencies, which may have been a main determinant of the evolution of the Discovery Ceremony. The male gradually learns to tolerate the female in its territory (Fjeldså 1982b, 2004). Complete Discovery Ceremonies occur a short time after spring arrival, and are, as soon as the birds appear to know one another individually, replaced by incomplete versions or other displays when birds meet after a separation. Probably no pair-bonds in Red-necked Grebes and other *Podiceps* species develop unless the birds know one another individually and have become sufficiently motivated to perform the Weed Ceremony after the Discovery Ceremony (Fjeldså 1982b). One may say that the ritualization of displays takes a form where expression of antagonistic elements is used to consolidate pair bonds instead of disrupting them (Fjeldså 2004).

As we shall discuss in more details below, the development of courtship rituals has taken a different course in grebes compared with other birds. Grebes are distinctive in having mutual ceremonies where the partners have identical, or ambivalent, roles. A courting grebe normally releases the same or reciprocal behaviour in its partner. The pair formation displays are well separated (in context and ritualization) from mating behaviour. While the water courtship (e.g. Discovery Ceremony) provides a mechanism enabling two birds to remain peacefully together, it does not immediately lead to mating (Fjeldså 2004).

Red-necked Grebes are monogamous, at least for one season (seasonal monogamy). The pair-bond often breaks down as the pairs split the broods or when they leave the nesting area. In all Red-necked Grebe families under observation in Turtle Mountain Provincial Park, Manitoba, one parent departed 1-3 weeks before its mate, so sustained monogamy is unlikely (De Smet

1983). Although a high level of mate fidelity (67% of the resighted pairs, $n = 21$) was found in a colour-banded Minnesota population of Red-necked Grebes, it is doubtful that this fidelity is due to year-round pairing (Stout and Nuechterlein 1999). It is very likely that territorial attachment by both sexes may result in contact with former mates and in an opportunity for renewing the pair-bonds in spring (cf. Ferguson 1981 for *Podiceps auritus* and Van der Poel 1984, 1985 for *P. cristatus*).

Similar Roles of the Sexes

A very striking feature of Podicipedidae is the almost total sexual ambivalence in displays and other social behaviours: the male and female play similar roles simultaneously or reciprocally, or show different roles interchangeably, either sex taking the initiative. Even mounting during the copulation can be reversed, and females mounting males is common in many grebe species and has also been reported in Red-necked Grebes (see 15.3.8). The behavioural dimorphism between the sexes is largely characterized by a differing frequency of certain behaviour patterns, and the only definite differences between male and female grebes seem to be the ability to fertilize and to lay eggs, respectively (Simmons 1985, Fjeldså 2004).

It should be stressed that male and female grebes not only play similar roles in displays, but also share other tasks. However, as already stated, the overall time-activity budgets of the sexes can differ. Kloskowski *et al.* (2012) studied Red-necked Grebes in Poland. They reported that males in the pre-laying period were involved in aggressive interactions at a higher rate than females, but there were no sex differences in the time spent on aggressive encounters. This was due to the fact that females participated in more prolonged territorial disputes with other *griseogena* pairs. The authors discovered that the most conspicuous difference concerned building activities: males spent substantially more time than females on platform-building. The greater participation in nest construction by males allowed the females to allocate more time to self-maintenance activities (foraging, preening, sleeping and resting) in the period prior to egg-laying. A positive relationship was found between the relative contribution of males to nest-building and later brood provisioning. Kloskowski *et al.* (2012) stated that this indicates that male nest-building is an honest indicator of future paternal effort. Males obtained copulations proportional to the time spent on nest-building,

and the extent of male participation in nest construction was of importance for explaining variation in clutch size. The authors suggested that greater investment of males in energetically demanding pre-laying activities is functionally similar to post-mating courtship feeding; it constitutes the males' indirect contribution to clutch production. The studies of Kloskowski *et al.* (2012) support the idea that the male contribution to nest building provides the female with an indication of the male's paternal quality.

15.3.3 Relations Within the Family Group

The young of grebes are precocial and semi-nidifugous. Although newly-hatched chicks can swim and dive feebly in case of need, they do not voluntarily stay long in the water. Their ability to regulate their body temperature seems poorly developed at first. In addition, their short down isolates poorly. They are very susceptible to draughts and chilling until their thermoregulation ability develops in the second week. They are brooded under the wings of their parents and spend most of their early lives snugly riding on the back of one or other of their parents (Fjeldså 1977b, 2004). At first, one adult carries all the young while the other brings food. The old bird carrying the young flaps its wings and dumps the young into the water at intervals. This often stimulates immediate defecation, and the young then climb back on it, or on the other parent. After some days the young may be fed in the water, which allows both parents to dive. The young are fed one prey item at a time, so the food provisioning is a serious work constraint (Fjeldså 2004) (see 16.5 for more details).

Sibling Competition (this topic is treated in more detail in 16.5.12)

During the back-brooding period in Red-necked Grebes (the first two weeks after hatching), the advantages of size and strength given to the first-hatched young by asynchronous hatching are enhanced by the establishment of a dominance hierarchy within the brood, reinforced by pecking. The larger chicks obtain most of the food and gain initial access to the parents' back by pecking and chasing the smaller siblings. The subordinates never retaliate and may eventually die (De Smet 1983, Kloskowski 2001a, 2003a). In this period, when carrying the young, the parents do not interfere in the sibling competition for food. However, after the back-brooding period, in the free-swimming phase, the parents show aggression to their offspring, especially to the older

chicks and the within-brood hierarchy of received food is gradually reversed. The junior chicks are also longer cared for than their older sibling. Thus, it is suggested that Red-necked Grebe parents change the within-brood investment allocation over time. In the first weeks after hatching (the back-brooding period), they allow biased food distribution and in consequence even brood reduction. Later, they intervene in resource allocation and attempt to equalize the post-fledging survival of all chicks. The parental aggression appears to be a means both for counteracting the competitive advantage of older sibs and for forcing the chicks to independence (Kloskowski 2001a).

Brood-division (see also 16.5.13)

Simmons (1955, 1989, 1997) described brood-division in grebes, especially in Great Crested Grebes. He wrote that, when carrying is over, *cristatus*-families of more than one surviving chick tend to be divided between the parents, this system becoming stable by the sixth week at the latest, each adult by then typically caring only or mainly for its "own" young (Simmons 1989).

Wobus (1964) found, from his studies in Oberlausitz, Germany, that in some but by no means all pairs of Red-necked Grebes there would be a partition of the brood between the male and female after a brief period in which both sexes cared for them jointly. As most broods in the study area of Wobus (1964) comprise two chicks, the adults would each take over the care of one of them. Now and then the two units separate to a large extent, each unit partly occupying different areas of the same pond. The division in some broods was such that the male would attack and chase away the female's chick and the female the male's (as recorded in the Great Crested Grebe), though in other divided broods two family units would sometimes rest together without any sign of friction. Brood-division in Oberlausitz was very rare on small ponds occupied only by a single pair but common on larger and well populated waters with a long unbroken border of aquatic vegetation.

In only one case was Wobus (1964) able to make detailed observations on the first stage of the division process which started on 27 June, four days after the hatching of the last chick of three (on 23 June), by which time it had died, the smallest surviving chick staying with the female, and the larger with the male, though the female was seen to feed the male's chick and the male to carry

both chicks. Three days later, on 30 June, the division was much more clear-cut, there being no exchange of young or feeding of the other young, but observations ended next day, on 1 July, when both chicks succumbed during a spell of inclement weather.

Kloskowski (2001a) studied 17 pairs of Red-necked Grebes that raised 2 or 3 chicks to independence (12 with 2 chicks, 5 with 3 chicks). His study was conducted at small fish-ponds in southeast Poland. In eight 2-chick families the parents divided the broods. Although the parents of the divided broods showed hostility more often to the offspring from the other family unit, they usually continued to provision the chicks from the other group.

Courtship Between Siblings

Young Red-necked Grebes and other Podicipedidae show forms of behaviour normally only associated with sexually mature birds. Adult-like water-courtship between siblings in *P. griseogena* occurs at times from the 4th week. They may perform Head-shaking or other pair-bonding behaviour. Older chicks sometimes solicit on raised sites (Fjeldså 1977a, Vlug 2002a).

It is not known whether these adult-like displays in young grebes just demonstrate the development of close individual bonds, or whether there is a hormonal basis for such behaviour in young birds (Fjeldså 2004).

Second Broods (see also 16.3.2 and 16.5.14)

Many Red-necked Grebes lose their eggs. However, they can lay up to 5 replacement clutches (Stout and Nuechterlein 1999). After successful hatching of the first brood, early breeding pairs may sometimes produce a second brood (Wobus 1961, 1964, Menzel 1971, Melde 1978, Axelsson 1988, Dittberner 1996, Axelsson 1997, Stout and Nuechterlein 1999, Kloskowski 2001b, Vlug 2005, Dittberner and Dittberner 2006). Of 163 observed breeding pairs in south-east Poland, 4 attempted a second brood and 2 were successful (Kloskowski 2001b). Vlug (2005) recorded 36 attempts to produce a second brood in Schleswig-Holstein, 27 were successful ($n = 10,349$ Red-necked Grebe pairs, 1969-2002). Stout and Nuechterlein (1999) write that there is only one record of a successful second brood in North America (but see 16.3.2). In Turtle Mountain Provincial Park, Manitoba, only one second clutch was attempted out of 110 pairs of Red-necked Grebes that were regularly observed (De Smet 1983).

Pairs with second broods nest in breeding waters with an abundance of food and start their first clutch early in the season (*cf.* Berndt 2010 for *Podiceps cristatus*). Apparently, only early breeding on territories with abundant food allows the Red-necked Grebe parents to overcome the conflicting pressures resulting from overlapping parental investment in successive reproductive attempts. Raising two broods is energetically costly and stressful, and the double-clutched parents (in Poland) become aggressive to their first brood offspring earlier than controls (Kloskowski 2001b).

The clutch of a second brood is usually initiated when the young from the first brood are still dependent and 3-5 weeks old (Wobus 1964, Menzel 1971, Kloskowski 2001b). Sometimes the beginning is much earlier: Melde (1978) observed near Kamenz, in eastern Germany, a female Red-necked Grebe laying eggs on the same days as the first brood chicks were hatching, and De Smet (1983) recorded a second clutch on Margaret Lake, Manitoba; laying of this clutch commenced 1-2 days before the hatching of the first.

In overlapping second broods of grebes, the large young of the first brood may assist in feeding their younger siblings (Fjeldså 1977b). However, in the Red-necked Grebe, the relations are often hostile, and the first brood young may show kleptoparasitic behaviour (Kloskowski 2001b) (see 16.5.14 for more details).

Departure

Adult Red-necked Grebes in Europe and North America usually leave the breeding waters up to 4 weeks before their young (Wobus 1964, Scholl 1974, Riske 1976, Vlug 1996, Stout and Nuechterlein 1999). The parents depart earlier from territories on small ponds than from territories on larger ones (Kloskowski 2003b). Mostly the adults depart singly, i.e. not together with the partner (Scholl 1974, De Smet 1983, Vlug 1996, Kloskowski 2003b).

During the study of De Smet (1983) in Manitoba, departure data were collected from the young of 11 broods: the immatures generally departed at 9-10 weeks of age, although a few left before they were 2 months old, and others remained beyond 70 days. As with the adults, most immature Red-necked Grebes departed their nesting lakes singly.

Frequently, one member of a pair abandons its mate and still dependent young (see 16.5.16).

15.3.4 Breeding Dispersion, Territoriality and Coloniality

Territorial Behaviour

Red-necked Grebes are highly pugnacious, intensely territorial birds and usually nest as isolated pairs. They do not only show intraspecific territoriality, but also interspecific (De Smet 1983, Stout and Nuechterlein 1999, Vlug 2002a, Fjeldså 2004).

The pairs defend their territory with threat displays, overt aggression, and vocal duets. Red-necked Grebes are very vocal in the breeding season and may use a loud, far-carrying Song and display-call or Whinny-braying (“uööh-Gebrüll” of Wobus 1964) as territorial advertisement and as display of pair unity. This call is commonly observed by the pairs at the territorial boundaries, particularly when other pairs approach. An intense Song and display-call duet occurs as Triumph Ceremony (term as used by Stout and Nuechterlein 1999) after territorial conflicts. The pairs on a territory respond to the neighbours’ calls (Wobus 1964, Cramp *et al.* 1977, Stout and Nuechterlein 1999, Vlug 2002a).

Defence of a breeding territory is not merely dominance with a spatial reference but can more properly be defined as a hierarchically organized “instinct” system whose first stage is a defensive one and includes avoidance and isolation from conspecifics. This means that the pairs first try to isolate themselves and find a “vacant” place, usually a pond, bay or inlet with no other grebes. Thereafter they try to prevent other grebes from entering the area (Fjeldså 2004).

Territory Types and Sizes

Type A territories (mating, nesting, and feeding ground for the young) predominate in Red-necked Grebes. Type B territories (mating and nesting ground, most foraging occurs elsewhere) are rather rare (see 16.2.5 for more details).

Klatt and Paszkowski (2005) stated that the number of conspecifics in their study area in Alberta has a larger effect on territory size than the abundance of food. Thus, high nesting densities may (sometimes) be explained more by intruder pressure than food abundance (see 16.2.5 for more details).

Colonies

Sometimes small colonies (up to 15 nests) of the nominate race are reported, and there are numerous reports of *Podiceps grisegena holboellii* in North America nesting in (“loose”) colonies. However, the authors usually present few data and the term “colony” often indicates some areas with a high nest density (see 16.2.5 for more details).

Definition of Avian Coloniality

Wittenberger and Hunt (1985) define a nesting colony as “a place where a number of individuals or pairs nest ... at a more or less centralized location from which they recurrently depart in search of food.” This definition includes true as well as semi-colonies (see below) and serves well as a working definition. However, at present there are no objective (nor even widely accepted) criteria as to how clumped nests must be to constitute a colony.

Two types of colonies can be distinguished, the true and the semi-colonies.

True Colonies

In the true colonial grebes the nest site selection is highly social, with the initial nests serving as epicentres from which the colony grows outward. The birds may show synchronization of egg-laying caused by the interaction of conspecifics. Nest-building activities, platform-courtship and promiscuous mating may promote this synchronization.

The true colonial grebes are more peaceful than the territorial and semi-colonial species. Unlike the Red-necked Grebe, aggression in *Podiceps nigricollis* and other true colonial species is only released at short range and mainly comprises unritualized, mobile attack-escape sequences (Fjeldså 1982b, 2004). The Hoary-headed Grebe and the species of the eared *Podiceps* group deviate from the territorial grebes by a simplification of agonistic behaviour (behaviour relating to combat), which is very likely conditioned by colony breeding. Stationary threat in Forward-display, typical of Red-necked Grebes and other territorial species, is suppressed, and Token-dives miss completely (Fjeldså 1982b, 2004).

Semi-colonies

Semi-colonies are nesting aggregations in which the individuals are independently attracted by a particular environmental feature. Even the most fiercely aggressive territorial grebes are able to breed in semi-colonies. In spring, the semi-colony formation in the Red-necked,

Great Crested and Slavonian Grebes begins with a number of initial pairs vigorously defending large areas of the future colony site. As additional pairs try to get a foothold, open fights are frequent. As the pressure increases and becomes persistent, the initial territory-holders cannot counter all the settlement attempts of numerous pairs and their resistance wanes. A gradual habituation to the close presence of established pairs occurs. When still more settlers come, they have to build ever closer to existing platforms, thereby contributing to a reduction of nest distances over time. Finally, the birds only defend the immediate vicinities of their chosen nest sites (see 16.2.5 for more details).

15.3.5 Agonistic Behaviour (see Fig. 56)

Agonistic behaviour is the complex of aggression, threat, appeasement (conciliation), and avoidance (retreat) that often occurs during encounters between members of the same species. When encountering a stranger or rival, many animals exhibit a mixture of aggression and fear, which manifests itself in various forms of agonistic behaviour, including ambivalent behaviour and conflict. Agonistic behaviour is usually typical of the species, often taking the form of characteristic displays (McFarland 2006). The term is also often used as synonymous with aggressive or antagonistic behaviour (Terres 1980, Fjeldså 2004).

Red-necked Grebes can be very pugnacious in the pair formation period and in the breeding-season. Agonistic behaviour is common in spring aggregations along the coast as well as in the breeding area, by night as well as by day, and often involves both members of a pair. Males are more likely to initiate attacks than females, and they attack from greater distances than females. When looking for a partner (Advertise) the grebes are often attacked resolutely by mated birds, often without preceding threat. On their breeding lakes, Red-necked Grebes are territorial and intra- and interspecifically aggressive, commonly threatening or making underwater attack dives against conspecifics and other waterbirds that enter their breeding territory (they sometimes even kill ducklings) (Cramp *et al.* 1977, Stout and Nuechterlein 1999, Vlug 2002a, Fjeldså 2004).

Unlike the gregarious and true colonial *Podiceps*-species, Red-necked Grebes show sustained postures in Forwards threat (Forward-display) and perform ritualized threat dives (Token-dives) (Fjeldså 1982b).

Physical Interactions

The grebes attack conspecifics during courtship and in defence of the territory. They often initiate swimming and diving pursuits, even after the intruder begins to swim away (Garner 1991, *cited in* Stout and Nuechterlein 1999).

The Red-necked Grebe may stalk or chase the rival in a series of Sinister-dives: the bird submerges from the Forward-display (see below) and swims rapidly just below the surface, the course perhaps slightly indicated by ripples. During the approach, the head may surface briefly once or twice. It attacks by jabbing at the underside of the victim with its bill ("Torpedoangriff", Wobus 1964) or by grabbing the feet of the victim. The potential victim often peers underwater or dives in response. It appears that the Sinister-dive in the Red-necked Grebe is less ritualized than in the Great Crested Grebe, with the ripples on the water not evident (Cramp *et al.* 1977, Stout and Nuechterlein 1999). A Red-necked Grebe also attacks by patter-flying over the water with its neck extended (Patter-attack) (see Fig. 57).

In a one-sided fight, the bird seizes its rival by the head or neck, attempting to force it under water. The victim tries to escape by pattering across the water (with or without use of the wings), by diving, or flying. In a full combat, both birds leap forwards and upwards to clash breast to breast, almost out of the water; they paddle with their feet, stab and wrestle with their bills. Usually they flap their wings vigorously to keep their balance (see Fig. 58, 59 and 60). If one bird loses its balance, the other one can get the upper hand. The winner pushes its opponent under water and bites it at the back of its head and neck (Cramp *et al.* 1977, Fjeldså 1977a, Fjeldså 2004; see drawing in Fjeldså 1977a, p. 25, and in Fjeldså 2004, p. 80). Prolonged fights usually attract the mates of the birds, which often also begin to fight. In Red-necked Grebes fights sometimes last several minutes.

Communicative Interactions

The agonistic displays grade into one another, differing primarily in the position of the crest (spread or not), the head (height), the neck (stretched or not), the bill (angle), the back-feathers (raised or not), and the wings (spread or not). These positions are combined to form a complex series of graded agonistic postures, many of which are used in combination with vocalizations (Stout and Nuechterlein 1999). The most extreme forms of

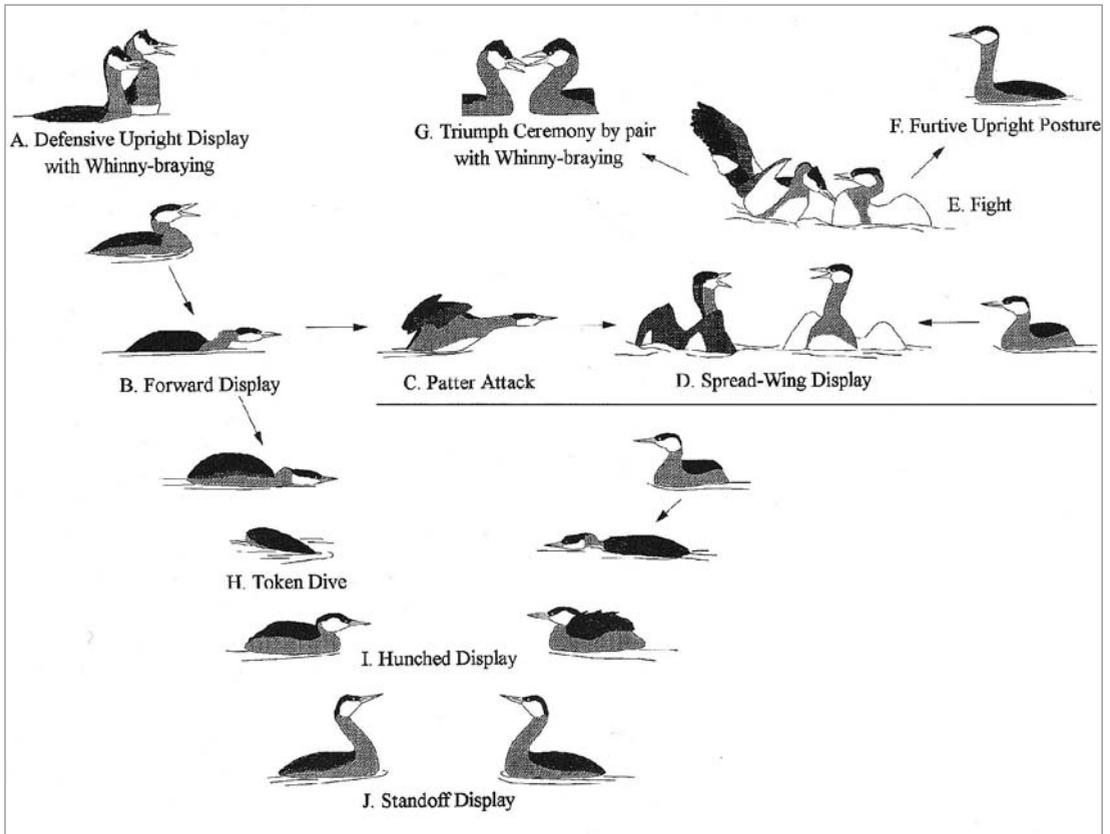


Fig. 56: Agonistic behaviours of the Red-necked Grebe; the displays grade from one to another. A. Defensive-upright display with Song and display-call (Whinny-braying). B. Forward-display. C. Patter-attack. D. Spread-wing display. E. Fight. F. Alarm or Furtive upright posture. G. Triumph Ceremony with Song and display-call (Whinny-braying). H. Token-dive. I. Hunched-display. J. Stand-off display. From: B E Stout and G L Nuechterlein (1999), Red-necked Grebe *Podiceps grisegena*. In A Poole and F Gill (eds.), The Birds of North America, No. 465, page 13. The Birds of North America, Inc., Philadelphia, Pennsylvania. Drawings by B E Stout from photographs by G L Nuechterlein, reproduced with kind permission of the authors

Fig. 56: Agonistische Verhaltensweisen des Rothalstauchers; die Verhaltensweisen gehen ineinander über. Für viele englische Namen der Verhaltensweisen gibt es in der deutschen Sprache kein direktes Pendant. So wird "display" sehr unterschiedlich übersetzt und auch angewandt. Die meisten deutschen Bezeichnungen sind aus Wobus (1964) und Konter (2010) übernommen. A. Abwehrhaltung mit "uööh-Gebrüll". B. Flaches Drohen. C. Überwasserangriff (Drohanflug, Fluglaufangriff). D. Ausgebreitete Flügelstellung. E. Kampf. F. Alarmhaltung. G. Triumphzeremonie mit "uööh-Gebrüll". H. Flachtauchen. I. Hohes Drohen. J. Vermeidungshaltung.

these agonistic displays have been named by Wobus (1964), Cramp *et al.* (1977), Stout and Nuechterlein (1999), Konter (2010), and others.

The Defensive-upright display is the most conspicuous agonistic display. The head, neck and breast are stretched high, the crests are raised, the tail is cocked, and the mandibles are open as a call is given (see photograph in Konter 2010, p. 217). It is usually seen as the mates join each other on their territory, nearly always in association with the loud, far-carrying diver like Song and display-call

(Whinny-braying) (Stout and Nuechterlein 1999). In response to the Song and display-call by intruding pairs, the mates on the territory usually first join together to give the Song- and display call in the Defensive-upright display, and then approach the intruders as a unit. The intensity of the display (indicated by the head height and the degree to which the crest is raised) is highly variable; it may decrease as the season progresses. The Defensive-upright display is also used as Triumph Ceremony following agonistic encounters (Stout and Nuechterlein 1999) (however, Cramp *et al.* 1977 write that the mates, in both



Fig. 57: Patter-attack. Photo: T Runge (Schleswig-Holstein)

Fig. 57: Überwasserangriff (Fluglaufangriff).



Fig. 58: Fighting Red-necked Grebes. Photo: T Runge (Schleswig-Holstein)

Fig. 58: Kämpfende Rothalstaucher.



Fig. 59: Fights sometimes last several minutes. Photo: T Runge (Schleswig-Holstein)

Fig. 59: Die Kämpfe dauern manchmal einige Minuten.



Fig. 60: Fighting birds. Photo: T Runge (Schleswig-Holstein)

Fig. 60: Kämpfende Vögel.

ances, may link up and perform the Triumph Ceremony assuming the *Hunched-display*; thus, the Triumph Ceremony of Cramp *et al.* 1977 is the same as the Greeting Ceremony of Stout and Nuechterlein 1999).

In the Forward-display (“*Flaches Drohen*”, see drawing in Wobus 1964, p. 53) (see Fig. 61, 62 and 63) the bird faces its opponent, the body-feathers flattened. When swimming towards the opponent, the neck may be straight, extended low over the water, the throat touching the water surface; when stopping, the neck is withdrawn, with a characteristic bend towards the body, and awash. At high intensity threat, most of the body is submerged and the bill somewhat raised (*Threat-lurking*) (Wobus 1964, Fjeldså 1973c, Cramp *et al.* 1977, Stout and Nuechterlein 1999) (see Fig. 62). The Forward-display is sometimes followed by *Sinister-dives* toward the victim. In other cases, it is followed only by *Token-dives* (“*Flachtauchen*”, Wobus 1964), in which the bird submerges as if to approach under water, but surfaces instead at or near the original spot, often near the territorial boundary (Wobus 1964, Stout and Nuechterlein 1999, Vlug 2002a) (see Fig. 64).

When at the territorial border, the Forward-display grades into the *Hunched-display* (German: “*Hohes Dro-*

hen”) in which the bird holds its head low but raises the back-feathers. The wings are partly lifted on the back. The grebe kinks the neck such that (in the most extreme case) the head is nearly held over the shoulders (Cramp *et al.* 1977, Stout and Nuechterlein 1999) (Fig. 63). Usually, the bill in this display is held horizontal or lowered, sometimes touching the water (Cramp *et al.* 1977). However, the bill may be raised, pointing obliquely upwards (“*Oblique Hunched-display*” of Konter 2010; see drawing in Wobus 1964, p. 54, and photograph in Konter 2010, p. 215).

Konter (2010) discerns an *Intermediate-threatening display* (“*Mittelhohes Drohen*”) (see photograph in Konter 2010, p. 215). In contrast to the Forward-display, the bird is not very low on the water surface, and, although its head is held relatively low (a little above shoulder height), it is held higher than in a high intensity Forward-display.

The Forward-display is sometimes followed by a *Patter-attack*, in which the grebe attacks its opponent by patting with flapping wings across the surface (see Fig. 57). This behaviour may be succeeded by the *Spread-wing display*: both birds face off in an upright posture,



Fig. 61: Forward-display. Photo: T Runge (Schleswig-Holstein)

Fig. 61: *Flaches Drohen*.



Fig. 62: High intensity Forward-display (Threat-lurking). Photo: T Runge (Schleswig-Holstein)

Fig. 62: Flaches Drohen, hohe Intensität.



Fig. 63: Stationary threat in Forward-display with back-feathers raised as in Hunched-display (at the territorial border, the Forward-display grades into the Hunched-display). Photo: T Runge (Schleswig-Holstein)

Fig. 63: Stationäres Flaches Drohen mit aufgestelltem Rückengefieder wie beim Hohen Drohen (an der Grenze des Brutreviers geht das Flache Drohen in das Hohe Drohen über).



Fig. 64: A Red-necked Grebe directly before a Token-dive. Photo: T Runge (Schleswig-Holstein)

Fig. 64: Ein Rothalstaucher unmittelbar vor dem Flachtauchen.

with the breasts extended out of the water and the wings partially unfolded (see photograph in Larsen and Wirdheim 1994, p. 3) (see Fig. 65 and 66). Usually, the Spread-wing display is accompanied by the Song and display-call. It often precedes physical attacks (Stout and Nuechterlein 1999).

In the extreme Alarm or Furtive-upright posture, all the feathers are depressed, the neck is stretched up and somewhat back, the bill is horizontal; as the bird swims away, the rear-end of the body may be low in the water, the front-end high (Cramp *et al.* 1977). A Red-necked Grebe outside its own territory or without a territory in a breeding pond is normally timid and restless at the sight of other grebes and often assumes the Furtive-upright posture and is prepared for diving or rapidly swimming away (Stout and Nuechterlein 1999, Vlug 2002a).

In stand-offs at close quarters, the birds may raise their head and hold the bill at an oblique angle, grading into the Stand-off display, with the body stiff and oriented broadside to the opponent (Kevan 1970, Stout and Nuechterlein 1999) (see Fig. 67). Birds assuming the Stand-off display usually swim very slowly, circling each other about a body length apart. Frequently there are

three or four grebes involved in this circling (Kevan 1970). Konter (2010) calls the circling of the birds "Parading in Stand-off display" (see photograph in Konter 2010, p. 221) (see Fig. 68). Such encounters generally end with the birds drifting apart, joining their mates, and swimming off calling. Sometimes the Stand-off display ends in fighting (Kevan 1970).

15.3.6 Water-courtship (see Fig. 69)

The main function of the Water-courtship displays of grebes is to reduce the disruption pressure in the union of two birds and to cement pair bonds. These displays do not lead to the actual mating. Therefore, Water-courtship and Platform-courtship are mutually exclusive, and almost always separated by periods of day to day activities (Fjeldså 1973c). The most complex displays mark the initial phase of pair formation, and the "formalities" are thereafter soon dropped. So, well-established partners show only a simple gesture (Fjeldså 2004).

The Water-courtship displays can be spectacular and involve both sexes in a variety of highly ritualized, apparently mechanical, sequences, which are among the most



Fig. 65: Spread-wing display. Photo: T Runge (Schleswig-Holstein)

Fig. 65: Ausgebreitete Flügelstellung.



Fig. 66: Spread-wing display of two Red-necked Grebes *P. g. holboellii*. Photo: A Konter (Canada)

Fig. 66: Ausgebreitete Flügelstellung von zwei Rothalstauchern *P. g. holboellii*.



Fig. 67: Stand-off display. Photo: T Runge (Schleswig-Holstein)

Fig. 67: Vermeidungshaltung.



Fig. 68: The two Red-necked Grebes *P. g. holboellii* with the neck stretched high are Parading in Stand-off display. Photo: A Konter (Canada)

Fig. 68: Die zwei Rothalstaucher *P. g. holboellii* mit gestrecktem Hals paradieren in Vermeidungshaltung.

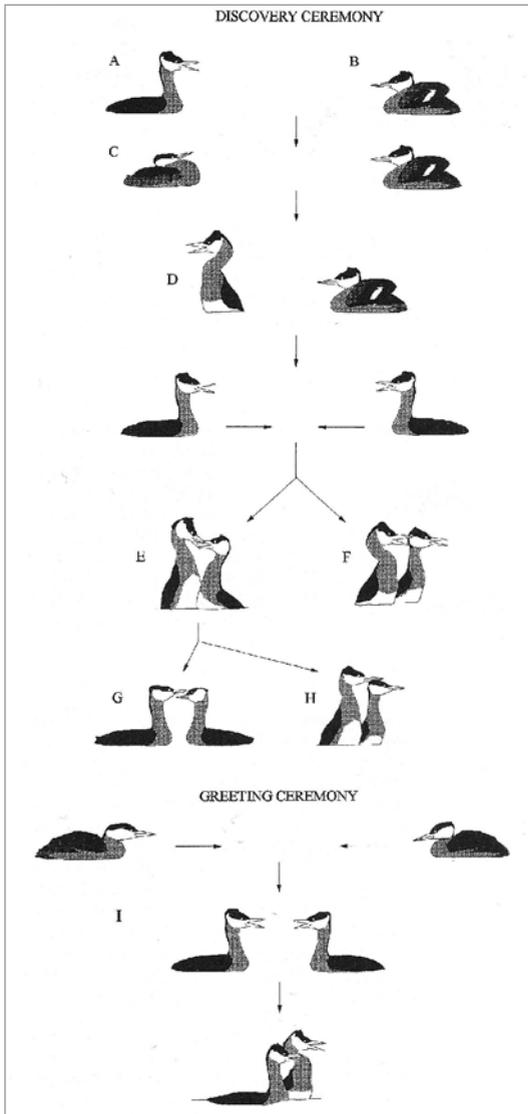


Fig. 69: Courtship displays of the Red-necked Grebe. A. Song and display-call (Whinny-braying). B. Cat-display. C. Bouncy-posture. D. Ghostly-penguin display. E. Penguin-dance. F. Parallel-rush. G. Slow Head-turning. H. Parallel-barging. I. Greeting Ceremony. From: B E Stout and G L Nuechterlein (1999), Red-necked Grebe *Podiceps grisegena*. In A Poole and F Gill (eds.), The Birds of North America, No. 465, page 14. The Birds of North America, Inc., Philadelphia, Pennsylvania. Drawings by B E Stout from S Cramp *et al.* (1977), and photographs by G L Nuechterlein, reproduced with kind permission of the authors

Fig. 69: Balzverhalten des Rothalstachters. A. "uööh-Gebrüll". B. Schwanstellung. C. Schaukelstellung. D. Steilauf tauchen (Geisterpose). E. Pinguintanz. F. Paralleles Vorschnellen. G. Wegsehen. H. Parallelschwimmen (aus Wobus 1964). I. Begrüßungszeremonie.

complex known in birds. In addition to their complexity, maybe their most peculiar feature is the degree of sexual ambivalence: in most displays male and female adopt the same posture, and in those displays where they have different roles, these are fully reversible. This even applies to the mating behaviour, as the female often mounts the male (reverse mounting), so in fact the only definite sexual differences are in the ability to sire young and to lay eggs (Fjeldså 2004).

The Water-courtship displays differ from agonistic behaviour mainly by the more stereotyped performance, the increase of extraneous elements, such as Head-shaking, weed presentation (Weed-dance), redirection of Ghostly-penguin display, and the development of compromise movements between attack and turning away (Parallel-barging) (Fjeldså 1973c).

Though the Water-courtship of the Red-necked Grebe is similar in some features to that of *Podiceps cristatus* and *P. auritus*, it apparently lacks any form of Habit-preening and Retreat Ceremony, and mate-feeding of the female by the male is rare and unritualized (Cramp *et al.* 1977, Stout and Nuechterlein 1999, Fjeldså 2004). Low Head-wagging is not very developed as the birds use a rather more or less intense Penguin-dance (often with only the male rising), which usually ends with a long period with Slow Head-turning in furtive attitudes, as the birds gradually drift apart (Fjeldså 2004). The species is also much more vocal, giving Song and display-call during most ceremonies (Cramp *et al.* 1977).

Stout and Nuechterlein (1999) write, that the (Water-) courtship displays in *Podiceps grisegena* include Whinny-braying (Song and display-call), Cat-display, Bouncy-dive, Ghostly-penguin posture, Weed-dance, Penguin-dance, and Head-turning (Head-shaking). These displays are often organized into Discovery Ceremony, Weed Ceremony, and Greeting Ceremony (Stout and Nuechterlein 1999).

Advertising

The Advertising of the Red-necked Grebe appears to be less specialized and frequent than in other *Podiceps* species (Cramp *et al.* 1977). The variability of the Advertising-call, facilitating individual recognition, possibly increases the difficulty in identifying the call. Advertising is performed by a lone bird in a posture similar to that adopted when singing (Song and display-call), with the

head raised and the feathers of the crests and hindneck erected (see drawing in Fjeldså 1977a, p. 31).

Red-necked Grebes use (the whinny-like portion of) the Song and display-call and the rather unspecialized Quacking-call as Advertising-call (Cramp *et al.* 1977, Stout and Nuechterlein 1999).

Storer (*cited in* Cramp *et al.* 1977) noted that in *P. g. holboellii* a loud, nasal “a a n”, somewhat similar to the comparable call of the Slavonian Grebe *P. auritus*, is (also) used as Advertising-call; it is uttered by either the male or the female, or both, prior to the Discovery Ceremony and also in combination with duet calls and, possibly, other notes. Perhaps, the nominate race does not use this loud, nasal call as Advertising-call. It is important to know whether the Advertising calls of *P. g. holboellii* differ in some aspects from those of the nominate subspecies because Advertising appears to be the first step in pair-formation (Storer 1969), and Nuechterlein (1981a) demonstrated that a difference in the number of notes in the Advertising-call provided a key for reproductive isolation between the Western Grebe *Aechmophorus occidentalis* and Clark’s Grebe *A. clarkii*.

The attitude of the Advertising bird (head raised and the feathers of the crests and hindneck erected) suggests a certain degree of alertness, and the calling birds run the risk of being attacked by mated individuals, and so the bird keeps at some distance from others. Advertising by one or both birds may precede the Discovery Ceremony (Fjeldså 1982b, 2004).

Head-shaking

Like all grebes, Red-necked Grebes show Head-shaking: the male and female face each other closely and turn, sway or shake their heads from side to side with the heads held high. The roles of the sexes are identical, and the movements are performed simultaneously or reciprocally. Head-shaking is often a part of ceremonies, but it also occurs separately. Two types of Head-shaking in Red-necked Grebes are discerned: Low Head-wagging, and Slow Head-turning.

As the birds meet after a separation, or in a hostile situation, they may perform Low Head-wagging (“Kopfschütteln” of Wobus 1964) while uttering the Song and display-call. It includes repeated shaking and rotating of the head rapidly from side to side with the bill open and lowered, the crests erected; the movements are of small

amplitude so that the bill tip inscribes a small arc (see drawing in Wobus 1964, p. 44) (see Fig. 70). It appears that Low Head-wagging is the lowest intensity level of the Penguin-dance (Wobus 1964).

The other type of Head-shaking, Slow Head-turning (“Wegsehen” of Wobus 1964), is associated with peaceful situations and performed silently: pointing the bill from side to side, entirely in a horizontal plane, in a deliberate, measured manner (see photograph in Wobus 1964, p. 42) (see Fig. 71 and 72). Low-head wagging, Penguin-dances and other ceremonies in Red-necked Grebes often end with a long period of Slow Head-turning in a furtive posture with heads held high and head and back feathers sleeked down, as the birds gradually move formally apart (Ceremonial Turning-away). Thus, Slow Head-turning (and parallel-looking) before the terminal Turning away from a ceremony, particularly developed in Red-necked Grebes, suggest intentions to turn away (Wobus 1964, Cramp *et al.* 1977, Fjeldså 1982b, VlUG 2002a, Fjeldså 2004).

Red-necked Grebes do not show any form of Habit-preening, a movement characteristically associated with Head-shaking in Great Crested and Slavonian Grebes (Fjeldså 1973c, Cramp *et al.* 1977) (see Fig. 23).

Penguin-dance

Penguin-dances may be two different displays: Plump and Tall Penguin-dances. It is probable, that the Red-necked Grebe only shows the tall version (Fjeldså 1982b). While treading water, the partners may rise up in the water and remain upright, with the breasts touching. The elevation varies, but the pair rarely rises high in the water. The birds maintain the upright position, in part by expanding the body plumage, which certainly increases buoyancy, and in part by moving the feet up and down. The neck leans back somewhat relative to the back. In the typical Penguin-dance (“Pinguintanz” of Wobus 1964), both birds give the Song and display-call and one bird (almost certainly the male) always rises much higher than the other (see photographs in Wobus 1964, p. 42, in Schmidt 1970, p. 367, and in Larsen and Wirdheim 1994, p. 3) (see Fig. 73, 74, 75, 76 and 77). Both partners also open the mandibles, and either (or both) may grasp at other’s bill or make short stabs towards its breast.

In the Red-necked Grebe, the Penguin-dance is particularly common, probably largely taking over the role of Head-shaking during the engagement period. As already



Fig. 70: Low Head-wagging. Photo: T Runge (Schleswig-Holstein)

Fig. 70: Kopfschütteln.



Fig. 71: Slow Head-turning. Photo: T Runge (Schleswig-Holstein)

Fig. 71: Wegsehen.



Fig. 72: Slow Head-turning, detail. Photo: T Runge (Schleswig-Holstein)

Fig. 72: Wegsehen, Detail.



Fig. 73: Two loudly calling grebes swim to each other in upright position. Photo: T Runge (Schleswig-Holstein)

Fig. 73: Unter Geschrei schwimmen zwei aufgerichtete Taucher aufeinander zu.



Fig. 74: Penguin-dance. Photo: T Runge (Schleswig-Holstein)

Fig. 74: Pinguintanz.



Fig. 75: Penguin-dance. One bird, almost certainly the male, rises higher than the other. Photo: T Runge (Schleswig-Holstein)

Fig. 75: Pinguintanz. Ein Vogel, höchstwahrscheinlich das Männchen, richtet sich höher als der andere Vogel auf.

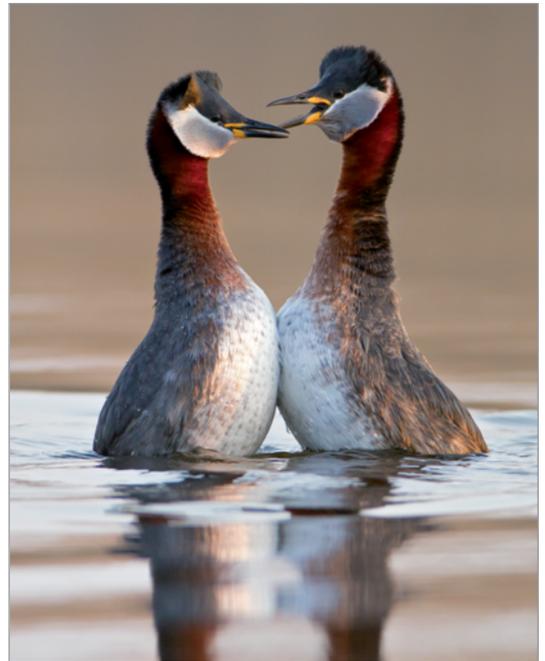


Fig. 76: Penguin-dance. Both birds give the Song and display-call. Photo: T Runge (Schleswig-Holstein)

Fig. 76: Pinguintanz. Unter lautem „uööh-Gebrüll“ vollzieht sich der Pinguintanz.



Fig. 77: Penguin-dance. Both partners open the mandibles, and may grasp at other's bill. Photo: T Runge (Schleswig-Holstein)

Fig. 77: Pinguintanz. Dabei können die Vögel einander in die Schnäbel greifen.

stated, it usually ends with a long period with Slow Head-turning in furtive attitudes, as the birds gradually drift apart. It not only forms part of other ceremonies, but also occurs separately (Cramp *et al.* 1977, Fjeldså 1982b, Stout and Nuechterlein 1999, Fjeldså 2004).

Fjeldså (1982b) considered the Penguin-dance as evolved from elements originally shown in combat. This is strongly supported by certain displays of White-tufted *Rollandia rolland* and Titicaca Flightless Grebes *R. microptera*, where it is very hard to tell upright display postures apart from overt fight behaviour. As already stated, dancing Red-necked Grebes may deliver bill-stabs and regularly grasp each-others bills during the initial phase of the dance. Red-necked and Slavonian Grebes may use the Tall Penguin-dance as threat against man near the nest. Thus, comparison, elements, as well as the similar context (and probably similar motivation) suggests that the Tall Penguin-dance evolved by ritualization of the state shown when combatants raise up to overthrow one another (Fjeldså 1982b).

Parallel-barging

Red-necked Grebes may perform Parallel-barging ("Parallelschwimmen" of Wobus 1964; see drawing in

Wobus 1964, p. 46, and photograph in Fjeldså 1977a, p. 38): the partners may turn during the Penguin-dance and swim slowly side by side through the water in the Penguin-posture, arching the upper neck and erecting the crests, giving the Song and display-call. Then they subside and move formally apart (Ceremonial Turning-away) (Cramp *et al.* 1977, Fjeldså 1982b).

Red-necked Grebes often Parallel-barge as varieties of Penguin-dances or aggressive Low Head-wagging. Contexts, the arching of the upper neck, erection of the plumes and the voice suggest a strong similarity with attack behaviour in the beginning, gradually replaced by flight tendencies towards the end (Fjeldså 1982b). Probably, Parallel-swimming is a less intense form of Parallel-barging, often used during Greeting and Triumph Ceremonies (see drawing in Fjeldså 2004, p. 185) (see Fig. 78 and 79).

Parallel-rush

The Penguin-dance is occasionally replaced by a Parallel-rush over the water, in which the birds orient side by side in an upright position and move rapidly forwards. Both birds call and one bird, almost certainly the male, rises higher than the other (Cramp *et al.* 1977, Stout and



Fig. 78: Probably, Parallel-swimming is a less intense form of Parallel-barging. Photo: T Runge (Schleswig-Holstein)

Fig. 78: Wahrscheinlich ist das hier gezeigte Parallelschwimmen eine weniger intensive Form als die in Wobus (1964), Seite 46, abgebildete.

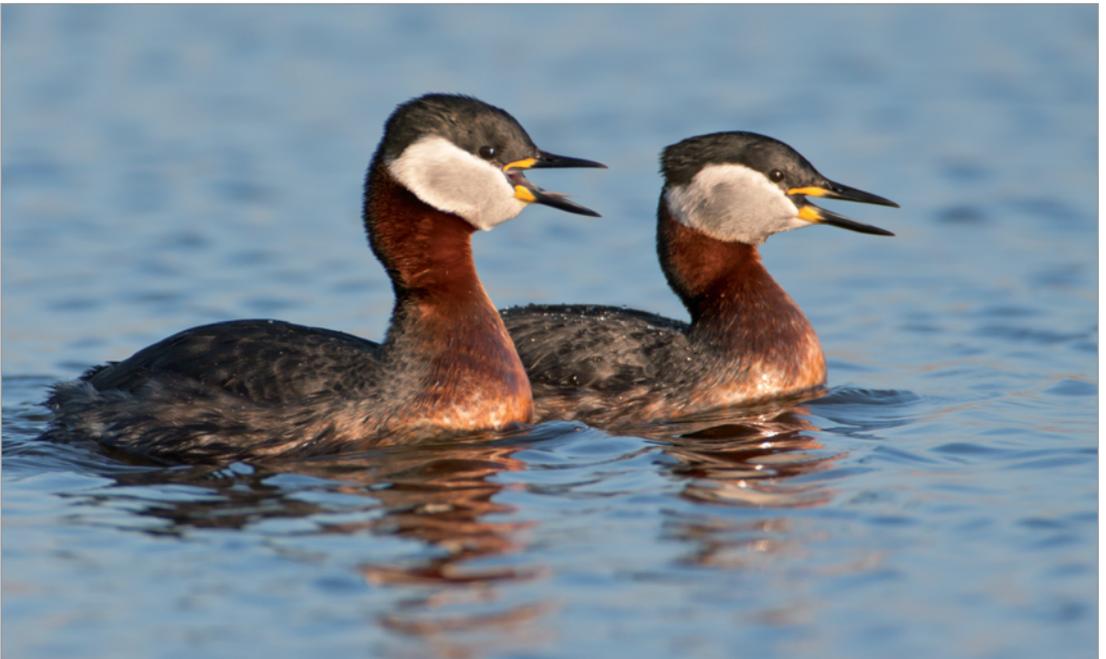


Fig. 79: Parallel-swimming is often used during Greeting and Triumph Ceremonies. Photo: T Runge (Schleswig-Holstein)

Fig. 79: Parallelschwimmen wird häufig während Begrüßungs- und Triumphzeremonien vorgeführt.

Nuechterlein 1999) (see Fig. 80 and 81). Thus, in contrast to Parallel-barging, the birds in the Parallel-rush swim rapidly.

Discovery Ceremony

The Discovery Ceremony (“Tauchbalz” of Wobus 1964) is a sequence in which each element releases the next. Advertising by one or both birds may precede the ceremony (Cramp *et al.* 1977, Konter 2004b). One of the birds repeatedly dives toward the other. During this Approach-dive, the bird occasionally emerges, 2-4 m away from the surface bird, in the Bouncy-posture (“Schaukelstellung” of Konter 2004b), with its head feathers sleeked down, the tail-tuft cocked, the head resting on the mid-back area and the breast puffed out; or showing its head only (see drawing in Stout and Nuechterlein 1999, p. 14, and photograph in Konter 2004b, p. 427). The surface bird, facing towards where the other bird dived, performs the Cat-display (“Schwanenstellung”, see drawings in Wobus 1964, p. 43, and in Cramp *et al.* 1977, p. 93, and photograph in Konter 2004b, p. 427) (see Fig. 82 and 83): lowering its head just in front of the shoulders by kinking its neck, the crests erect (at high intensity of the display), and the wings raised (slightly) over the body, but normally not spread

(Cramp *et al.* 1977, Fjeldså 1982b, Stout and Nuechterlein 1999). The Cat-display in the Red-necked Grebe is, as a rule, not so striking as in the Great Crested Grebe, which adopts the Wing-spread posture (partly opening the wing and rotating them forward in a V on each side of the body so that the white pattern of their upper surfaces is displayed frontally) (Simmons 1975b) (see Fig. 22). The bird performing the Cat-display is stationary, but pivots to face the approaching bird each time it emerges. The approaching bird performs the Ghostly-penguin display 3-5 m, and occasionally up to 8 m or 10 m away from the bird in the Cat-display (Wobus 1964, Cramp *et al.* 1977, Stout and Nuechterlein 1999, Konter 2004b; see photographs in Schmidt 1970, p. 367, and in Konter 2004b, p. 427) (see Fig. 84). In this display (“Steilauftauchen” of Wobus 1964, and “Geisterpose” of Konter 2004b) the head appears above the water, the neck curiously arched down, but the body emerging in an erect position. While the bird rises, as though in slow motion, the neck is kept bent over until the body is partly out of the water. Then the head is raised and held almost at right angles to the now vertical neck. The bird emerges with its back to the bird in the Cat-display while uttering the Song and display-call loudly and then turns slowly towards its display partner, which usu-



Fig. 80: Parallel-rush. Photo: T Runge (Schleswig-Holstein)

Fig. 80: *Paralleles Vorschnellen.*



Fig. 81: Parallel-rush. Note the bow wave. Photo: T Runge (Schleswig-Holstein)

Fig. 81: Paralleles Vorschnellen. Beachte die Bugwelle.



Fig. 82: Cat-display. Photo: T Runge (Schleswig-Holstein)

Fig. 82: Schwanenstellung. Wobus (1964, Seite 43) nannte das Cat-display bei Haubentauchern Katzenstellung, bei Rothalstauchern jedoch Schwanenstellung.



Fig. 83: A striking Cat-display. Photo: T Runge (Schleswig-Holstein)

Fig. 83: Eine auffallende Schwanenstellung.



Fig. 84: A bird performing the Ghostly-penguin display. The bird in the foreground (out of focus) in the Cat-display. Photo: T Runge (Schleswig-Holstein)

Fig. 84: In der Geisterpose steil auftauchender Vogel (Steilauftauchen, Wobus 1964) mit Vogel in Schwanenstellung (unscharf im Vordergrund).

ally also starts to call (Cramp *et al.* 1977, Vlug 2002a, Konter 2004b). Typical Ghostly-penguin displays are restricted to *Podiceps*-species and vary little, but in the Red-necked the performance is exceptionally stereotyped and slow (4-6 sec.) and performed farther away from the Cat-displaying bird (Fjeldså 1982b, 2004). The Ghostly-penguin bird, still calling, joins the other bird. Both rise breast to breast in the Penguin-dance, subside, and perform Slow-Head Turning (Wobus 1964, Cramp *et al.* 1977). The Discovery Ceremony ends as the birds move stiffly and formally apart, the Ceremonial Turning-away, or they may sometimes perform Parallel-barging before subsiding and Turning-away (Cramp *et al.* 1977, Konter 2004b).

Incomplete Discovery Ceremonies, which are common in true colonial *Podiceps*-species and semi-colony-breeding Great Crested Grebes, are rare in Red-necked Grebes (Fjeldså 1982b).

After the pair-bond is well established in Red-necked Grebes, the Discovery Ceremony is replaced by the Greeting Ceremony (of Stout and Nuechterlein 1999) (see below).

The Discovery Ceremony plays a central role in the initiation of pair-bonds. It seems to be necessary to permit two strangers to come into close mutual contact (Fjeldså 1973c). In territorial grebe species paired birds often attack Advertising (“Display-calling”) strangers on long range, usually by a long under-water attack, although sometimes patter-flying or flying at the victim. It appears that the Discovery Ceremony contains many elements from this attack, but allochthonous elements are added, the critical stage in the “attack” is directed away from the partner, and a definite sequence has evolved. All the extraneous elements are movements which are frequent in conflict situations during attack or combat. The ceremony ends as a stereotyped escape from the fight situation (Fjeldså 1982b).

Storer (1969) thinks that it is highly significant that the bird performing the Ghostly-penguin display always does so while facing away from the second bird. Thus we can postulate that a balance or near-balance in agonistic components is achieved by the bird in the more defensive posture (Cat-display) facing toward, and the bird in the more aggressive posture (Ghostly-penguin) facing away, from the bird with which it is performing the ceremony. From this point on in the ceremony, the performance of both birds is similar.

Weed Ceremony

Red-necked Grebes may perform a Weed Ceremony (“Pflanzenbalz” of Wobus 1964) after a completed Discovery Ceremony, especially later in the pair formation (*cf.* the Weed Ceremony of *Podiceps cristatus* in Simmons 1975b). Both birds make a deliberate Weed-dive, in which they collect bits of green or partially decayed vegetation, emerge, and swim rapidly towards each other in threat posture (Fjeldså 1982b, Stout and Nuechterlein 1999). With their heads rising as they approach, they meet in the Weed-dance (similar to the Penguin-dance but with weeds held in their bills), accompanied by loud calling (Wobus 1964, Cramp *et al.* 1977, Stout and Nuechterlein 1999). Both birds subside into the water and drop the weeds, concluding the ceremony with Slow Head-turning (Stout and Nuechterlein 1999).

Greeting Ceremony

When the pair bond is well formed, the Greeting Ceremony (of Stout and Nuechterlein 1999) replaces the Discovery Ceremony. It is often stimulated by hearing neighbouring pairs. The mates approach each other in a hunched posture, in which the birds hold their heads low and raise the back-feathers. Then they rise more or less out of the water and give the Song and display-call, swimming side by side with the head and crests erected. After meeting, the pair sometimes concludes with Slow Head-turning or by performing a brief Penguin-dance. The Greeting Ceremony is especially intense after agonistic interactions (Stout and Nuechterlein 1999).

Cramp *et al.* (1977) described the Greeting Ceremony of Stout and Nuechterlein (1999) as “Triumph Ceremony”. However, they give fewer details than Stout and Nuechterlein (1999) (see also “Triumph Ceremony” of *Podiceps auritus* in Fjeldså 1973c).

15.3.7 Nest-site Selection-displays

Ceremonial-building

During the nest site selection, a Red-necked Grebe may place plants in front of its mate. Sometimes the male and female simultaneously present vegetation to each other (Ceremonial-building) (see 16.2.1 for more details).

Inviting-display-on-the-water

Once the grebes have settled in a territory, the pair seeks out sites, typically together. A characteristic form of behaviour in these early days is the Inviting-display-on-the-water. Male or female, or sometimes both simulta-

neously, floats immobile with the back turned to the mate and the head held forward and low, the neck kinked (see photographs in Wobus 1964, p. 51, and in Konter 2007a, p. 271) (see Fig. 85). This behaviour is similar to one form of soliciting (the Inviting-display) shown later upon the platform (see below) but occurs typically on open water off stands of covers or in the edge of, or among sparse, flooded vegetation. In general, the behaviour does not lead to copulation (Simmons 1975b) (however, see below).

The Inviting-display-on-the-water is best considered a form of incipient platform-behaviour that is often but not always associated with nest site-selection early in the cycle (Wobus 1964, Stout and Nuechterlein 1999).

At a pond near Raisdorf, Schleswig-Holstein, Konter (2007b) observed both partners of a pair performing the Inviting-display-on-the-water in turns and the behaviour appeared to be embedded in a more complex process. In spite of the fact that the Red-necked Grebes here already owned a good platform, it seemed as if the female now disagreed with the former choice of the site. Indeed, the Inviting-displays were followed by the female offering nesting material to its mate in the middle of the

pond and some Ceremonial-building was observed there.

Konter (2007a) saw the Inviting-display on the water surface of the Baltic Sea near the coast of the island of Fehmarn, Schleswig-Holstein, where no breeding habitat exists. Here it is probably more a form of courtship to attract the attention of the sexual partner and could help pair formation (Konter 2007a).

On very rare occasions, the Inviting-display-on-the-water leads to copulation. An apparent copulation after this display (and some incipient Ceremonial-building by one member of the pair) on open water by a pair of Red-necked Grebes was observed on 1 May 1965 at Spenard Lake, Anchorage, Alaska (Hemming 1968): "The male was seen to emerge from a dive with a piece of vegetation in its bill. The plant material was then dropped and picked up several times. Suddenly the male seemed to become alert, picked up the weed, and began swimming toward the female, who was approximately thirty feet away. The two came together with necks arched, until their bills appeared to touch. Several times the male turned to the side and then back and again presented the plant material to the female. This activity lasted 15 to 20



Fig. 85: Inviting-display-on-the-water. Photo: T Runge (Schleswig-Holstein)

Fig. 85: Einladungsbalz auf offener Wasserfläche.

seconds. The female then assumed an inviting posture with the neck extended and the fore part of the body lowered in the water so that the basal portion of the neck was nearly submerged, while the cloacal region was quite high. The male swam to the female and placed the plant on her back, near the cloaca. The plant immediately slid into the water but was replaced several times by the male. The female then began to move very slowly forward while maintaining the inviting posture. The male followed, without the weed, and gently nudged the cloacal region of the female with his breast. The male then, with crest up, wings closed, and neck stretched forward, hopped onto the female's back, while the female continued to move forward. Mounting resulted in the female being pushed quite low in the water, with only her head and a small portion of her back above the water. Vigorous paddling with the feet, as indicated by forward movement, probably prevented the female from becoming completely submerged. Mounting lasted three to five seconds and was followed immediately by calling and a bill-touching display. The birds then became quite passive and moved away in a normal swimming attitude. At no time during the above activities was there any sign of aggression."

15.3.8 Platform-courtship and Copulation (see Fig. 86)

This behaviour is similar to the other *Podiceps* species. It includes two forms of soliciting (the Inviting-display and the Rearing-display), the pre-mounting behaviour, the copulation, and the Post-copulatory display with Water-treading and Post-copulatory Slow Head-turning. The Post-copulatory display in *Podiceps grisegena* is very stereotyped and ritualized (Cramp *et al.* 1977, Fjeldså 1982b).

Pairs of Red-necked Grebes copulate after constructing a platform, which may or may not become the nest. They rarely attempt to copulate off the platform on submerged logs, artificial nests, on open water or on dry land (Johnstone 1953, Schmidt 1961, Hemming 1968, Wobus 1964, Kevan 1970, Cramp *et al.* 1977, De Smet 1983, Stout and Nuechterlein 1999, Vlug 2007) (see 15.3.7). Pairs in Podicipedidae often engage in repeated mounting attempts in a short period, sometimes five or six copulations in a 15- to 20-min. period. The minimum period between two copulations in Red-necked Grebes is 3 minutes (Wobus 1964, Nuechterlein and Storer 1989, Fjeldså 2004).

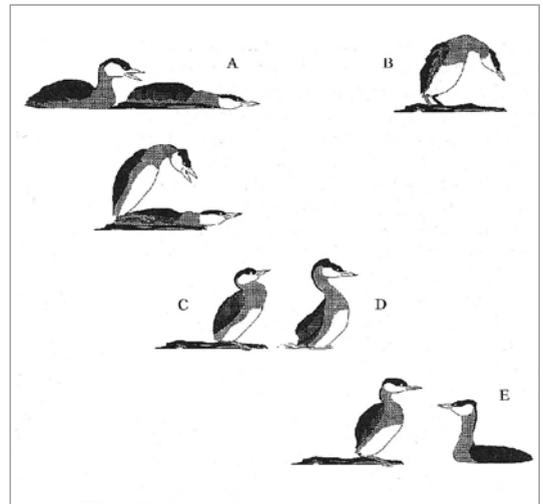


Fig. 86: Copulatory and Post-copulatory displays of the Red-necked Grebe (Platform-courtship and copulation). A. Inviting-display. B. Rearing-display. C. Ecstatic posture. D. Post-copulatory Water-treading. E. Post-copulatory Slow Head-turning. From: B E Stout and G L Nuechterlein (1999), Red-necked Grebe *Podiceps grisegena*. In A Poole and F Gill (eds.), The Birds of North America, No. 465, page 15. The Birds of North America, Inc., Philadelphia, Pennsylvania. Drawings by B E Stout from T Schmidt (1970), S Cramp *et al.* (1977), and personal observations of B E Stout, reproduced with kind permission of the authors.

Fig. 86: Kopulationsverhalten- und Verhalten nach der Kopulation (Plattform- oder Paarungsbalz) des Rothalstauchers. Die deutschen Bezeichnungen stammen aus Wobus (1964) und Vlug (2007). A. Einladungsbalz. B. Winkelstellung. C. Ekstatische Stellung. D. Postkopula-Wasserretzen. E. Wegsehen nach der Kopulation.

Soliciting

Inviting-display

The female Red-necked Grebe (or the male in reverse mounting) springs on to the platform, and performs the Inviting-display: the bird leans the neck forwards and lays motionless on the platform, usually oriented away from the partner. The neck is partly extended, characteristically bent about the middle (kinked) with the head very low, and the crests flattened, the nape-skin pulled forwards (see photographs in Schmidt 1970, p. 369, and in Wobus 1964, p. 52) (see Fig. 87). The bird gives the Purring-call ("Knätschen" of Wobus 1964), a drawn-out, largely unarticulated "(kn)ääääääää" (Wobus 1964, Cramp *et al.* 1977).

The Inviting-display is characteristic of all *Podiceps* species. *Tachybaptus* shows a probably more primitive behaviour, the Prone-display, like a defeated grebe with the neck drawn in, the bill sloping 45° and oriented away



Fig. 87: Inviting-display on platform. Photo: A Konter (Schleswig-Holstein)

Fig. 87: Einladungsbalz auf einer Plattform.

from the mate. *Rollandia* adopts the Prone-display as a transition state before the true Inviting-display, while it is entirely lost in the *Podiceps*-species (Fjeldså 1982b).

Rearing-display

Before the Inviting-display, the soliciting Red-necked Grebe on the platform may assume an ecstatic, stiff posture, the Rearing-display (“Winkelstellung” of Wobus 1964): it stands very high on its feet, the feet widely apart, and leans the body partly forwards. The neck is bent over and the bill points downwards. The crests are flattened precisely as in the Inviting-display. The ventral plumage is fluffed, as if to open the brood-patch, the mantle feathers are raised, and the folded wings lifted at the tip and vibrated (Wing-quivering), which is sometimes repeated (see photograph in Schmidt 1970, p. 369) (see Fig. 88). Sometimes, the feathers of the crests and the neck of *Podiceps grisegena* may be more or less erected during Wing-quivering (A Konter). The Rearing-display ends as the bird lowers its throat nearly to the platform and lays down, Inviting. If the partner does not come to the nest after some time, the bird may raise its neck, rise up again, and repeat the Rearing and Wing-quivering (Schmidt 1970, Fjeldså 1973c, 1982b).

According to a detailed analysis, the Rearing-display is ritualized from activities shown by a grebe ascending a nest and preparing itself to lie down and incubate. This origin was confirmed by the less ritualized Rearing in *Rollandia* (Schmidt 1970, Fjeldså 1982b).

Pre-mounting Behaviour and Copulation

The behaviour of the bird in the water (usually the male) during soliciting is varied. It may drift or swim aimlessly about in the vicinity of the platform; or preen; or collect, bring, and incorporate material, and it gives soft calls. A full response to Inviting ends with pecking towards the rear end of the Inviting bird, a gradual flaring of the nuptial plumes, and leaping suddenly out of the water on to the soliciting bird’s back, then giving the loud Rattling-call, a deep, trilling “u” sound turning immediately into a rapid series of higher “r” sounds. This call is repeated 3-6 times by the copulating bird (see photographs in Wobus 1964, p. 52, in Schmidt 1970, p. 370 and in Larsen and Wirdheim 1994, p. 3) (see Fig. 89). The mounting bird shows some foot-pushing before it finds its balance (sometimes it falls off, but notwithstanding such blunder, the birds perform a normal Post-copulatory display). It continues to call as it stands, more or less erect and supported on the flat of the tarsi, with the neck



Fig. 88: Rearing-display. Photo: T Runge (Schleswig-Holstein)

Fig. 88: Winkelstellung.



Fig. 89: Copulation. Photo: A Konter (Schleswig-Holstein)

Fig. 89: Kopula.

and head arched forward, bill open, for some 5-10 seconds while copulating. The bird on the nest (the soliciting bird) curves the neck and slightly raises the head when mounted (Wobus 1964, Simmons 1975b, Cramp *et al.* 1977, Fjeldså 1982b, Stout and Nuechterlein 1999, VlUG 2002a).

Post-copulatory Display

After 5-10 seconds of copulation, the mounting bird stops calling as it suddenly waddles forward and dismounts over the head of its partner, forcing it momentarily under water, and lands upright with its breast high out of the water, with rapid foot-splashing, the head held high, the neck extended and leaned partly back and the crests erect (see photograph in Larsen and Wirdheim 1994, p. 3). This Post-copulatory Water-treading is more ritualized than in other *Podiceps*-species. The partner remains on the platform and assumes a stiff Ecstatic posture: rising to almost vertical attitude, it puffs the breast out, curves the neck, and presses the head firmly against the neck (like in the Bouncy-display) (see photograph in Schmidt 1970, p. 370) (see Fig. 90). The male in the water turns and faces the female to perform an exceptionally long bout of Post-copulatory Slow Head-turning (see photograph in Schmidt 1970, pp. 372-3) (see Fig. 91) (Wobus 1964, Simmons 1975b, Cramp *et al.* 1977, Fjeldså 1982b, Stout and Nuechterlein 1999, VlUG 2002a, Fjeldså 2004).

“Platform-courtship” and Copulation on a Dry-land Site

On 7 May 2006 L Sielmann observed a pair of Red-necked Grebes performing “Platform-courtship” (Rearing-display and Inviting-display) and copulation on a dry part of a pond on the island of Fehmarn, Schleswig-Holstein, Germany. The birds did not build a platform. The Post-copulatory display was nearly omitted: The soliciting bird did not show the Ecstatic posture and the mounting bird, landing up-right on dry ground, did not carry out the ritualized Post-copulatory Water-treading (of course, treading on water was not possible, however, it did not even attempt the treading phase on land), and only an inconspicuous Slow Head-turning was performed (VlUG 2007).

Reverse Mounting

Females mounting males is common in many grebe species (Nuechterlein and Storer 1989, Fjeldså 2004, Hayes and Turner 2017) and has also been reported in Red-necked Grebes (Storer 1969). Reverse mounting behaviour is not a matter of mistaking the sex of the partner because

mountings by birds of the same sex are very rare. It is not abnormal behaviour in Podicipedidae, but apparently constitutes a regular and integral part of the courtship behaviour of Podicipedidae. Whether dominance reversal or stimulation of the ovaries or both are involved cannot be determined (Nuechterlein and Storer 1989).

Reverse mountings occur chiefly early in the cycle of platform behaviour but are rare during or immediately preceding egg laying (Storer 1969, Nuechterlein and Storer 1989). Usually, there is no cloacal contact; and ejaculations are not confirmed to occur (Fjeldså 2004). In reverse mountings, females of *Podiceps grisegena* give a loud, open-billed, male-like call, and (in *Podiceps occipitalis* at least) the males are more likely to Rearing and Wing-quivering prior to Inviting the female to mount (Nuechterlein and Storer 1989, Stout and Nuechterlein 1999).

Platform-courtship in Red-necked Grebes Nesting Semi-colonially

During the pre-laying period, Red-necked Grebes in a colony engaged in more platform behavioural events, spent significantly more time performing these events, and used Inviting and copulation behaviour more than their solitary counterparts (Lake Osakis, Minnesota; Klatt 2003). It is possible that this is a strategy for ensuring ownership of platforms and nests in a prime nesting habitat. It is perhaps also a method to guard the nests against intraspecific brood parasitism, which may be greater in areas where pairs breed closer together. Along with investing in nest sites, each male may also invest in the female through mate guarding and frequent copulation. Since males provide parental care, females may increase paternity certainty by allowing them to copulate more frequently. Thus, in a colony pairs tended to copulate more often during the platform period than did solitary pairs. Red-necked Grebes breeding in a colony tolerated conspecifics at closer distances which suggests that those breeding in higher aggregations may expend more energy when dealing with conspecifics (Klatt 2003).

15.4 Interspecific Behaviour

15.4.1 Non-predatory Interspecific Interactions

Nesting Associations with Other Species (this topic is treated in more detail in 16.2.6)

Red-necked Grebes frequently associate with nesting Coots *Fulica atra*. Although Coots may destroy or eat



Fig. 90: Bird on the platform in Ecstatic posture. Photo: A Konter (Schleswig-Holstein)

Fig. 90: Der Vogel auf der Plattform zeigt die Ekstatische Stellung.

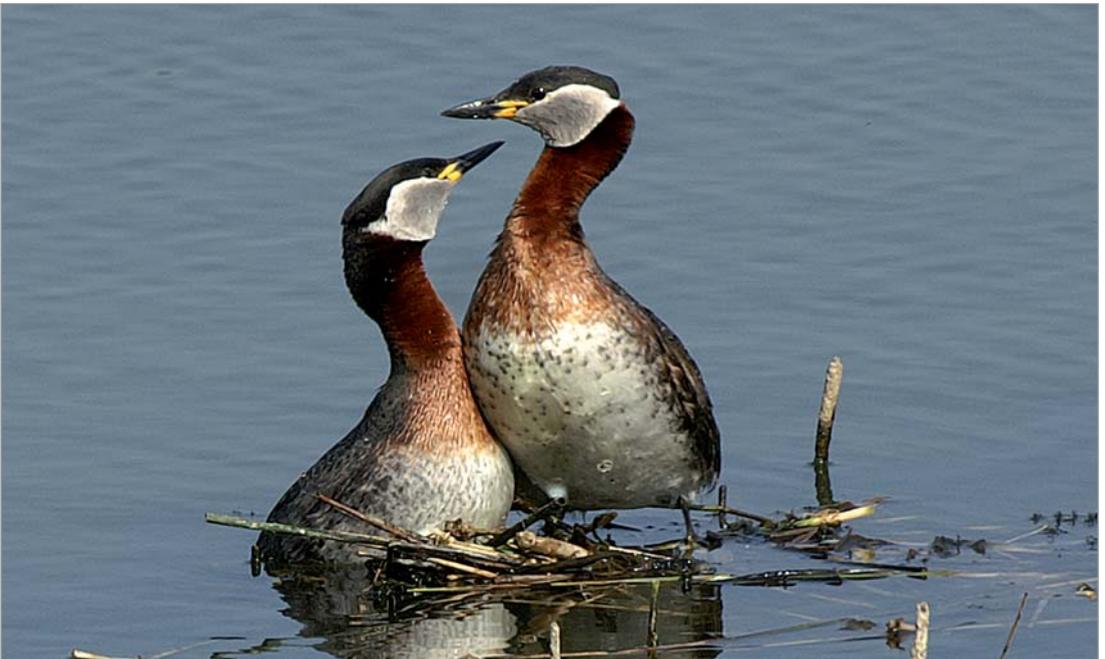


Fig. 91: Post-copulatory Slow Head-turning. Photo: A Konter (Schleswig-Holstein)

Fig. 91: Wegsehen nach der Kopulation.

grebe eggs, it appears that the majority of the grebes in these associations join already settled and nesting Coots. The risk of losing eggs may be outweighed by the protection that the highly pugnacious Coots provide because of their fierce nest defence.

Red-necked Grebe pairs will sometimes nest within colonies of Black-headed Gulls *Larus ridibundus* or Black Terns *Chlidonias niger*, but the tendency to nest in association with small Laridae and Sternidae is much less marked than in Black-necked Grebes.

Hybridization and Courtship with Other Species of Grebes

Hybridization is rare in Podicipedidae; it appears that differences in Advertising-calls normally prevent it (Nuechterlein 1981a). Hybridization sometimes occurs when conspecific mates are hard to find.

There is one observation of a hybrid between a Red-necked Grebe and a Great Crested Grebe, but there seems to be no published report (McCarthy 2006).

Courtship and an unsuccessful breeding attempt (the nest was abandoned) of a Red-necked Grebe paired with a Great Crested Grebe were observed at Brunn am Gebirge, near Wien (Vienna), Austria, in 1983 (Dvorak *et al.* 1993).

A Red-necked Grebe displayed courtship behaviour to a Great Crested Grebe in 2010, 2011 and 2012 at the Weissenau, Thunersee (Switzerland). In 2012 a nest was seen at the place where the birds were observed (Schuster *et al.* 2014).

Some records of hybridization in other grebes in Europe are known. In the summer of 2002 a Pied-billed Grebe raised one young in a lake in Norway, on the “wrong” side of the Atlantic. The appearance of this chick was intermediate between those of Pied-billed and Little Grebes, suggesting that the adult bird had mated with a Little Grebe (Fjeldså 2004). There is a possible case of interbreeding of Slavonian Grebe and Black-necked Grebe in Scotland (Dennis 1973). In spring 2006, at a site in central England, a Slavonian Grebe paired with a Great Crested Grebe, laid eggs, and produced two young, which unfortunately did not survive (Toon 2007).

Red-necked Grebes Rearing Chicks of Great Crested, Western and Clark’s Grebes

There are records of adult Red-necked Grebes rearing young Great Crested, Western and Clark’s Grebes. These Red-necked Grebes were usually seen with one foster child and no young of their own (see 16.5.17 for more details). Observations on Duck Lake, Creston Valley, British Columbia, probably explain the almost complete absence of larger Red-necked Grebe chicks in mixed families with Western or Great Crested Grebes (Van Damme 2006). During the 2006 season, six pairs of Red-necked Grebes nested within, or at the periphery, of a Western Grebe colony on Duck Lake. Van Damme (2006) discovered a nest with three Red-necked and two Western Grebe eggs. A fortnight later the Red-necked Grebe pair of this nest was recorded with one Western Grebe and three *grisegena* chicks. The Western Grebe chick was larger in size, obtained most food and gained more access to the foster parents’ back than its smaller “siblings”. It acted aggressively toward one of the Red-necked Grebe chicks by jabbing at it with its bill (*cf.* normal sibling competition, see 15.3.3). A week after the last chick hatched, Van Damme (2006) only saw the Western Grebe, and there were no surviving *grisegena* chicks. It seems likely that the three smaller young did not survive the competition from the larger Western Grebe chick.

Commensal Feeding Associations

Red-necked Grebes typically forage alone. However, at wintering and moulting sites, commensal feeding associations with scoters have been recorded (see 14.3.10 for more details).

Wintering Red-necked Grebes associating with Velvet Scoters *Melanitta fusca* synchronized their activities with those of the scoters: when a scoter stopped feeding so did the grebe, but instead of seeking a new scoter which was actively feeding, the grebe continued its association with the original scoter. Grebes kept close to their chosen scoter, both while they were feeding and when not feeding. In feeding associations, the grebe dived a few seconds after the scoter it accompanied. Scoters were never seen to attack or show hostility toward the grebes or to try to avoid them. The association appears to be a route whereby naive first-year birds can more easily obtain prey. Presumably scoters make prey so easily available that they constitute an attractive food resource to the grebes even though the most commonly available prey, polychaetes, may be nutritionally less favourable. The

grebes associating with scoters are often birds of the year. The association of grebes with scoter diminishes over the winter: presumably the grebes gradually become more skilled at capturing fast-moving prey, enabling them to adopt the more demanding but energetically favourable pursuit of diving for fish (Byrkjedal *et al.* 1997).

Interspecific Food Kleptoparasitism

Many gull species are kleptoparasites, stealing food from grebes (Ulfvens 1988, Henriksen 1993, Fjeldså 2004). Kleptoparasitism by Black-headed Gulls *Larus (Chroicocephalus) ridibundus* on Red-necked Grebes has been observed on breeding waters in Schleswig-Holstein, Germany (J J Vlуг).

Peculiar is the observation of a young Coot *Fulica atra* (about six weeks old) stealing a little fish from an adult Red-necked Grebe at the moment this adult bird was giving it to one of its young (Schleswig-Holstein; J J Vlуг).

At a Washington wintering site, Red-breasted Mergansers *Mergus serrator* were observed stealing food from Red-necked Grebes that brought the food to the surface (McDougall, *cited in* Stout and Nuechterlein 1999).

Agonistic Interactions with Other Species

1. Red-necked Grebes attacking other species

During the breeding season, the Red-necked Grebe is very aggressive towards other species in defence of its nest or territory. This interspecific aggression appears greatest during territory establishment and after hatching. The males are more likely to initiate attacks than females, and they attack from greater distances than females (Stout and Nuechterlein 1999). Attacks are reported on humans (by the adult bird during banding of a young), Common Muskrat *Ondatra zibethicus*, many species of ducks, Great Northern Diver (Common Loon) *Gavia immer*, other species of grebes, Double-crested Cormorant *Phalacrocorax auritus*, Great Blue Heron *Ardea herodias*, coots *Fulica atra* and *F. americana*, Black-headed Gull *Larus ridibundus* and other gulls, and crows *Corvus* (Wobus 1964, Sage 1973, Spletzer 1974, Chamberlin 1977, De Smet 1983, Garner 1991, Stout and Nuechterlein 1999).

Red-necked Grebes are most aggressive towards other species of grebes and diving ducks, which are competitors for food or nest-sites, and are attacked more frequently and from a greater distance than other waterbirds, such as dabbling ducks (Spletzer 1974, Garner 1991,

Stout and Nuechterlein 1999, Vlуг 2002a). De Smet (1983) also noted that the Red-necked Grebes in Turtle Mountain Provincial Park in Manitoba were more tolerant of dabbling duck species, but displaced competitors for food or nest-sites such as most Pied-billed Grebes *Podilymbus podiceps*, Eared Grebes (Black-necked Grebes), Canvasbacks *Aythya valisineria*, Ring-necked Ducks *Aythya collaris*, Buffleheads *Bucephala albeola*, and Hooded Mergansers *Lophodytes cucullatus* that encroached upon their territory. In instances where Red-heads *Aythya americana* and Ruddy Ducks *Oxyura jamaicensis* were displaced, however, the Red-necked Grebes may have been guarding against parasitism. Many Canvasback nests found in the Turtle Mountains during the study of De Smet (1983) had been parasitized by Red-heads and Ruddy Ducks, and one instance of Redhead parasitism on an active Red-necked Grebe nest was noted.

The species may exclude the Bufflehead *Bucephala albeola* from ponds (Donaghey 1975, *cited in* Stout and Nuechterlein 1999). Sage (1973) observed a pair with young in Alaska, which on one occasion drowned two of a brood of young Pintails *Anas acuta* that had approached close to the brooding platform, by holding them under water. Red-necked Grebes were also observed killing Wood Duck *Aix sponsa* and Common Goldeneye *Bucephala clangula* ducklings (Stout and Nuechterlein 1999).

Agonistic interactions with other grebes are common where the species breed sympatrically. The agonistic displays of the Red-necked Grebe are more or less the same as those of other species of grebes and the birds “understand” each other.

Observations show that the nominate *grisegena* may chase away the Slavonian Grebe *P. auritus* (Fjeldså 1973a) and the Black-necked Grebe *P. nigricollis* (Scholl 1974, Spletzer 1974, Koop 1998) from breeding sites suited to both. According to Fjeldså (1973a), the Slavonian Grebe has virtually disappeared from a number of localities as a result of an increase in numbers of the Red-necked Grebe. Interspecific territorialism does occur and naturally the smaller *auritus* is physically subordinate, and rarely maintains itself, being left with only smaller suitable waters that lack a dense plant life (Fjeldså 1973a, Cramp *et al.* 1977). However, it is still not clear to what extent the competition of Red-necked and Slavonian Grebes affects the habitat choice of the latter.

Attacks are also reported on Little Grebes *Tachybaptus ruficollis* (Schleswig-Holstein; Spletzer 1974; R K Berndt, A Konter, J J Vlug), Western Grebes *Aechmophorus occidentalis* and Pied-billed Grebes *Podilymbus podiceps* (North America; Stout and Nuechterlein 1999).

Chamberlin (1977) described an attack of a male Red-necked Grebe on two immature Pied-billed Grebes in Michigan: "At hatching the male became strikingly territorial towards other species. On one occasion the male drove off 2 immature Pied-billed Grebes that were foraging at least 40 m from the nest. The male approached one of the Pied-bills in a very pronounced threat attitude, hunched very low on the water. The male dived and in the same instant the Pied-bill half ran, half-flew 3-4 m across the water. The male surfaced and continued to pursue the Pied-bill in a threat attitude. When the male dived a second time the Pied-bill flew off. The male then turned his attention to the other young grebe and with a similar sequence of actions drove it away."

2. Agonistic encounters with Great Crested Grebes

In Europe, numerous agonistic encounters with Great Crested Grebes *P. cristatus* are recorded (Spletzer 1974, Fjelds  1977a, Oldekop 1996). There are accounts of Great Crested Grebes pushing a Red-necked Grebe under water, seizing it by its head or neck, and dragging it through the water (Schleswig-Holstein) (Vlug 2002a). Spletzer (1974) discovered that in water bodies where Red-necked Grebes outnumber Great Crested Grebes, fights between them are frequently to the disadvantage of the larger species, as the Red-necked Grebes normally win here. However, Great Crested Grebes are at an advantage in larger and deeper lakes with high fish densities (Spletzer 1974, Fjelds  2004). Because Great Crested Grebes very occasionally usurp the territory of Red-necked Grebes, it is possible that interspecific competition for breeding places may limit the number of Red-necked Grebes in some wetlands suited to both species. However, both species are sufficiently separated ecologically to be able to limit competition to a large extent (Vlug 1993, 2000).

3. Other waterbirds attacking Red-necked Grebes

Podiceps griseigena may be attacked by numerous other waterbirds. There is a record of a Red-necked Grebe found dead with stab wounds in the abdomen, inflicted by a Western Grebe (Storer and Nuechterlein 1992). The species may also be attacked by Pied-billed Grebes. Great

Northern Divers *Gavia immer* cause Red-necked Grebes to flee and generally can displace them (Stout and Nuechterlein 1999).

15.4.2 Predators and Response to Predators

Predation on Adults and Chicks (this topic is discussed in more detail in 12.4.1)

Eagle Owl *Bubo bubo*, Great Horned Owl *B. virginianus*, White-tailed Eagle *Haliaeetus albicilla*, Goshawk *Accipiter gentilis*, and Peregrine Falcon *Falco peregrinus* have been cited as likely predators of adults, which are most vulnerable during incubating (Wobus 1964, De Smet 1987, Stout and Nuechterlein 1999).

A number of (semi aquatic) land predators such as Raccoons *Procyon lotor* and the American Mink *Mustela (Neovison) vison* may occasionally be a threat to grebes nesting or loafing in narrow vegetation zones near the shore line, or in water-bird colonies.

Many aerial and some (semi aquatic) land predators may be a threat to grebe chicks, e.g. gulls *Larus*, crows *Corvus*, Marsh Harrier *Circus aeruginosus*, Red Kite *Milvus milvus*, Goshawk *Accipiter gentilis*, White-tailed Eagles *Haliaeetus albicilla*, Grey Heron *Ardea cinerea*, and American Mink *Mustela (Neovison) vison* (Wobus 1964, Vlug 2002a; J J Vlug).

When not on their parent's back, small grebe chicks may be taken by large predatory fish, such as Rainbow Trout *Oncorhynchus mykiss* or Pike *Esox lucius* (Simmons 1955, De Smet 1983, Stout and Nuechterlein 1999, Imberti *et al.* 2011).

Predation on Eggs (this topic is treated in more detail in 12.4.2)

Predators on eggs of Red-necked Grebes and other Podicipedidae include crows *Corvus*, gulls *Larus*, Marsh Harrier *Circus aeruginosus*, Red Kite *Milvus milvus*, Coot *Fulica atra*, American Coot *F. americana*, Great Blue Heron *Ardea herodias*, American Mink *Mustela (Neovison) vison*, Raccoon *Procyon lotor*, Muskrat *Ondatra zibethicus*, Eurasian Otter *Lutra lutra*, Red Fox *Vulpes vulpes*, Stoat *Mustela erminea*, Pine Marten *Martes martes* and Wild Cat *Felis silvestris*.

Although Raccoons are significant predators on grebe eggs in some areas, the main egg predators in most districts are crows *Corvus* and gulls *Larus*. Human disturb-

ance during the incubation period causes the grebes to leave their nest and increases the predation risk by crows and gulls. There are reports of Carrion Crows *Corvus corone* specializing in robbing eggs in colonies of Great Crested Grebes after human intrusion (Vlug 1983). Eggshells, with a hole laterally, are usually found on land, sometimes on an open or somewhat elevated point on the adjacent shore meadow (Stout and Nuechterlein 1999, Fjeldså 2004).

Response to Predators

Predation on Podicipedidae is only infrequently recorded, but it may have played a significant role in shaping the behaviour of grebes. Their nocturnal migration may mainly be determined by predation risks relating to their poor manoeuvrability (Fjeldså 2004). Predation on grebes and their eggs also influenced their nest-site selection. Since nest-sites near the shore are most vulnerable to mammalian predators while those far offshore are most exposed to wave action and egg-stealing gulls, these threats play against one another when grebes choose nest-sites. Eggs are easily replaced but especially mammalian predators threaten the lives of incubating adult grebes. Probably, the nest-site selection of grebes evolved primarily as a response to mammalian predators and less to wave action (Fjeldså 2004).

Males and females often try to drive away potential predators when these approach the nest. Incubating birds defend their nests from egg predators by jabbing with the bill (Stout and Nuechterlein 1999). Frequently, grebes give the Hissing-call when defending the nest, e.g. when Coots try to destroy the eggs or use the nests of grebes for their own ends (Schleswig-Holstein; A Konter). Red-necked Grebes nesting on Lake Osakis, Minnesota, reacted to Great Blue Herons *Ardea herodias* with a loud, hissing threat whenever they came close to their nest. This tactic generally was effective against herons, which did not appear to seek out grebe nests (Nuechterlein *et al.* 2003).

When aerial predators, such as Marsh Harriers, approach a nest, the incubating bird may adopt a characteristic threat display: it raises the spread wings, showing the entire prominent white patch on the secondaries. At the same time, the bird leans its stretched neck backwards, pointing the bill upwards at an oblique angle, and gives the Hissing-call (Vlug 2002a; photograph in Spillner 1970, p. 276).

When disturbed by mammalian predators or humans, the incubating bird frequently gets up quickly and, if it has time, covers the eggs with sodden loose nest material, dives away to open water, where it sometimes exhibits vigorous, apparently unconcerned preening with agitated motions. On open water, the birds dive in response to threat (Vlug 2002a).

Nuechterlein and Buitron (2002) discovered that many Red-necked Grebes on Lake Osakis, abandoned their nests for extended periods during at least two of the three nights that they were monitored. By leaving their nests at night, the birds may be decreasing their exposure to nocturnal predators that prey on adults (see 16.4.4 for more details).

The Penguin-posture is frequently shown by Red-necked Grebes during human disturbance near the nest (Fjeldså 1973c). When humans approach an incubating bird, it may give the Hissing-call, meanwhile showing a Defensive-upright display with the head, neck and breast stretched high, and the crests raised (see photograph in Wobus 1964, p. 41, and account and photograph in Sage 1973).

Red-necked Grebes rarely perform a Splash-dive (escape-dive, crash-dive) during human disturbance at the nest: emerging very briefly, they suddenly beat both feet upwards, sending up a spray of water of more than 2 m high as they disappear in “fold-in-middle” dive (Wobus 1964; J J Vlug).

When approached by humans, other mammals and over flying raptors, especially if the chicks are present, the adults give the Alarm-call: a short, sharp, irregularly spaced tick (“äck”) (Wobus 1964, Stout and Nuechterlein 1999).

16. Breeding

Why birds breed when they do and why they lay a certain clutch size etc., seem at first sight to be relatively simple questions, and one might naively imagine that they require only simple answers. This is very clearly not the case. Nature is often complex, and many life history traits are influenced by a wide range of factors and often in subtle ways (Birkhead *et al.* 2014).

Since Wobus (1964) wrote his paper on the Red-necked Grebe many studies have been carried out in various

nesting populations, but there are still more unanswered than answered questions. Recognizing individual birds by colour-banding can reveal many new facts about the breeding behaviour of the species. However, it is difficult to catch and mark adults and large young, and the research worker has to spend long hours of observation, and so there are very few studies based on colour-banded Red-necked Grebes.

Because the breeding and reproductive behaviour penetrates all aspects of life, in this chapter a number of topics which are also treated elsewhere are covered.

16.1 Pair-bond

16.1.1 *Pair Formation, Mate Fidelity, and Territorial Attachment* (these topics are treated in more detail in 15.3.2)

Most Red-necked Grebes probably pair up during spring migration within large assemblages along the migration route, and as late as the arrival at the breeding waters before serious nesting behaviour begins. Although the majority of the birds give the appearance of being paired on arrival at the nesting waters, unsynchronized actions and frequent changes of partners show that a number of these grebes are not definitively paired at this stage. The pair formation in *Podiceps* species is a long process and begins before establishing true territories.

Red-necked Grebes are monogamous, at least for one season (seasonal monogamy). It is very likely that territorial attachment by both sexes may result in contact with former mates and in an opportunity for renewing the pair-bonds in spring.

16.1.2 *Similar Roles of the Sexes* (this topic is treated in more detail in 15.3.2)

A very striking feature of Podicipedidae is the almost total sexual ambivalence in displays and other social behaviours: the male and female play similar roles simultaneously or reciprocally, or show different roles interchangeably, either sex taking the initiative. The behavioural dimorphism between the sexes is largely characterized by a differing frequency of certain behaviour patterns, and the only definite differences between male and female grebes seem to be the ability to fertilize and to lay eggs, respectively.

It should be stressed that male and female grebes not only play similar roles in displays, but also share other tasks. However, as already said, the overall time-activity budgets of the sexes can differ.

16.2 Nest, Nest-building and Nest-site

Grebes have become independent of firm land by building floating nest platforms and back-brooding their young. Both behaviours are universal in grebes, suggesting that they were well developed before the differentiation of modern species began (Fjeldså 2004).

We may assume that the ancestors of grebes built their nests on humid ground at marshy lake margins, and that they gradually shifted to reed-beds growing in water, as they thereby got away from nest predators that often follow the shoreline. Since grebes have no near now-living relatives, and since the habit of building floating nests is universal in grebe species, there is no way to document the transition (Fjeldså 2004).

16.2.1 *Nest-site Selection*

Soon after arrival, Red-necked Grebes begin searching for potential nest sites around which they establish their territories (De Smet 1983). Male and female swim around together, examining shoreline emergents, and entering likely cover. These inspections are characterized by a specific behaviour, an important component of which appears to be “bobbing” of the heads back and forth in an (American) Coot-like manner similar to that displayed by Slavonian (Horned) Grebes during nest site selection (Ferguson 1977, De Smet 1983). They may evaluate the site by diving and peering beneath the surface, presumably checking the underwater environs of potential nest sites (De Smet 1983).

The birds frequently build several flimsy platforms before constructing the definitive nest. The platforms are used for soliciting and copulation. The pairs are not consistent in their choice of platforms, but shift from one platform to another, adding nest material and soliciting. Occasionally, members of a pair seem to prefer different sites; then the activity of one bird centres on one site while its mate's activity centres on another. Kevan (1970) saw that one bird of a pair of Red-necked Grebes invited on one platform while its mate was inviting on another. After a few days, activity centred on one site, and this became the definitive nest. The platform that will finally contain the eggs is that

one which, while not necessarily the last to be made, is the last to have joint construction done at it by male and female before the onset of ovulation (Simmons 1955).

Nest-site Selection-displays

1. Ceremonial-building

During the nest site selection, a Red-necked Grebe may place plants in front of its mate. Sometimes the male and female simultaneously present vegetation to each other (Ceremonial-building). Chamberlin (1977) observed this behaviour in Red-necked Grebes in Michigan: "One bird picked up a piece of vegetation floating on the water, turned and swam to within several centimetres of the other and dropped it. A lily pad was presented once; a bulrush and then some unidentified vegetation was presented; strands of water milfoil were presented 3 times; and unidentified vegetation was presented once. During a fifth presentation both birds simultaneously presented vegetation to the other and then turned away. Immediately after one presentation both birds called in unison and after another the birds turned tail-to-tail (bodies almost touching) and simultaneously dipped their bills and shook their heads." The behaviour may occur on a fixed spot, often before any platform is made, like a mutual "agreement" about where to start nest-building. It appears that it is in the Great Crested Grebe more ritualized than in *Podiceps grisegena*. This ritualized building of *cristatus* is much as in the Little Grebe, the male and female repeatedly and formally picking up and dropping the same piece of material alternately while more or less facing each other (mutual Ceremonial-building) (Simmons 1975b, Fjelds  1982b).

2. Inviting-display-on-the-water

The Inviting-display-on-the-water is similar to one form of soliciting (the Inviting-display), but occurs typically on open water. This behaviour is often associated with nest site-selection early in the cycle (see 15.3.7 for more details).

16.2.2 Nest-building

Begin of Nest-building

Photoperiod is the main driver for seasonal events, but it is recognized that many other factors, including food-availability, nest-site availability, nest material, and social interactions all influence whether a bird comes into breeding condition (see 16.3.2). Birds have the flexibility to respond adaptively to variation in conditions (Birkhead *et al.* 2014).

Nest-building may begin as soon as the Red-necked Grebes arrive on the breeding waters, perhaps especially in birds paired with the same partner as in the previous year (Stout and Nuechterlein 1999, Vlug 2002a). However, many pairs start later. Wobus (1964) wrote that *P. grisegena* pairs begin to build a few days until two weeks after their appearance on the nesting ponds.

Building

New nests are built for each breeding season, but not necessarily for new clutches within the same season. Pairs raising a second brood may reuse their old nest, and the old nest may also be used for re-nesting (Wobus 1964, Stout and Nuechterlein 1999, Fjelds  2004). Kloskowski (2001b) saw in his study area in South-East Poland that all pairs of *Podiceps grisegena* which raised a second brood or attempted it, re-nested within the same territories. Red-necked Grebes occasionally construct brooding platforms (De Smet 1983).

As already stated, Red-necked Grebes frequently build a few (one to three) flimsy platforms before constructing the definitive nest (Wobus 1964, Kevan 1970). The former are only used for soliciting and copulation, and only one may become the definitive nest and be used for egg-laying and incubation (see 16.2.1). The distance between two copulation platforms can be 2-10 metres (Wobus 1964).

Male and female participate equally in nest-building (Garner 1991, *cited in* Stout and Nuechterlein 1999). The general scheme of construction, in spells of persistent building, is to bring as much material as possible in a short time and to pile it up for later arrangement (Simmons 1955) (see Fig. 92). The nest material is most often deposited on top of some dead reeds or stems that have been broken by the wind, or in a small gap between some plants. In this way, the nest is usually more or less firmly anchored among emergent or floating vegetation (Fjelds  2004). The birds collect predominantly emergent and submergent vegetation, often sodden and partially decayed, mixed with bottom sediments. The nest materials differ with the location of the nest, but plant species that are most abundant are used (Kevan 1970, Vlug 2002a). Most nest material is gathered within 10 metres of the nest site, although Kevan (1970) saw a Red-necked Grebe carrying a stick approximately 25 metres, and Wobus (1964) observed that the grebes travelled occasionally more than 50 metres.



Fig. 92: Grebes often bring a large cargo of weed to the nest. Photo: T Runge (Schleswig-Holstein)

Fig. 92: Die Taucher bringen häufig eine große Ladung Pflanzen zum Nest.

The birds begin the nest-building with more buoyant materials which are able to support a load, such as small dead waterlogged branches or undecayed reed-stems, up to 1.5 m long, broken off from the source or collected from the surface of water. After completion of the base, partially decayed vegetation is particularly used, mainly obtained from below the surface by diving (Wobus 1964, De Smet 1983, Stout and Nuechterlein 1999, Vlug 2002a). The birds always swim fast across the surface on their way to deposit the material, never diving along en route as they may when bringing food for the young (Wobus 1964, Simmons 1955) (see Fig. 93). When the grebe reaches the site, it immediately deposits its load, usually on to the slope of the platform. If it is very active in collecting, it will then move quickly away to forage anew (Simmons 1955). During these intensive nest building bouts, one Red-necked Grebe brought material to the nest 25 times in a period of 5 minutes (Wobus 1964). A platform that supports the weight of a female bird can be made within ten minutes (Wobus 1964), and in two to three hours it supports a mating pair (Kevan 1970, Fjeldså 2004). A complete nest that can be used for egg-laying can be made in 24 hours, although 4-7 days is more normal (Fjeldså 2004).

As the mound of nest material grows, the birds become more careful in the placement of the material and circle the nest before depositing the latest load (Kevan 1970). In the final stages of nest building, one partner frequently sits on the nest. The central depression for the eggs is formed by the bird piling weed up round itself as it sits, receiving materials brought by the mate, and so it constructs the rim of the nest (Simmons 1955, Wobus 1964, Stout and Nuechterlein 1999, Vlug 2002a). This “sideways building” or “sideways throwing” in Podicipedidae is a stereotyped behaviour which can be shown as part of normal nest-building, but may also be a displacement behaviour – a nervous “sparking over” – when a bird is simultaneously influenced to leave the nest and to stay: if the motivation to incubate is strong (especially when chicks vocalize inside the eggs), the bird vigorously pulls plant material up along its flanks, but if the tendency to breed is low, it will instead preen its plumage (Fjeldså 2004).

The platform is given solidity chiefly by the incidental movements of the large lobed toes, but occasionally deliberate trampling is seen (Vlug 2002a). Significant amounts of new material are added to the nest throughout the whole incubation period, especially in response



Fig. 93: Grebes always swim fast to bring materials to the nest. Photo: T Runge (Schleswig-Holstein)

Fig. 93: Die Taucher schwimmen stets schnell, um Material zum Nest zu bringen.

to changes in the water level and wave action (Wobus 1964, Stout and Nuechterlein 1999, Vlug 2002a). Temperature probes placed in floating nests of Red-necked Grebes before windy periods were often buried 15 cm in 4 days (Stout and Nuechterlein 1999). At the time of egg laying nests of *P. grisegena* were just flat heaps of vegetative material, 1-2 cm above the water level (Kloskowski *et al.* 2012). However, halfway into the incubation period the majority of the nests have well-shaped dry cups. Abandoned nests are easily identified by lack of freshly added nesting material.

Building by Unpaired Birds

Occasionally, unpaired birds build a platform. In the breeding seasons from 1986 to 1991 a solitary Red-necked Grebe was observed on the Edersee (Eder Reservoir) near Herzhausen in the district of Waldeck-Frankenberg, Hessen (Hesse). In 1986, 1987, 1989, 1990 and 1991 the bird showed nest-building, defended a territory against Great Crested Grebes and was highly vocal (Burkhardt 1995, Hessische Gesellschaft für Ornithologie und Naturschutz 2010; R Enderlein). The same behaviour of an unpaired Red-necked Grebe was recorded by Dietzen *et al.* (2011) on the Sangweiher near Daun, Rheinland-Pfalz (Rhineland-Palatinate), in 2009.

Davis (1983) made an interesting observation of a solitary Red-necked Grebe making nest-building movements in winter. On 22 November 1979, at Chouet Bay in the island of Guernsey, English Channel, he saw a Red-necked Grebe feeding in company with a Red-breasted Merganser *Mergus serrator*. After ten minutes the two moved 90 metres apart and the grebe climbed on top of a rock covered in Bladder Wrack *Fucus vesiculosus* standing 0.5 m above the surface of the water. The bird then settled down and, using its bill, arranged the wrack around itself in the form of a nest; after five minutes, it climbed down and started to swim around the rock in an agitated manner.

Building of Brooding Platforms

After hatching is completed, Red-necked Grebe pairs usually resort to nearby open water or to the edge of a reed bed, where one adult (the guard adult) generally remains with the young while the mate forages for and brings food to the young. However, in Turtle Mountain Provincial Park, Manitoba, De Smet (1983) saw that in at least three instances, the empty nest was used as a brooding platform until 1-2 weeks after hatching. At least 8 other pairs of Red-necked Grebes constructed open-water brooding platforms 1-3 weeks after the

young hatched. These platforms were used sparingly as a resting site for the young and occasionally the guard adult. Even though 20% of the successful pairs in the study of De Smet (1983) brooded their young on the nest or a brooding platform, other studies of the Red-necked Grebe reported only isolated cases where the abandoned nest or platform was used (e.g. Wobus 1964) or where a new brooding platform was constructed. A pair that Sage (1973) studied in southern Alaska had a brooding platform at the edge of a bed of sedges and about nine metres from the nest. About once an hour the parents would bring the young to this platform where they would be brooded by one of the adults for 10-15 minutes.

Returning to the nest after hatching chicks is a normal behaviour in pied-bills *Podilymbus*, dabchicks *Tachybaptus*, and White-tufted Grebes *Rollandia rolland*. They often return for 2-3 weeks to brood the young on the nest by night and during bad weather, and sometimes build extra platforms for brooding and loafing (Fjeldså 2004).

16.2.3 Nest Characteristics

Nest Structure, Size and Composition Matter

The nest is a compact mound of partially decayed aquatic vegetation with a shallow depression for the eggs. The great mass of the nest is under water. The nests are usually floating and anchored to the emergent and submergent vegetation or are built up from the lake bottom or submerged stumps, logs, or beaver caches. The completed nests vary in size and shape depending on the site chosen and changing water levels during incubation (Wobus 1964, Cramp *et al.* 1977, Stout and Nuechterlein 1999, VlUG 2002a) (see Fig. 94).

As already stated, significant amounts of new material are added to the nest throughout the whole incubation period, especially to counter changes in the water level and wave action (Wobus 1964, VlUG 2002a). The first egg is often laid on a water-soaked and flimsy platform, where the nest-cup is barely indicated. However, most nests have well-shaped dry cups halfway into the incubation period (Fjeldså 2004). Due to changes in the water level, two nests in eastern Germany towered 25 cm above the water during hatching, and it was difficult for the adults to climb these (Wobus 1964). There is a strong correlation between nest size (height, diameter) and water depth at the nest site (Kloskowski *et al.* 2012). The

nest-size also depends on the buoyancy of the material. Where there is plenty of fresh aerenchymatous plant material, or where fermentation proceeds rapidly (because of high temperatures and pH), the birds apparently do not need to add much more material to keep the nest floating. So, these nests remain small. In boreal lakes with cold water and a low pH, and only rotting plant debris available, the buoyancy of the nest is low, and the grebes must add new material daily throughout the whole incubation period (Fjeldså 2004). Such nests may in the end weigh more than 20 kg (after draining the water), much more than the nest weights of 9 and 13 kg given by Wobus (1964).

The nest cup diameter is influenced by the size of the bird and the number of eggs laid in the nest (Bocheński 1961, Wobus 1964).

For nest building, the grebes use a wide variety of emergent and submergent plants, especially partially decayed materials from the lake bottom, but also mud. The plant species favoured depend on the availability and buoyancy.

Dittberner and Dittberner (2006) found many plant species as nest material in the nests of *P. griseogena* in the Uckermark, Germany, e.g. culms of Common Reed *Phragmites australis*, Amphibious Bistort *Polygonum amphibium*, hornwort (coontail) *Ceratophyllum*, culms of sedge *Carex*, pondweed *Potamogeton*, bulrush (cattail) *Typha*, algal bloom, aerial roots of White *Nymphaea alba* and Yellow Water-lilies *Nuphar lutea*, bur-reed *Sparganium*, stalks of mugwort *Artemisia*, comfrey *Symphytum*, grass Gramineae (Poaceae), club-rush (bulrush) *Scirpus*, Bittersweet Nightshade *Solanum dulcamara*, Reed Sweet-grass *Glyceria maxima*, bog (peat) moss *Sphagnum*, crowfoot *Ranunculus*, and duckweed *Lemna*.

On Astotin Lake, Alberta, pairs nesting in open water used pondweed *Potamogeton* to construct their nest while those in emergent vegetation used the species that were most abundant. In areas of the lake where Beavers *Castor canadensis* were active, the Red-necked Grebes used sticks at the base of their nests. In 85% of 78 nests in Astotin Lake sedges *Carex* were used as nest material, in 40% pondweed *Potamogeton*, in 14% sticks and in 12% cattails *Typha* (Kevan 1970).

Club-rushes (bulrushes) *Schoenoplectus* and decayed vegetation were the major component in about one-



Fig. 94: Red-necked Grebe nest with eggs. Photo: T Runge (Schleswig-Holstein)

Fig. 94: Rothalstauchernest mit Gelege.

quarter of 217 Red-necked Grebe nests found in Turtle Mountain Provincial Park, Manitoba (De Smet 1983). Other major components that occurred in 5-15% of the nests were filamentous algae, Sago Pondweed (Fennel Pondweed) *Potamogeton pectinatus* (*Stuckenia pectinata*), Clasping Leaf Pondweed *Potamogeton richardsonii*, hornworts (coontails) *Ceratophyllum* and water milfoils *Myriophyllum*. Although sticks were rarely the major component, they represented a minor component in more than one-third of the nests in Turtle Mountain Provincial Park (De Smet 1983).

The nests of Red-necked Grebes in British Columbia were low accumulations of nearly submerged, usually decaying, aquatic vegetation including pondweeds *Potamogeton*, water milfoils *Myriophyllum*, and filamentous algae, sometimes mixed with mud and invariably lined with living or dead club-rush (bulrush) *Scirpus* (*Schoenoplectus*), cattail *Typha*, sedges *Carex*, mosses *Bryophyta*, water-lilies Nymphaeaceae, rootlets, twigs, horsetails *Equisetum*, or leaves (Campbell *et al.* 1990).

Nests near Yellowknife, Northwest Territories, were constructed of a variety of plant materials, including sedges *Carex* in 75% of the nests, sphagnum mosses *Sphagnum*

in 60%, cattail *Typha* in 43%, horsetail *Equisetum* in 29%, and pond-lily *Nuphar* in 26% (Fournier and Hines 1998).

Wheeler (2001) studied Red-necked Grebes at Whitefish Lake in Ontario in 1993 and 1994. She showed that 84% of 121 nests investigated in 1994 were constructed primarily with Wild Rice *Zizania palustris*, the most abundant emergent species in the study area. The major components of the remaining nests included water-lily *Nymphaea*, Common Water Crowfoot *Ranunculus aquatilis*, Water Horsetail *Equisetum fluviatile* and club-rush (bulrush) *Scirpus* (*Schoenoplectus*). Early in the breeding season, from late May to early June, most of the nests and platforms were constructed of old, decaying Wild Rice stalks from the previous year, and fewer with new Wild Rice stalks as they came available.

The old Wild Rice nests were typically very densely packed, compact and contained large amounts of mud. From the middle of June through the remainder of the nest-building period, nests consisted primarily of new growth Wild Rice. These nests were characteristically larger than old Wild Rice nests and much looser in construction. In all cases, the plant species that was predom-

inant in the nest was also the most abundant species immediately adjacent the nest site.

One hundred and six of the 121 of the nests observed at Whitefish Lake were floating nests attached to the lake substrate by a column of sub-surface vegetation and detritus. Closer investigation revealed that some underwater fixture, log, twigs or significant rise in the lake substrate served as an anchor for these nests (Wheeler 2001).

Nest Measurements

The nest dimensions are extremely variable and depend among other things on the site chosen, changing water levels, nest materials and the building activities of the birds before and during incubation. Most authors did not mention when they measured the nests, which means that the data are not fully comparable.

The measurements (cm) of *P. grisegena* nests in eastern Germany (Wobus 1964) were:

Dimension	n	Mean	Min.	Max.
Water depth	55	67.0	25.5	100.0
Diameter nest just above the water level	55	37.0	18.0	50.0
Diameter nest below water level	33	57.0	37.0	90.0
Diameter nest cup	43	13.5	5.0	18.0
Height nest above water	48	4.7	2.7	10.5
Total height of nest	40	47.0	18.0	93.5
Depth of nest cup	45	3.1	1.5	7.0

Dittberner and Dittberner (2006) measured 102 Red-necked Grebe nests in the Uckermark, Brandenburg in eastern Germany:

1. Mean outside diameter of the nest 27.4 cm (range 18.0-93.0 cm),
2. mean inside diameter of the nest 9.5 cm (range 7.1-22.3 cm),
3. mean depth of the cup 3.0 cm (range 1.1-9.0 cm),
4. mean height of the nest 5.5 cm (range 1.2-9.1 cm).

Of 26 Red-necked Grebe nests in British Columbia (Campbell *et al.* 1990) the ranges of nest measurements were:

1. Outside diameter 33-122 cm,
2. inside diameter 18-28 cm,
3. height 8-25 cm.

The measurements (cm) of Red-necked Grebe nests at Whitefish Lake, Ontario for 1993 and 1994 (Wheeler 2001) were:

Dimension	n	Mean	SD	Min.	Max.
Outside diameter	48	98.6	34.8	57.0	235.0
Inside diameter	69	53.2	8.4	36.0	85.0
Cup diameter	68	16.4	0.6	0.0*	22.0
Cup depth	64	4.2	1.9	0.0*	7.0
Height nest above water	68	6.9	2.8	1.0	14.0
Water depth	67	50.4	18.8	26.0	108.0

* Wheeler (2001) remarked, that the cup diameter and cup depth were often underdeveloped in newly constructed nests.

Temperature of the Nest

Bocheński (1961) wrote that it is well-known to field observers that the nests of Podicipedidae are especially warm in the last stage of incubation. He measured the temperature in 14 nests of Black-necked Grebes at the end of the incubation period (in a few nests the young birds were just beginning to hatch). Thermometers were inserted into three places of each nest and the temperature measured after 10 minutes. Bocheński (1961) concluded that the temperature in the nest material was constant and higher than the temperature of the surrounding water by 1°C or more. He said that the warmth was especially caused by the body heat of the incubating bird, but also by the solar heat accumulated in the layer covering the eggs and the heat derived from the putrefying (decomposing) nest material. The last acted only indirectly by slowing down the cooling of the nest after it was left by the incubating bird, especially at advanced stages of incubation. However, a long time before Bocheński (1961) published his paper on the nesting biology of the Black-necked Grebe, Schiermann (1927) carried out investigations on the nests of Great Crested Grebes. According to this author, the nest temperatures of grebes are not higher than those of other water birds (Coot *Fulica atra*, Common Pochard *Aythya ferina* and Moorhen *Gallinula chloropus*), and it could not be established that heat is generated by the putrefying plant material. On the other hand, Schiermann (1927) believed that his data showed that the layer of nest material used for covering the eggs is a good heat insulator.

Fjelds  (2004) stated that in regions with a fairly warm summer the temperature of the bottom of the nest-cup of grebes may be maintained by rotting plant material, but this is certainly not the case near the sub-arctic distribution limit of Podicipedidae, where nest-cups are often very cold. Apparently, grebe embryos are remarkably hardy to cold and survive long periods of chilling (see 16.4.8).

16.2.4 Nest-site Characteristics

Compared with many other waterbirds, a grebe is much more limited in its choice of nesting place, largely because of its physical specializations as a highly efficient diver. Sites have, therefore, to be accessible from the water, either at the water's edge or among flooded vegetation (as long as the nest can be anchored); even then, the grebe can make only the lowest of leaps to get out of the water (Simmons 1974).

The nest-site selection by grebes involves a response to interrelated variables of water depth, proximity to open water, vegetation density, wave action, proximity to the shore and availability of nest materials. The nest-sites selected generally offer proximity to fairly deep, open water allowing an easy access to and from the nest; relatively unobstructed visibility and maximum distance to the shore for protection against land predators; and a solid anchorage, maximum distance to open water, and minimum distance to the opposite shore for protection against wind and waves.

The nests of Red-necked Grebes are often built in flooded emergent vegetation such as a fringe of reeds and reed-beds along a stretch of water, or near small areas of open water in large marshes (Vlug 2002a).

Nest-site Selection and Water Depth

The water depth at the nest varies but is rarely < 20 cm. Nests in water depths of 20 cm or less are vulnerable to becoming stranded because of a drop in the water level (Kevan 1970), and are deserted because the birds can no longer swim to them. The maximum water depths are usually limited by the availability of suitable anchorage objects, but even when deep-water anchorage sites are available, Red-necked Grebes usually prefer depths of less than 1 metre, probably because of a positive correlation between water depth and wave action (De Smet 1983).

The range of regional means of water depth at the nest was 42-80 cm. The water depth at the nest in different areas (cm) was:

Area	n	Mean	Min.	Max.	Author
Eastern Germany	55	67	25.5	100	Wobus (1964)
Kamenz, Sachsen (Saxony)	?	60	50	80	Melde (1978)
Ponds near Warsaw	20	65	35	85	Gotzman (1965)
Astotin Lake, Alberta	93	42	20	81	Kevan (1970)
British Columbia	?	?	20	360	Campbell <i>et al.</i> (1990)
Marsh adjacent to Duck L., British Columbia	63	80			Ohanjanian (1986)
Yellowknife, Northwest Territories	89	63	16	163	Fournier and Hines (1998)
Turtle Mountains, Manitoba *	219	54.9	15	140	De Smet (1983)
Whitefish Lake, Ontario	67	50.4	26	108	Wheeler (2001)

* Nests anchored to the lake bottoms (offshore reefs) were in shallowest water (mean depth 38.7 cm, $n = 6$); those anchored to Beaver *Castor canadensis* food caches were in deepest water (mean depth 79.3 cm, $n = 9$). Although the Red-necked Grebe nests in Turtle Mountains were found in water depths of 15-140 cm, more than 96% of the nests were in water depths of 20-100 cm (De Smet 1983).

To anchor their floating nests and hatch their young, Red-necked Grebes on Lake Osakis, Minnesota, preferred sheltered emergent vegetation in water at least 0.5 m deep (Nuechterlein *et al.* 2003).

In the Uckermark, Brandenburg, the minimum water depth at the nest was 20 cm, the maximum 300 cm (Dittberner and Dittberner 2006). The distribution of 228 nest-sites in relation to the water depth there was as follows:

1. depth 20-50 cm: 44 nests (19%),
2. depth 51-100 cm: 120 nests (53%),
3. depth 101-200 cm: 61 nests (27%),
4. depth >200 cm: 3 nests (1%).

Distance of Nests from Shore and Open Water

The distance of nests from shore and open water depends on many variables such as wave action, solid anchorage facilities, accessibility, and predators.

The habitat for feeding also plays a role in the selection of the nesting site. Gotzman (1965) reported that the distance between the nest of Podicipedidae and the open water depends upon the location of the nest territories in relation to the feeding grounds. Species feeding near their nests, e.g. *Tachybaptus ruficollis* nest at quite a distance from the open water, whereas those feeding in the open water, *Podiceps cristatus* and *Podiceps nigricollis*, build their nests at the edges of the emergent vegetation. *Podiceps griseogenus* takes an intermediate position in feeding habitat and also in the choice of its nesting site. The distance between the nest site in the emergent vegetation and the open water of fourteen Red-necked Grebe nests was c. 10 m, and of 6 other nests 30-50 m ($n = 20$ Red-necked Grebe nests) (Gotzman 1965).

Dittberner and Dittberner (2006) found a nest in the Uckermark, Brandenburg, at a distance of 2 m from shore on 23 May 1991. As a rule this distance is larger in eastern Germany.

On Astotin Lake, Alberta, the distance from the nests in the emergent vegetation to open water was measured. The majority (83%) of the nests in the sedge *Carex* marshes were found closer to open water than to shore: the mean distance to open water was 4.0 metres with a range of 0.3 to 15.5 metres. Nests in the bulrushes *Scirpus* tended to be farther from open water, the mean distance being 6.1 metres with a range of 1.5 to 12.0 metres. Nests with loose density vegetation between them and open water tended to be farther from open water than those separated from it by medium density vegetation. The mean distance to shore in the sedge *Carex* marshes was 10.6 metres with a range of 1.8 to 27.4 metres. Nests closer to shore tended to be in shallower water and were more subject to stranding and subsequent desertion (Kevan 1970).

In Turtle Mountain Provincial Park, Manitoba, the average distance to the closest shore was 24.0 m ($n = 219$ nests). The average distance ranged from 12.0 m ($n = 9$) for nests anchored to Beaver *Castor canadensis* food caches to 38.5 m ($n = 29$) for nests anchored to flooded willow *Salix* stumps (De Smet 1983).

Of 48 nests near Yellowknife, Northwest Territories, for which distances were measured, the mean distance from shore was 14.8 ± 1.7 m (range 3.1-65.0 m, median 12.0 m) and the mean distance to open water was 1.5 ± 0.3 m (range 0-12.5 m, median 0.7 m). All nests were farther than 3 m from shore and 90% were located within 3 m of open water (Fournier and Hines 1998).

Most nests in British Columbia (81%; $n = 674$) were positioned among or at the edge of emergent vegetation. Other nests were built in open areas. The nests were placed from 0.6 to 91 m from shore (Campbell *et al.* 1990).

The mean distance from shore for Red-necked Grebe nests at Whitefish Lake, Ontario was 48.3 m (SD 6.0 m, range 0.0-385.9 m, $n = 155$) (Wheeler 2001).

Nest-site Selection, Species of Plants and Stem-densities

1. Nest-site and vegetation

As already stated, the nests of Red-necked Grebes are often built in flooded emergent vegetation such as fringe of reeds and reed-beds along a stretch of water, or near small areas of open water in large marshes (see Fig. 94 and 95). In Central Europe Common Reed *Phragmites australis*, cattail *Typha*, sedge *Carex*, horsetail *Equisetum*, Reed Sweetgrass *Glyceria maxima*, club-rush (bulrush) *Scirpus* (*Schoenoplectus*), bur-reed *Sparganium* and rush *Juncus* are commonly used for cover and anchorage. The nests are often anchored to flooded or trailing willow *Salix* or flooded alder *Alnus*. The birds may also use floating vegetation such as Yellow Water-lily *Nuphar lutea*, White Water-lily *Nymphaea alba*, Amphibious Bistort *Polygonum amphibium*, Common Water Crowfoot *Ranunculus aquatilis* and Broad-leaved Pondweed *Potamogeton natans* (see below). Occasionally, the birds anchor their nests to Bogbean *Menyanthes trifoliata* (Tischler 1941, Wobus 1964, Melde 1978, Dittberner 1996, Vlug 2002a; J J Vlug).

As in Central Europe, the nests in North America are most often built in flooded emergent vegetation, and also in open water on thick mats of submergent vegetation, or anchored to the lake bottom or submerged tree stumps, logs etc. (Stout and Nuechterlein 1999).

Bulrush (club-rush) *Scirpus*, cattail *Typha*, sedge *Carex*, willow *Salix*, and horsetail *Equisetum* are commonly used for cover and anchorage, but the birds may use other available vegetation, such as pond lily *Nuphar*, es-



Fig. 95: A grebe on its nest, keeping watchful eye on its surroundings. Photo: T Runge (Schleswig-Holstein)

Fig. 95: Ein Taucher auf seinem Nest, aufmerksam die Umgebung beobachtend.

pecially when other emergents are lacking (Stout and Nuechterlein 1999).

In 1968 and 1969, at Astotin Lake, Alberta, the majority of the nests were found in emergent vegetation (c. 70%). In both years, Water Sedge *Carex aquatilis* and Spangle-top Grass *Scolochloa festucacea* marshes were favoured as nest sites (57% of 327 nests); willow stumps *Salix* (9%), cattail *Typha* (8%), reed *Phragmites* (3%) and bulrushes *Scirpus* (2%) were less often used. Four percent of the nests were anchored to fallen trees and 14% were found in open water ($n = 327$; 1968 and 1969) (Kevan 1970).

Of 89 nests examined near Yellowknife, Northwest Territories, all were anchored to emergent vegetation or trees. The most commonly used emergents were Broadleaf Cattail (Common Bulrush) *Typha latifolia* (39% of the nests), sedges *Carex* (20%), willows *Salix* (18%), and Water Horsetail *Equisetum fluviatile* (15%). The remaining nests were anchored to bulrush (club-rush) *Scirpus*, Water-arum (Bog-arum) *Calla palustris*, Marsh Cinquefoil *Potentilla palustris*, flooded (dead) alder *Alnus*, and Yellow Pond-lily (Variegated Pond-lily) *Nuphar variegata* (Fournier and Hines 1998).

Wheeler (2001) found a large breeding population of Red-necked Grebes on Whitefish Lake (3,015 ha) in the district of Thunder Bay in 1993 (59 pairs) and 1994 (39 pairs) (see 16.2.3). The population was strongly associated with uncultivated Wild Rice *Zizania palustris* stands in shallow bays in the west end and northwest shoreline of the lake. The Wild Rice stands provided concealment from predators, adequate shelter from the wind and high waves, and abundant nest material for the nests of the Red-necked Grebes.

2. Nest-site and stem-densities

Gotzman (1965) defined four classes of emergent vegetation density:

1. Full density: the emerged parts of the plants are in contact with each other, forming a dense compact thicket very difficult to force one's way through,
2. great density: the emerged portions of the plants are not in contact with each other, but a man finds it rather difficult to go through; leaves a distinct trace behind him in the form of a belt of destroyed vegetation,
3. medium density: it is possible to walk through

without any difficulty, a trace will, however, remain behind,

4. loose density: patches of open water surface are found between the individual plants or their clumps, walking is possible with no difficulty or damage to the vegetation.

In addition to being protected from wind and waves, grebe nests should ideally be firmly anchored, readily accessible, and situated a safe distance from shore (De Smet 1983). Red-necked Grebes meet these requirements by nesting in medium and loose density emergent vegetation.

In the study area of Gotzman (1965) near Warsaw, 80% of the nests of *Podiceps grisegena* were found in medium density vegetation ($n = 20$ nests).

On Astotin Lake, Alberta, Water Sedge *Carex aquatilis* and Spangletop Grass *Scolochloa festucacea* marshes were favoured as nest sites (see above). In these marshes the vegetation was growing in hummocks and was classed as loose density vegetation. Willows *Salix* were also in this classification. Cattail *Typha* grew only at full density and at loose density. Nests in cattail were found only in vegetation of loose density. When the amount of cattail growing at loose density was calculated, the utilization was found to be 3.6 times the availability. Nests in reeds *Phragmites* and bulrushes *Scirpus* were found in vegetation of medium density (Kevan 1970).

Nests in Open Water

The nests in Europe are frequently clearly placed in open water (see Fig. 96), sometimes at a large distance from shore, within emergent vegetation clumps [e.g. tussocks (clumps) of club-rush (bulrush) *Schoenoplectus* or tussocks of sweet-grass *Glyceria*, which are often not much larger than the nest], on mats of algal bloom or on mats of submergent vegetation (e.g. water milfoils *Myriophyllum* and hornworts *Ceratophyllum*), in fields of floating White *Nymphaea alba* and Yellow Water-lilies *Nuphar lutea*, Amphibious Bistort *Polygonum amphibium*, Common Water Crowfoot *Ranunculus aquatilis* and Broad-leaved Pondweed *Potamogeton natans*, or anchored to the lake bottom, submerged sticks, stumps, or logs. Thus, although Red-necked Grebe nests are most frequently built in flooded emergent vegetation, a number of nests are found on open sites, especially when emergent vegetation is lacking, quite often without shielding vegetation, completely open to view (e.g. 22% of the nests in

the area around Leipzig were completely open to view, Höser *et al.* 1998) (Wobus 1964, Scholl 1972, Makatsch 1974, Melde 1978, 1986, Dittberner 1996, VlUG 2002a, Dittberner and Dittberner 2006). Nests placed in open water are inaccessible from the mainland bank and thus protected against land predators. However, they can be vulnerable to wave actions, and the open water nests that are not hidden by screening vegetation easily fall victim to aerial predators such as crows, gulls and harriers (though this is offset to some extent by the deliberate covering of eggs, and even young, with nest material) (Simmons 1974, Fjeldså 2004; J J VlUG).

Locally, the number of nests in open water can be large, but fully free floating, un-anchored, nests are very rare in all areas (Wobus 1964, Melde 1986; J J VlUG). Dittberner and Dittberner (2006) found a Red-necked Grebe nest on a free-floating tussock (clump) of sedge *Carex* in the Uckermark, Germany.

Also, in North America the nests are often found in open water on thick mats of submergent vegetation, especially water milfoils *Myriophyllum*, or anchored to the lake bottom or submerged stumps, logs, or Beaver *Castor canadensis* food caches (Stout and Nuechterlein 1999).

On Astotin Lake, Alberta, fourteen per cent of 212 nests found in the summer of 1969 were in shallow open water. Seventy per cent of the open water nests were established toward the end of June. Many of these nests were suspected to be re-nests because equal numbers of old nests were found nearby in the marshes. In late June of 1969 two nests in open water were moved over 30 metres by a storm and deserted after the storm even though the eggs were undisturbed (Kevan 1970).

In Turtle Mountain Provincial Park, Manitoba, Red-necked Grebes nested within open water submergent vegetation (29.2%), within open water emergent clumps (16.9%), near the open water/emergent vegetation interface (8.7%), or anchored their nests to sticks, stumps, or to the lake bottom (23.7%), or nested within emergent bands (21.5%) ($n = 219$ nests) (De Smet 1983).

On Duck Lake (1,300 ha in size), British Columbia, all Red-necked Grebes nested on accumulations of Eurasian Water Milfoil *Myriophyllum spicatum*. Over three years of study complete clutches were found only in areas where accumulated milfoil was of high or medium density (Ohanjanian 1986) (see below).



Fig. 96: A grebe returning to the nest. Photo: T Runge (Schleswig-Holstein)

Fig. 96: Ein Taucher kehrt zum Nest zurück.

Nest-site Selection and Predators

One factor influencing the nest-site selection is the presence of predators. However, the actual nest locations may represent a compromise between a number of opposing factors. To anchor their floating nests, Red-necked Grebes on Lake Osakis, Minnesota, preferred sheltered emergent vegetation in water at least 0.5 m deep. Nests that were located farther from the mainland or over deeper water presumably were safer from terrestrial predators such as Raccoons *Procyon lotor*. Experimental nest platforms on the lake showed that even 10 m of open water can greatly reduce access to the nests by mammalian predators. Nests farther from shore may still be vulnerable to more aquatic mammals, such as Mink *Mustela vison*, and to aerial predators, such as Great Blue Herons *Ardea herodias*, Great Horned Owls *Bubo virginianus*, gulls and corvids (Nuechterlein *et al.* 2003).

Nests far from shore may be safer from terrestrial predators, but stem densities of emergents generally decrease with water depth, and so these nests are more vulnerable to destruction by wind and wave action. Risks from waves (which do not threaten the lives of incubating adults) and predators (which do), therefore appear to play against one another when grebes are choosing nest

sites, and actual nest locations may represent a compromise between these factors (Nuechterlein *et al.* 2003). Because eggs are easily replaced but especially mammalian predators threaten the lives of incubating adult grebes, it is probable that the nest-site selection of grebes evolved primarily as a response to this threat and less to wave action (Fjelds  2004).

Nest-site Selection and Wind and Wave Exposure

Wave action causes major nest losses within most grebe species, especially those nesting on larger lakes (Speirs *et al.* 1944, Riske 1976, Vlug 1983, Goc 1986, Zimmermann and Schieweck 1988, Storer and Nuechterlein 1992, Nuechterlein *et al.* 2003, Fjelds  2004, Vlug 2005) (see 12.2.2 and 16.3.5 for more details). On Lake Osakis over 40% of all Red-necked Grebe nest losses were wind related (Nuechterlein *et al.* 2003). The impact of wave action varies among nesting areas and years, presumably in relation to the amount and density of the previous year's vegetation that remains to serve as a breakwater. Initiating nests early, and repeatedly replacing destroyed nests, appear to be common tactics among many species of grebes (Nuechterlein *et al.* 2003).

De Smet (1983) believed that Red-necked Grebes in Turtle Mountains, Manitoba, selected nest-sites with minimal amounts of wind and wave exposure. Nests located in lakes smaller than 20 ha in size ($n = 74$) were significantly less exposed than those in 20-30 ha lakes ($n = 47$) or those within bays of larger lakes ($n = 42$). Nests located within lakes exceeding 30 ha but not within well-enclosed bays ($n = 57$), were significantly more exposed than nests within any of the other sites. Nests within large lakes received additional wave protection by being situated in shallower water (mean 50 cm) than those in lakes of less than 30 ha (mean 60 cm).

Breeding Red-necked Grebe pairs arriving on Lake Osakis, a large (2,537 ha), wind-blown lake, were highly attracted to several large floating Lesser Bulrush (Narrowleaf Cattail) *Typha angustifolia* mats that had broken off and drifted away from the mainland to become „islands“ snagged within rooted emergent beds. These mats provided prime nesting habitat protected from waves and predators, which was chosen by nearly 40% of the breeding population of 80-100 pairs. During most years of the period 1995-98, pairs that established nests on those mats hatched earlier in the season and had larger clutches and broods (Nuechterlein *et al.* 2003) (see 16.3.5 for more details).

Of 55 complete clutches found in Eurasian Water Milfoil *Myriophyllum spicatum* on Duck Lake, BC, c. 38% were in high density accumulations and c. 62% were in medium. No complete clutches were found in low density accumulations. All nests constructed in May, prior to the build-up of substantial amounts of milfoil, were lost by wave action. Nests in an adjacent marsh were anchored to Broadleaf Cattails *Typha latifolia*. A dense wall of these plants protected the nests from wind and wave damage. Hatching success in the marsh was significantly greater than on Duck Lake and the young hatched about one month earlier (Ohanjanian 1986) (see 16.3.5 for more details).

Roles of Innate Mechanisms and Learning for Nest-site Selection

The relative roles of innate mechanisms and of learning for nest-site selection in grebes were studied by comparing nest-sites of second calendar year and older Slavonian (Horned) Grebes in Lake Mývatn and the

surrounding pothole areas in Iceland (the age of the birds was determined from egg measurements) (Fjeldså 1973a, 2004). First-time breeding females settled mainly in bays and ponds completely fringed by sedges *Carex*, even though the extension of vegetation as such did not always offer a good measure of protection or concealment. There seemed to be a tendency that the first-time breeding females were very dependent on the occurrence of supra-aquatic vegetation. They further tended to settle in places with less extensive sheets of open water. Thus, young birds probably preferred to see themselves completely surrounded by emergent vegetation. Older birds, on the other hand, appeared to rely on parameters that are more essential. They preferred to place their nests in dense protective patches of vegetation, irrespective of how extensive these were, or they liked to place their nests close to the best feeding areas, irrespective of whether there was emergent vegetation at all. The older birds were remarkably good at finding safe sites even on exposed coasts, where this gave access to rich feeding habitats near thermal wells in Lake Mývatn. Their nest-sites comprised cavities among grassy tussocks along the shore or among emerging rocks at coasts where aquatic vegetation was lacking. Experienced birds, which used aberrant nest sites in Lake Mývatn, had a large nesting success, much above the average for the entire population (Fjeldså 1973a, 2004).

16.2.5 Distance Between Nests of Conspecifics, Breeding Dispersion and Colonies

Territoriality

Red-necked Grebes are highly pugnacious, intensely territorial birds and usually nest as isolated pairs. They do not only show intraspecific territoriality, but also interspecific (De Smet 1983, Stout and Nuechterlein 1999, VlUG 2002a, Fjeldså 2004).

1. Territory types and sizes, population densities

Type A territories (mating, nesting, and feeding ground for the young) predominate in Red-necked Grebes. Type B territories (mating and nesting ground, most foraging occurs elsewhere) are rather rare. Type A territories in Oberlausitz, Germany, ranged from 1 to 6 ha (Wobus 1964). The mean territory size in a study area in North Dakota for pairs with young was $1.39 \text{ ha} \pm 0.35 \text{ SE}$ ($n = 8$), and for pairs without young $1.09 \text{ ha} \pm 0.26 \text{ SE}$ ($n = 14$) (Garner 1991, *cited in* Stout and Nuechterlein 1999).

Several factors are likely to influence territory type and size such as the characteristics of the nesting habitat, food quantity, intruder pressure, and amount of normal or high-quality nest-sites.

Territories of type A, the combined breeding and feeding territories, are found in smaller ponds or in well secluded bays of larger lakes. Here the territory borders are physical barriers and easier to defend than invisible lines determined through intraspecific conflict. Territories in Podicipedidae average smallest where food is abundant, and it seems that the tendency to attack is correlated with the abundance of food. In poor food situations the territory is defended more fiercely than in rich food situations (Ejelds  1973d).

Very small ponds with an abundance of food suffice to feed a brood of young. In Schleswig-Holstein, Germany, Red-necked Grebe pairs sometimes nest and raise young on inland-ponds of 0.05-0.12 ha. However, many single pairs occupy entire small ponds of 1-3 ha and larger. These ponds could support more than one pair (Vlug 2005). The aversion to close neighbours secures hegemony of unnecessarily large areas in some pairs. However, intruder pressure can compel solitary pairs to accept neighbours.

Klatt and Paszkowski (2005) examined the influence of factors determining the territory size in Red-necked Grebes breeding on small boreal lakes (15-240 ha) in Alberta. Their results showed that the size of territories is inversely related to the density of conspecifics and of fish (i.e. food) abundance. Although food abundance is important for breeding Red-necked Grebes, the authors showed that the number of conspecifics in their study area has a larger effect on territory size than the abundance of food. Thus, high nesting densities may (sometimes) be explained more by intruder pressure than food abundance.

Lakes and ponds with large quantities of macroinvertebrates and small fish may attract many Red-necked Grebes, so that the intruder pressure increases. When these breeding waters offer enough shielding vegetation between the nest-sites, the nest densities can be very high.

An example is Struckteich (14 ha), a well-vegetated breeding water with an abundance of aquatic arthropods in Schleswig-Holstein (Germany). In 2000 54 Red-

necked Grebe pairs nested here (= 3.86 breeding pairs/ha) (Vlug 2011) (see Fig. 29).

2. Distance between nests of conspecifics

In Central Europe, single pairs often occupy an entire small pond. In larger breeding waters, as a rule, the nests are scattered. However, the distance between 2 active Red-necked Grebe nests is occasionally only 2 metres, for example in densely populated breeding waters near the Baltic Sea on the island of Fehmarn (food-flights, see 11.3.1) (Vlug 1998). Dittberner and Dittberner (2006) found, in the Uckermark, nearest-neighbour distances of 2 m, 2.5 m, 6 m and 7.5 m, and Gordienko (1981) recorded 1-2 metres in the Naurzum Lakes, North Kazakhstan. Wheeler (2001) observed a minimum distance of 1.5 m on Whitefish Lake, Ontario. Even distances less than 1 metre have been reported (for example in the semi-colonial Red-necked Grebes on Lake Osakis, Minnesota; Nuechterlein *et al.* 2003).

Colonies

1. Reports of colonies of Red-necked Grebes

Sometimes small colonies (up to 15 nests) of the nominate race are reported, e.g. near Reinfeld in Schleswig-Holstein, Germany (Hagen 1913), on the Drausensee (Jeziro Dru no), a lake near Elbing (Elbl g) in former Prussia (in present day Poland) (Tischler 1941), and in the Volga Delta (Markuze 1965). Extremely high breeding population densities are found on lagoons and other shallow wetlands near the Baltic Sea (up to 40 pairs, in 2017, on a 3-ha pond near Westermarkelsdorf on the island of Fehmarn = 13.3 breeding pairs/ha) (see Fig. 32). Because foraging occurs outside the breeding water (the adult Red-necked Grebes make food flights to the adjacent sea), we can classify the grebes in these wetlands as (semi-) colonial breeding birds (see below for the definition of avian coloniality and see 11.3.1 for more details).

There are numerous reports of *Podiceps grisegena holboellii* in North America nesting in ("loose") colonies, e.g. Bent (1919), Palmer (1962), Godfrey (1986) and Johnsgard (1987). However, the authors usually present few data and the term "colony" often indicates some areas with a high nest density (see below).

Wheeler (2001) studied a breeding population of Red-necked Grebes at Whitefish Lake, Ontario in 1993 and 1994. As already stated, this population (1993 59 pairs) was strongly associated with uncultivated Wild Rice *Zizania palustris* stands in shallow bays of the lake. She

gave a more precise description of colony breeding in the species. The mean inter-nest distance for nearest neighbour at Whitefish Lake was 27.2 m, range 1.5–185.0 m ($n = 148$ nests). Wheeler (2001) considered this population to be semi-(or loosely-) colonial.

2. Definition of avian coloniality

Nesting colonies can be defined as a place where a number of individuals or pairs nest at a more or less centralized location from which they recurrently depart in search of food. Nests or territories at the centralized colony site occur in a relatively small area, whereas foraging normally occurs outside that area (Wittenberger and Hunt 1985). This definition includes true as well as semi-colonies and serves well as a working definition.

3. True colonies

True coloniality, in which the birds nest together as a result of social attraction between conspecifics, in the Podicipedidae family only occurs in the Podicipedini-*Poliiocephalus* clade. It has evolved in 9 of 13 species of this clade [in the Hoary-headed Grebe *Poliiocephalus poliiocephalus*, the five eared *Podiceps* species (Black-necked Grebe *Podiceps nigricollis* and its four South American relatives), the two swan grebes (Western Grebe *Aechmophorus occidentalis* and Clark's Grebe *A. clarkii*) and perhaps in the Great Grebe *Podiceps major*] (Vlug 2012).

In true colonial grebes such as Black-necked *Podiceps nigricollis* and Hoary-headed Grebes *Poliiocephalus poliiocephalus*, the nest site selection is highly social, with the initial nests serving as epicentres from which the colony grows outward. The birds may show synchronization of egg-laying caused by the interaction of conspecifics. Nest-building activities, platform-courtship and promiscuous mating may promote this synchronization (Vlug 2012).

The true colonial grebes are more peaceful than the territorial and semi-colonial species. Unlike the Red-necked Grebe, aggression in the true colonial species is only released at short range and mainly comprises unritualized, mobile attack-escape sequences (Fjelds  1982b, 2004). The Hoary-headed Grebe and the species of the eared *Podiceps* group deviate from the territorial grebes by a simplification of agonistic behaviour (behaviour relating to combat), which is very likely conditioned by colony breeding. Stationary threat in Forward-display, typical of Red-necked Grebes and other territorial species, is suppressed, and Token-dives miss completely (Fjelds  1982b, 2004).

4. Semi-colonies

Semi-colonies are nesting aggregations in which the individuals are independently attracted by a particular environmental feature. Even the most fiercely aggressive territorial grebes, such as Red-necked, Great Crested and Slavonian Grebes, are able to breed in semi-colonies (Vlug 2012).

In a number of large lakes, semi-colony formation may be explained by a lack of nest-sites and an abundance of food. In such lakes the grebes often have to breed in inferior habitat and frequently lose their clutch or young. However, some semi-colonies of Red-necked, Slavonian and Great Crested Grebes are located in breeding waters with alternative nest-sites, and occupy relatively rare, high-quality habitat (Vlug 2012).

During 1995-98 Nuechterlein *et al.* (2003) studied the dynamics of the nesting dispersion in a population of 80-100 Red-necked Grebe breeding pairs on Lake Osakis, a large, wind-blown lake in central Minnesota. The grebe pairs on the lake were highly attracted to several large floating Lesser Bulrush (Narrowleaf Cattail) *Typha angustifolia* mats. These mats provided prime nesting habitat protected from waves and predators, which was chosen by nearly 40% of the breeding population. Most pairs establishing nests on these "islands" averaged 5-10 simultaneously active neighbours within 50 m, compared to pairs that established territories along the shoreline, most of which had no neighbours within 50 m. The semi-colonial Red-necked Grebes of this population gained selfish benefits from the relatively rare, high-quality habitat rather than from the proximity of conspecifics (Nuechterlein *et al.* 2003, Sachs *et al.* 2007) (see also 16.2.4).

In spring, the semi-colony formation in the Red-necked, Great Crested and Slavonian Grebes begins with a number of initial pairs vigorously defending large areas of the future colony site (this is in contrast to the initial pairs in true colonial grebes which only claim small areas). As additional pairs try to get a foothold, open fights are frequent. These fights sometimes last for several minutes. Red-necked Grebes breeding in a semi-colony engage in more overt aggressive behavioural interactions (threat, underwater pursuit, chase and fights) and spend more time conducting platform behaviour during the pre-nesting period than their solitary counterparts. As the pressure increases and becomes persistent, the initial ter-

ritory-holders cannot counter all the settlement attempts of numerous pairs and their resistance wanes. Aggression of the settled birds decreases during egg laying and after clutch completion. This reduction in aggressiveness has also been observed in territorial pairs, but the semi-colonial grebes tend to be more reluctant than solitary conspecifics to leave the nest vacant and unguarded from competitors and predators and permit other pairs to nest in between them. A gradual habituation to the close presence of established pairs occurs. When still more settlers come, they have to build ever closer to existing platforms, thereby contributing to a reduction of nest distances over time. Finally, the birds only defend the immediate vicinities of their chosen nest sites (Fjelds  1973d, Koshelev and Chernichko 1985, Klatt 2003, Nuechterlein *et al.* 2003, Fjelds  2004, Klatt *et al.* 2004, Konter 2008a, b, 2011).

5. Origins of coloniality in grebes

The breeding aggregations in Red-necked Grebes without obvious adaptations to the social environment suggest that these semi-colonies represent the earliest stages of coloniality (Sachs 1998, Sachs *et al.* 2007). Due to the study of the semi-colonies of Red-necked and Great Crested Grebes and many other studies, a preliminary hypothesis on the origin and evolution of coloniality in this family can be given (McAllister 1958, Fjelds  1973d, Nuechterlein 1975, Blinov *et al.* 1981, Fjelds  1981, 1982b, Vlug 1983, Burger 1984, Fjelds  1985, Koshelev and Chernichko 1985, Goc 1986, Moskal and Marszałek 1986, Fjelds  1988, O'Brien 1990, Storer and Nuechterlein 1992, Henriksen 1993, Boe 1994, Sachs 1998, Cullen *et al.* 1999, Stedman 2000, Vlug 2002a, Nuechterlein *et al.* 2003, Fjelds  2004, Klatt *et al.* 2004, Vlug 2005, Sachs *et al.* 2007, Konter 2008a, Vlug 2012):

The first grebes probably lived in a closed habitat, i.e. marshes with mosaics of aquatic vegetation and open spaces such as channels intersecting the reed marsh. It is very likely that they were territorial because it is generally agreed that territorial (solitary) nesting is the ancestral condition in birds. However, it is reasonable to believe that the first grebes sometimes nested in high densities.

The genus *Rollandia* is the oldest, most unspecialized ("primitive") branch in the extant grebes, and the two species of golden grebes indeed show highly territorial behaviour and sometimes a crowding together of the territories. It is perhaps justified to assume that the flexible

nesting dispersion of the golden grebes represents the ancestral state in grebes.

The earlier grebes gave rise to two main lineages, the Podilymbini and Podicipedini. The species of the Podilymbini (dabchicks and piedbills) retained the ancestral states, i.e. territoriality and a preference for breeding and feeding on open spaces in swamps. In their habitat the number of prey animals is restricted, and it is likely that natural selection preserved the territorial nesting system. Their solitary hunting may also be vital because they pursue rather big and agile arthropods and fish which likely are chased away if many grebes forage in the same area. The birds, especially the dabchicks, prefer to stay nearby cover of some kind, where they can hide themselves when in peril.

Most likely, the genus of white-haired grebes *Poliiocephalus* is basal to the Podicipedini lineage (swan grebes *Aechmophorus* and the *Podiceps* species). The Hoary-headed Grebe *Poliiocephalus poliocephalus* is the most gregarious grebe species.

The Podicipedini species and the Hoary-headed Grebe left the closed marsh habitat and went to the more open wetlands with (rather) large open foraging areas. The Hoary-headed Grebe and the eared *Podiceps* species (Black-necked Grebe and its South American relatives) do not actively pursue their prey like the dabchicks and piedbills. They are searchers and simply pick small slow-moving prey from the vast supply that is found in some wetlands. Their food items are easily caught and not a contested resource, show a rapid population turnover and a patchy occurrence. This eliminated the possible advantages of individual food exploitation and breeding on dispersed territories. The birds often feed in flocks and adopted true coloniality as a breeding system.

The remaining Podicipedini species, i.e. the swan grebes, the Slavonian (Horned) Grebe *Podiceps auritus*, the Great Crested Grebe and (to a much lesser extent!) the Red-necked Grebe, retained the ancestral pursuing feeding techniques and concentrate on fish (*Podiceps cristatus* and *Aechmophorus*) or take a mixed diet of fish and aquatic arthropods (*Podiceps griseigena* and *P. auritus*). They normally forage singly on larger open lakes. The two swan grebes nest in true colonies, but the Slavonian, Great Crested and Red-necked Grebes are highly territorial and only occasionally breed in semi-colonies.

When the Podicipedini species occupied large waters, a shortage of nesting sites or a scarcity of ideal sites in relation to the large feeding areas forced many of them to nest in aggregations (semi-colonies). Perhaps, the hostility here was not as great as in small pools because abundance of food seems to decrease the tendency to attack. At the beginning, coloniality in these birds had no beneficial component. On the contrary, there was a larger risk of nest parasitism, egg loss, intraspecific infanticide, ectoparasite transmission, etc. The individuals only gain selfish benefits from the relatively rare (high-quality) nesting habitat and not from the proximity of conspecifics. As already stated, it is possible that the semi-colonies of Red-necked and Great Crested Grebes represent the earliest stages of coloniality.

However, once semi-coloniality had arisen, adaptations were to expect to maximize the benefits and minimize the costs of the new social environment, thus a gradual development into true coloniality may be supposed. Among these secondary adaptations are a reduction of pugnacity and the development of breeding synchronization. The nest site selection became highly social.

Because of their specialization as foot-propelled diving birds, grebes are not very capable of pursuing and attacking predators. It may be assumed that gulls and terns were important in the origin of grebe coloniality. They not only provide an early warning system, but they also actively pursue predators and drive them away (Blinov *et al.* 1981, Nuechterlein 1981b, Fjeldså 2004, VlUG 2012). Grebes are often attracted to colonies of gulls and terns and may breed near the gulls in (semi-) colonies of their own. An example is the breeding population of *Podiceps cristatus* on Lake Braband, Denmark, in the period 1985-89 (Henriksen 1993). Great Crested Grebes nesting with a distance of 30 m of Black-headed Gulls *Larus (Chroicocephalus) ridibundus* usually formed groups (semi-colonies) of 3-36 nests, but grebes nesting at a mean distance of 240 m (range 60-560 m) from the gulls nested well dispersed and solitary.

Grebes in mixed colonies synchronized their breeding activities with those of the larids (Goc 1986, VlUG 2012). The grebes in these colonies were (and are) more successful in their reproduction than other grebes (Blinov *et al.* 1981, Burger 1984, Goc 1986, Salonen and Penttinen 1988, Henriksen 1993, VlUG 2012). If nesting together with larids was selected for, it is imaginable that

the transition from semi- to true coloniality in grebes took place (partly) in or near gull colonies (VlUG 2012).

16.2.6 Nesting Associations with Other Species

Nesting Association with Coots

Red-necked Grebes frequently associate with nesting Coots *Fulica atra* (Onno 1960, Makatsch 1974, Melde 1978, Buchko *et al.* 1995, Höser *et al.* 1998). In total, 31% of 55 Red-necked Grebe nests in the Oberlausitz, eastern Germany (Wobus 1964), 71% at Naurzum Lakes, North Kazakhstan (Gordienko 1980), and 80% in the Volga delta (Markuze 1965) were found near nests of *Fulica atra*.

The minimum interspecific nest distances were 0.38, 0.5, 1.0 and 1.1 m (Wobus 1964, Dittberner 1996, VlUG 2002a, Dittberner and Dittberner 2006), and the mean distance was 3.5 m in the Oberlausitz ($n = 55$ nests) (Wobus 1964), and 2.2 m in North Kazakhstan (Gordienko 1980).

Not only Red-necked but also Great Crested Grebes often nest near Coots (Onno 1960, Schifferli 1967, VlUG 1983, Goc 1986, Konter 2002). Although Coots may destroy and eat grebe eggs, or occupy grebe nests (Schifferli 1967, Borrmann 1969, Goc 1986, Kloskowski 2000, Konter 2002, Fjeldså 2004), it appears that the majority of the grebes in these associations join already settled and nesting Coots (Onno 1960, Wobus 1964, VlUG 2002a, Fjeldså 2004). The risk of losing eggs may be outweighed by the protection that the highly pugnacious Coots provide because of their fierce nest defence. The Coot accepts a zone of "armed neutrality" towards the larger grebe that can fight back (Fjeldså 2004).

Nesting Association with Mute Swans

The nests of Red-necked Grebes are occasionally found near the nest of a Mute Swan *Cygnus olor*. The minimum interspecific nest distance in Schleswig-Holstein was 1 m (VlUG 2002a).

Nesting Association with Black-necked Grebes

There are reports of Red-necked Grebe nests in Black-necked Grebe *Podiceps nigricollis* colonies, e.g. on the Felchowsee (Lake Felchow) in the Uckermark (minimum interspecific distance 2.8 and 4.5 m) (Dittberner 1996, Dittberner and Dittberner 2006), on the Ruppertsdorfer See (Lake Ruppertsdorf) in Schleswig-Holstein (Koop 1998, VlUG 2000), and in the western part of the Ukraine (Buchko *et al.* 1995).

Nesting Association with Great Crested Grebes

Although Great Crested Grebes may occasionally displace Red-necked Grebes from the breeding site (Spletzer 1974) or force them to abandon their nest with eggs (Kloskowski 2000), the two species sometimes nest close together. In water bodies from which the adult Red-necked and Great Crested Grebes make foraging flights to the Baltic Sea, the minimum interspecific nest distance was only 2 metres (the minimum distance between 2 active Red-necked Grebe nests there was also 2 metres, see 16.2.5) (Vlug 1998).

In May 2014, three Red-necked Grebe nests, together with five nests of the Great Crested Grebe, were found on the edge of a small island with a Black-headed Gull *Larus (Chroicocephalus) ridibundus* colony in the Sulsdorfer Wiek, Schleswig-Holstein (R K Berndt, I Fahne, J J Vlug).

In Sachsen (Saxony), the distance between nests of *P. grisegena* and *P. cristatus* was quite often only a few metres (Höser *et al.* 1998). On the Zschornaer Teiche (ponds of Zschorna), Sachsen (Saxony), a Red-necked Grebe nest was found within a Great Crested Grebe colony in 1971, and another *grisegena* nest at a distance of 10 m from a *cristatus* colony in 1965 (Hummitzsch 1975).

Nesting Association with Western Grebes

Van Damme (2006) stated that six pairs of Red-necked Grebes nested within, or at the periphery, of a Western Grebe colony at Duck Lake, British Columbia, in 2006.

Nesting Association with Laridae and Sternidae

Red-necked Grebe pairs will sometimes nest within colonies of Black-headed Gulls *Larus (Chroicocephalus) ridibundus* or Black Terns *Chlidonias niger*, but the tendency to nest in association with small Laridae and Sternidae is much less marked than in the Black-necked Grebe (Vlug 2002a). Onno (1960) wrote that in Estonia the species avoids nesting within gull colonies. However, in other countries, e.g. Germany and Hungary, one or more pairs will sometimes nest within colonies of Black-headed Gulls or Black Terns (Hennicke 1903, Wobus 1964, Dittberner 1996, Dittberner and Dittberner 2006).

Von Homeyer (*cited in* Hennicke 1903) found some nests of the Red-necked Grebe, together with nests of the Black-necked Grebe, within a large Black-headed Gull colony on Velencei-tó (Lake Velence) in Central Hungary. The majority of the nests of *P. grisegena* were built at one side of the gull colony, and those of *P. nigricollis* at the other side.

As already stated, three Red-necked Grebe nests, together with five nests of the Great Crested Grebe, were found on the edge of a small island with a Black-headed Gull colony in the Sulsdorfer Wiek, Schleswig-Holstein. The minimum distance between a Red-necked Grebe nest and a gull nest was 1 metre (R K Berndt, I Fahne, J J Vlug). In the Uckermark, Brandenburg, the minimum distance between a *grisegena* and a Black-headed Gull nest was 3 m, and between a *grisegena* and a Black Tern nest 1.8 m (Dittberner 1996, Dittberner and Dittberner 2006).

Breeding associations between grebe species and marsh-dwelling gulls and terns appear to be common. The best documented cases are for the Black-necked Grebe, which maintains a world-wide association with gull and tern species occurring within its range, and for the Western *Aechmophorus occidentalis* and Clark's Grebes *A. clarkii*. Nuechterlein (1981b) studied Western Grebe colonies associated with Forster's Terns *Sterna forsteri* on the Delta Marsh, Lake Manitoba. Such colonies were impossible to approach undetected. The Western Grebes appeared to be "parasitizing" the alarm call system and aerial perspective of Forster's Terns. Playback experiments showed that the grebes discriminate the tern's alarm call from other common vocalizations, such as the basic call. During playbacks, however, no grebes showed the extreme alarm reaction seen during actual disturbances, i.e. leaving their nests, diving and leaving the colony area. This suggests that visual cues from the terns, such as mobbing behaviour, may be required to elicit a grebe's full alarm response (Nuechterlein 1981b). As a consequence of being limited to a water-surface perspective, breeding grebes appear to be using the above mentioned flight adaptations and aerial alarm system of gulls and terns to reduce their vulnerability to approaching predators (see 16.2.5 for more details).

16.3 Eggs and Clutches

16.3.1 Eggs

The eggs of the Red-necked Grebe resemble closely those of other grebes in general appearance and vary greatly in size, so that it is not always easy to identify them (Bent 1919) (see Fig. 94).

Colour of Eggs, and Surface Texture

The egg shell of Podicipedidae is light turquoise covered by a chalky white layer. Because of the porosity of this chalky layer, the eggs of Red-necked (see below) and

other grebes soon change colour from light turquoise to white, and then to buff and gradually various shades of rusty to earthy brown, depending on the kind of nest material (Fjeldså 2004).

The eggs of Red-necked Grebes are not glossy (Cramp *et al.* 1977). The colour is light blue, often fading to chalky white or dull white within 24 hours of being laid. Over several days, the eggs become increasingly stained and scratched by the wet nest material during incubation, sometimes to irregular dark tan, dark brown, reddish-brown, or almost black, depending on the composition of the nest materials (Wobus 1964, Cramp *et al.* 1977, Stout and Nuechterlein 1999; see photographs in Makatsch 1974, p. 399). Coues (*cited in* Shufeldt 1914) stated that the eggs are rough, whitish, either inclining to pale greenish or with “buffy” discolouration.

Bent (1919) wrote: “The color of the clean, freshly-laid egg varies from pale bluish white to “cartridge buff,” but the color, which is never quite pure, soon becomes partly or wholly obscured by muddy, dirty, nest-stains and the egg is often plastered over with mud and bits of nest material, giving it a dark mottled appearance. Much of this can be washed off, but the stains seem to be indelible.”

Eggshell

1. Eggshell weight

The eggshell weight (g) of the eggs of the Red-necked Grebe was:

Subspecies	Weight	Range	Author
nominate	2.95	2.43-3.55	Schönwetter (1967)
nominate	2.91	2.15-3.52	Makatsch (1974)
nominate	2.81	2.43-3.37	Rey, <i>cited in</i> Makatsch (1974)
nominate	3.23	2.57-4.12	Rosenius, <i>cited in</i> Makatsch (1974)
<i>holboellii</i>	3.25	3.09-3.83	Schönwetter (1967)
<i>holboellii</i>	3.57		Makatsch (1974)

2. Eggshell thickness

The eggshell thickness of eggs of the nominate race is 0.29 mm, and of *Podiceps grisegena holboellii* 0.30 mm (Schönwetter 1967).

The mean eggshell thickness of 112 eggs collected in Wisconsin before 1947 (pre-DDT period) was 0.357 mm, and of 2 eggs collected in the state after 1970 was 0.350 mm ($n = 2$); in Ontario, 0.338 mm ($n = 6$) (Faber

and Hickey 1973, *cited in* Stout and Nuechterlein 1999) (see 12.3.2 for more details).

Forsyth *et al.* (1994) found that eggshell thickness of Red-necked Grebes nesting in Manitoba declined significantly during the years following the introduction of DDT (post-1947) and had only recovered partially by 1983 (DDT was banned in 1972), whereas the Alberta population did not appear to have undergone any significant decrease in shell thickness (see the table with mean Ratcliffe indices below; these indices are highly correlated with shell thickness).

The mean Ratcliffe index of shell thickness [weight (mg)/length x breadth (mm)] for 112 Wisconsin eggs collected before 1947 was 1.84. In 1970, 3 Wisconsin eggs had a mean Ratcliffe index of 1.62 (Faber and Hickey 1973, *cited in* Stout and Nuechterlein 1999).

The average Ratcliffe index for 29 Red-necked Grebe eggs collected in Turtle Mountains, Manitoba, in 1980-81 (1.72) was significantly less than the Ratcliffe indices for 112 eggs collected in Wisconsin prior to 1947 (mean 1.84) and for 186 eggs collected in central Alberta in the early 1970s (mean 1.86) (De Smet 1987).

Mean Ratcliffe indices of Red-necked Grebe eggs from Manitoba, Saskatchewan and Alberta before, during and following the ban of DDT use in North America (Forsyth *et al.* 1994) were:

Period	Manitoba	Saskatchewan	Alberta
Pre-1947	1.80 ($n = 33$)	1.78 ($n = 19$)	1.82 ($n = 29$)
1948-71	1.49 ($n = 10$)	1.56 ($n = 10$)	1.85 ($n = 253$)
1972-83	1.70 ($n = 31$)	1.79 ($n = 46$)	1.84 ($n = 77$)

Substantial eggshell-thinning, cracking of eggs, inviable eggs and high mortality during hatching were primarily attributed to high levels of PCBs, DDE, dieldrin, and other organochlorines in the eggs of Red-necked Grebes in North America. Especially studies conducted in Central Alberta in 1971-1976 and in Southwest Manitoba in 1980-81 suggested that the effects of organochlorine contaminants contributed to a reduced productivity of Red-necked Grebes (Riske 1976, De Smet 1987, Stout and Nuechterlein 1999) (see 12.3.2 for more details).

3. Eggshell structure

The eggshell of Podicipedidae is covered by a chalky white layer of calcium phosphate, as in flamingos, and

unlike the porous outer layer in pelicaniform eggs, which is of carbonate (Fjeldså 2004). Spheres of a nut-like morphology – a “kernel” formed from spherules contained in a “shell” of globular sub-units – are a unique feature of the phosphate-rich cover on the eggshells of Red-necked Grebes and (at least five) other grebe species (Board *et al.* 1984). Investigations showed that the spheres did not give a pattern with X-ray diffraction; the innermost ones were embedded in the dense crystalline layer on the outer surface of the calcitic portion of the shell. Electron-probe microanalysis revealed that the cover of spheres contained principally oxygen, calcium, phosphorus and sulphur, and infra-red analysis demonstrated the presence of phosphate. The outer surface of the stratum of spheres was bounded by a thin, fissured layer of amorphous material (Board *et al.* 1984).

When eggs of American Coots *Fulica americana* and of Grey Leghorn Chickens *Gallus gallus* were incubated in contact with liquid water in the laboratory, they increased in mass, whereas Black-necked Grebe eggs, incubated under the same conditions, decreased in mass. When eggs of grebes and chickens were placed in contact with a solution of methylene blue, the contents of the chicken eggs were stained blue, whereas the contents of the grebe eggs were not stained. When chicken eggs were incubated in nests of Black-necked Grebes, they increased in mass and rotted; Black-necked Grebe eggs in the same nests declined in mass and did not rot (Sotherland *et al.* 1984). In contrast to liquid water, water vapour conductance of grebe eggshells is large. Eggshell water vapour conductance in Pied-billed Grebes was 2.7 times greater than for other bird eggs of similar mass and incubation period. This high vapour conductance is the result of a threefold increase in pore density (Davis *et al.* 1984). These data show that the grebe eggshell layer acts as a barrier to diffusion of liquid water, yet still permits a rapid exchange of water vapour. The eggshell structure shows adaptations to wet nests.

We must conclude from the work of Sotherland *et al.* (1984) that it is not simply asphyxiation (lack of oxygen) that is potentially dangerous for embryos of grebes: microbial contamination is also a problem. Eggs can be contaminated by bacteria (rotting) and their route is through the egg’s pores. Micro-organisms are most effectively transported in water so waterproofing the eggshell is what keeps microbes at bay. The waterproofing has to be done in a way that still allows the embryo

inside the egg to breathe and this is achieved by covering the pores with shell accessory material, and most effectively by a layer of microscopic spheres which creates a surface that by its physical nature repels water and hence is unwettable (Board *et al.* 1984, Birkhead 2016).

Shape of Eggs

All eggs of Podicipedidae are biconical; they are fusiform to elliptical or sub-elliptical, in contrast to most other bird eggs, which have a round and a more pointed end (Fjeldså 2004).

The eggs of Red-necked Grebes are variably shaped, long elliptical to sub-elliptical (usually intermediate), with a biconical tendency (Palmer 1962, Harrison 1975, Baicich and Harrison 1997, Stout and Nuechterlein 1999, Harrison and Castell 2002). Bent (1919) stated that in shape the eggs vary from nearly ovate to elliptical oval, elongate ovate or to nearly fusiform (Bent 1919).

The mean radii of curvature of the ends of North American eggs are $11.40 \text{ mm} \pm 0.86$ and $8.38 \text{ mm} \pm 0.80$ SD. The elongation is $1.54 \text{ mm} \pm 0.067$ SD; the bicone is -0.155 , and the asymmetry $+0.129$ ($n = 20$, 1 egg/clutch) (Palmer 1962).

Length and Breadth Measurements of Eggs

1. *Podiceps grisegena grisegena*

The length and breadth (diameter) measurements of the nominate subspecies *Podiceps grisegena grisegena* in different areas (mm) were:

Area, Author	<i>n</i>	Mean	Max.	Min.
Palaearctic, Hartert (1912-21)	100	50.65 x 33.99	57.0 x 35.5 55.4 x 36.5	46.7 x 33.8 50.0 x 30.0
Palaearctic, Schönwetter (1967) *	100	51.0 x 34.2		
Europe, Harrison (1975)	?	50.6 x 34.9		
Central Europe, Makatsch (1974)	80	50.52 x 33.97	54.9 x 32.2 49.6 x 37.1	46.4 x 34.3 49.1 x 30.7
Uckermark, Germ., Dittberner and Dittberner (2006)	305	52.85 x 37.23	57.2 x 34.0 49.7 x 39.9	44.1 x 31.1 51.4 x 30.4

* Schönwetter (1967) wrote that the length ranged from 46.7-58.0 mm, and the breadth from 30.0-37.3 mm.

Area, Author	n	Mean	Max.	Min.
Oberlausitz, Germ., Wobus (1964)	162	50.2 x 34.5	55.4 x 35.2 52.3 x 36.8	44.4 x 31.8 47.0 x 31.6
Sweden, Rosenius, <i>cited in</i> Makatsch (1974)	99	52.31 x 34.58	58.0 x 35.0 51.0 x 37.5	46.0 x 34.7 49.8 x 31.0
Finland, Sandman, <i>cited in</i> Hennicke (1903) **	29	53.52 x 35.26		

** The mean egg size in northern Europe is probably somewhat larger than in other European areas (but cf. Dittberner and Dittberner 2006, Uckermark).

2. *Podiceps grisegena holboellii*

The eggs of *Podiceps grisegena holboellii* are on average slightly larger than those of the nominate race. The length and breadth (diameter) measurements of the subspecies *Podiceps grisegena holboellii* in different areas (mm) were:

Area, Author	n	Mean	Length (range)	Breadth (range)
East Asia, Tacza- nowski, <i>cited in</i> Ma- katsch (1974)	14	53.9 x 35.5		
North America, Bent (1919)	60	53.7 x 34.5	49.0-64.5	30.0-37.5
North America, Palmer (1962)	20	55.74 x 36.10		
Astotin Lake, AB, Kevan (1970)	102	54.9 x 35.7	50-60	31-40
Turtle Mtns., MB, De Smet (1983)	923	54.3 x 35.8	45.3-62.5	32.5-39.5
Yellowknife, NT, Fournier and Hines (1998)	333	53.5 x 35.3		
Lake Osakis, MN, Stout and Nuechter- lein (1999)	192	54.4 x 35.9	49.4-60.3	32.2-41.1
Whitefish Lake, ON, Wheeler (2001)	327	54 x 35	45-59	24-39

The mean volume of 327 eggs from Whitefish Lake, Ontario, was 35.2 cc ± 3.9 SD (range 15.1-46.1) (Wheeler 2001).

Variation in Egg-size, Intra-clutch Variation

Kevan (1970) indicated that intra-clutch variation of the Red-necked Grebe on Astotin Lake, Alberta, was slight, the greatest difference in length being 7 mm and in width 5 mm. But De Smet (1983) remarked that these figures were quite substantial, however, when compared to the maximum length and width variance in her entire sample (10 mm and 9 mm, respectively). In the Turtle Mountains, Manitoba, maximum intra-clutch variation in length (13.25 mm) was more pronounced than maximum intra-clutch width variation (4.25 mm). Among 135 Red-necked Grebe clutches with 4 or more eggs, intra-clutch variation in length averaged 3.6 mm (SD = 2.27), compared to an average width difference of only 1.3 mm (SD = 0.82). One pair that consistently alternated between a small egg and a large egg throughout its laying cycle, had length differences of up to 13.25 mm between successive eggs and corresponding width differences of only 3.25 mm (De Smet 1983).

In Podicipedidae, most often the first-laid egg in a clutch has the smallest measures, volume and mass (weight) (egg mass is highly correlated with egg volume) (Forbes and Ankney 1988, Henriksen 1995), but apart from this, the pattern of egg-size variation is variable: the egg-size (volume) may increase in laying sequence in large clutches and the largest clutches had the largest eggs, while the opposite is often found in small clutches of the same grebe species, indicating clutch-size regulation by follicle resorption. Dissection of Slavonian (Horned) Grebes shot in the laying period suggest that 4-8 follicles in the ovary enter the final phase of rapid growth, compared with an average of 3.8 eggs laid for 770 complete clutches from Iceland and northern Norway (Fjeldså 1973d, 2004).

The positive correlation between clutch size and average egg size is even pronounced under poor feeding conditions (birds breeding in the poorest lake-types) and other severe situations. The volumes of initial and replacement clutches are uncorrelated, so in case of re-nesting a large clutch may be followed by another large clutch after a few days. All this (and other facts discussed below) suggests that the egg laying in grebes is not much constrained by energy reserves available to the female. This is in strong contrast to the situation in many other precocial birds, which lay larger eggs. In general, adult grebes may have relatively stable food reserves during the breeding season (Fjeldså 2004).

Mass (Weight) of Eggs, Yolk and Development Mode of Young

1. Mass (weight) of eggs

The weight (mass) (g) of (fresh) eggs was:

Subspecies	Weight	n	Author
nominate race	30.5 g	100	Schönwetter (1967)
nominate race	30.6 g		Makatsch (1974)
nominate race	25-32 g		Heinroth (1922)
<i>holboellii</i>	34.9 g	95	Schönwetter (1967)
<i>holboellii</i> , MN	32.3-44.2 g	13	Eichhorst, cited in Stout and Nuechterlein (1999)

The eggs of Podicipedidae are small compared with the size of the bird – 3-4% of the average female's body mass in large grebes to 6-8% for the smallest species (Heinroth 1922, Fjeldså 2004). In Red-necked Grebes, the egg mass is c. 4.5% (*Podiceps grisegena grisegena*; Heinroth 1922, Schönwetter 1967) and 3-4% (*P. g. holboellii*; Stout and Nuechterlein 1999) of the average female's body weight. In typical precocial (nidifugous) birds the egg weight is much higher: 14.2% of the female's body mass in Anseriformes (ducks, geese, and swans) and 17.4% in Charadriiformes (shorebirds). The figures of Podicipedidae (3-8%) are better comparable to those of altricial (nidicolous) birds such as Piciformes (woodpeckers and toucans) (6.6%) and Passeriformes (songbirds) (7.7%) (O'Connor 1984).

2. Yolk

The relative yolk size of Podicipedidae eggs is very small compared with precocial birds, c. 25% (Fjeldså 2004). In larger grebe species 22% of the egg-volume is yolk, in dabchicks 29-31% (Fjeldså 1977b). In the Red-necked Grebe 22% of the egg-weight is yolk ($n = 2$ eggs; one egg of 28 g had 6.3 g yolk, another egg of 32 g had 6.7 g yolk; Heinroth 1922). The yolk components do not increase proportionally with egg mass, and hence the energy content is poorly correlated with egg size (Slavonian and Pied-billed Grebes) (Arnold 1989).

In precocial birds the mean yolk content of eggs is 36.6% \pm 0.82 SE, and in altricial birds it is 21.8% \pm 0.65 SE (O'Connor 1984).

3. Development mode of young

The yolk of an egg provides the main reserves of food materials for the developing embryo and correspond-

ingly varies between species. Precocial (nidifugous) species have proportionally more yolk in their eggs than have altricial (nidicolous) species and the yolk itself is also rich in lipids. Since the eggs of precocial species are also unusually large for the species body size, the total yolk and lipid contents are substantially above those of altricial species. Part of this extra lipid fuels the greater developmental maturity of the precocial hatchlings and part provides the food reserve until they can find their own food (O'Connor 1985).

Although newly-hatched grebe chicks are covered with down (in fact the fine, terminal barbs of the still undeveloped feathers), grebes are not typical precocial birds because their eggs are small and do not have much yolk (see above). Podicipedidae show a relatively small energy investment in the eggs and are income breeders, i.e. they do not utilize (much of) their body reserves for egg formation, but use (mainly) nutrients acquired on the breeding grounds (Paszkowski *et al.* 2004, McParland *et al.* 2010, Kloskowski and Trembacowski 2015; but *cf.* Forsyth *et al.* 1994).

More facts indicate that grebes are not typical precocial birds. Newly-hatched grebe young can swim and dive feebly in case of need, but they do not voluntarily stay long in the water because they have an imperfectly developed endothermy and the short down isolates poorly; the chicks may soon become chilled. The badly developed endothermy of grebe young have not been studied in well-controlled experiments, but field observations indicate that they soon become sluggish if left in cold water (Fjeldså 1977b, 2004).

The significance of the relatively small energy investment in the grebe eggs is that the energy input is instead divided between both parents and spread over a considerable time – almost to the same degree as in altricial species. The reproductive strategy of grebes is probably related to their feeding habits: their feeding ecology requires some training (Fjeldså 2004). This is very unlike the situation in waterfowl, especially in diving ducks, which have large eggs and highly developed precocial young with excellent thermal independency. Their food is relatively easy to obtain even for small young and may be very abundant along the lakeshore. Such birds invest all their energy at once in large high-energy eggs, which give rise to autophagous chicks (Fjeldså 1977b).

It must be concluded that grebes do not have typical precocial, but semi-precocial (Stout and Nuechterlein 1999) or sub-precocial young (like rails, cranes and divers) (Gill 2007).

16.3.2 Egg-laying

Timing of Breeding

An important factor influencing the survival of young grebes is food, and the ultimate factor governing the timing of the breeding season is the availability of food for the nestlings. The parents must commence their breeding cycle much earlier than the period of peak food abundance, since there is a considerable interval between the commencement of breeding and hatching of the young. However, Red-necked and other grebes live in unstable habitats and the food supply can fluctuate from time to time and from water to water and is often unpredictable. Moreover, many other variables may influence the time of egg-laying. In the following text factors that are probably responsible for the pre-laying interval are discussed.

Pre-laying Interval or Pre-nesting Interval

The pre-laying interval (or pre-nesting interval, De Smet 1983) refers to the length of time from arrival on a nesting lake until clutch initiation. This interval is very variable. Even when Red-necked Grebes arrived paired, Wobus (1964) found that they delayed clutch initiation for about two weeks. Most birds begin later (Wobus 1964), and Red-necked Grebes in Schleswig-Holstein wait two to six weeks after arrival before laying eggs (J J Vlug). In the Turtle Mountains, Manitoba, the interval between arrival and clutch initiation was determined for 55 Red-necked Grebe pairs and ranged from 11 to 42 days (average 19.7 days) (De Smet 1983).

These data reveal that members of a Red-necked Grebe pair may remain together for weeks without being able to breed, waiting for opportunities to lay eggs. The birds show the ability to respond rapidly to local or temporal changes and opportunities for successful breeding. During the waiting period they often have to face serious competition from other grebes for their mates and sites (Simmons 1970b; J J Vlug). It is against such a background that the significance of the elaborate courtship of Podicipedidae needs to be assessed. The most intense and frequent Water-courtship occurs during the "engagement" phase, immediately following the initial pairing up, and especially during the establishment of

territory and the seeking of suitable nest-sites (however, cf. Stout and Nuechterlein 1999 in 15.3.2). The function of the Water-courtship is both bond-forming and bond-maintaining, keeping the pair intact until breeding can get underway (Simmons 1970b).

Long delays in clutch initiation dates in Podicipedidae have been attributed to several factors such as fluctuations in the food supply, high levels of intraspecific aggression, insufficient growth of emergent cover, delayed reproductive development of one-year-old birds, water level fluctuations and inclement weather conditions (De Smet 1983).

Vlug (1993) wrote that fish ponds with an outlet for water are normally drained in winter and replenished with water in spring, and because it takes some time before we find an abundance of arthropods in these newly filled ponds again, egg-laying of *Podiceps grisegena* here begins later than in natural ponds.

Two factors that were probably responsible for delays in clutch initiation dates in the Turtle Mountains were intraspecific aggression and high winds. Intraspecific aggression probably contributed to significantly longer delays in clutch initiation for 32 Red-necked Grebe pairs that nested near one or more other pairs (mean 21.5 days after arrival) than for 23 isolated pairs (mean 17.1 days). Behavioural observations at dense-nesting sites also indicated that considerable interference occurred between pairs nesting near each other. High winds were also responsible for delays. On many occasions, completed platforms were destroyed by waves during 1 or 2 days of high winds. Following this, most Red-necked Grebe pairs initiated construction of a new platform in a more sheltered portion of their territory (De Smet 1983).

Increased exposure to wind and waves may not always lead to delays in clutch initiation dates but may delay hatching dates. Clutch initiation dates were similar for Duck Lake (exposed to wind and waves), BC, and a marsh adjacent to Duck Lake (protected from wind and waves), but hatching dates were not. In both areas the females began egg-laying in the first days of May. The first eggs in the marsh hatched during the last week of May while the nests on Duck Lake did so 5 weeks later in the first week of July. All clutches in the marsh had hatched by mid-July, however in the lake hatching continued until mid-August. This was because all nests constructed on Duck Lake in May, prior to the build-up of substantial amounts of protecting Eurasian Water Milfoil *Myrio-*

phyllum spicatum, were destroyed by wave action, and the Red-necked Grebes had to produce replacement clutches. Nests in the marsh were anchored to Broadleaf Cattails *Typha latifolia*. A dense wall of these plants protected the nests from wave damage and a large number of the first clutches were successful (Ohanjanian 1986).

Fjelds  (2004) stated that late breeding of Podicipedidae (especially of *Podiceps auritus*) typically occurs at sites that were not occupied the previous year, or where the breeding failed. It may also be related to long borderline conflicts between neighbour pairs, but the number of clutches started per day during the main laying period is only moderately affected by bad weather: new clutches are started at an almost normal rate in periods with sleet and snow and temperatures close to zero, but clutch-sizes are reduced. However, Red-necked Grebes and other Podicipedidae sometimes abstain from nesting if the water levels are unstable.

Period of Clutch Initiation

The whole period of clutch initiation (for initial and replacement clutches) and the main period of clutch initiation (initial and replacement clutches) of Red-necked Grebes were:

Area, Author (<i>n</i> = number of clutches)	<i>n</i>	Clutch initiation, whole period	Clutch initiation, main period
<i>P. g. grisegena</i>:			
Schleswig-Holstein, Germ., Scholl (1974)	213	early April to mid-July	first half of May
Uckermark, Germ., Dittberner (1996)	204	late March to early July	74% late April to late May
SE Poland, Kloskowski (1999, 2000)	154	late April to early July	76% in May (<i>n</i> = 102)
Estonia, Onno (1960)	66	early May to mid-June	88% mid-May to early June
West Ukraine, Buchko <i>et al.</i> (1995)		22 April to 3 June	77% first 3 weeks of May
<i>P. g. holboellii</i>:			
Astotin Lake, Alberta, Kevan (1970)	101	4 May to 2 July 1969	69% 11 May to 31 May
Turtle Mts., Manitoba, De Smet (1983)	219	4 May to 9 July	77% mid-May to mid-June
British Columbia, Campbell <i>et al.</i> (1990)	703	2 May to 15 August	58% 2 June to 20 June
Yellowknife, NT, Fournier and Hines (1998)	32	21 May to 21 June	84% 24 May to 5 June

In northern areas, the birds enter their nesting grounds on average much later than in southern areas, e.g. Red-necked Grebes reach their breeding waters in northern Sweden not until May (Larsen and Wirdheim 1994), and in central Yukon, the first birds, and the highest numbers, are seen in the third week of May (earliest 16 May 1996) (Sinclair *et al.* 2003); the main migration through the interior of Alaska is in mid-May (Kessel, *cited in* Stout and Nuechterlein 1999). Consequently, clutch initiation of Red-necked Grebes in northern areas is on average later than in southern countries. In Yellowknife, Northwest Territories, the first eggs were laid on 21 May (Fournier and Hines 1998), and in Yukon adults on nests have been noted from 19 May to 2 July, and thirteen nests with eggs were recorded from 24 May (1 egg, likely an incomplete clutch) to 23 June (Sinclair *et al.* 2003). Clutch initiation in Turtle Mountain Provincial Park, southernmost Manitoba, begins earlier (4 May) (De Smet 1983).

Behaviour During and Following Egg-Laying

There are no detailed descriptions of the egg-laying behaviour of *Podiceps grisegena* (see photographs in Sielmann 1981, pp. 154-5), but it seems reasonable to assume that this behaviour is the same as in Great

Crested Grebes. Wiechmann (1974) observed the laying process of *Podiceps cristatus*: "This begins when the female sitting on the nest suddenly raises and then quivers the closed wings a little without opening them. After one to two minutes this behaviour is replaced by treading movements of the feet (of the sitting bird, JJV). Although the bird does not raise herself at all, these movements slowly push her on to the edge of the nest, and any eggs already laid become visible. When her cloaca is approximately above the nest hollow, rhythmic movements of the orifice indicate that the egg is coming, which then appears as a bright whitish-green patch in the widening cloaca. Slowly, almost hesitatingly, the egg is squeezed out (...); deposition occurs after more than half a minute of intensive pressing.

Because part of the upper femur, as in all grebes, is developed in such a way that the legs protrude far back on the body, the cloaca is lifted so much when the bird is lying on the nest that the egg is ejected horizontally.

Once the egg is laid, the female raises herself and beats her wings, only half open, for one or two minutes (...). After a further period of standing over the nest hollow, she slips into the water. She may resume incubating after she has jumped up on to the nest platform again, or she may leave this to the male; in the latter situation she accompanies him to the nest, as if to reassure herself that laying has been successful."

Egg-laying Interval

Most grebe species lay eggs at intervals of one day, although they sometimes skip a day. Red-necked, Slavonian (Horned), and Great Crested Grebes more often lay every other day (Fjelds  2004). Eggs can be laid at any time of the day but most usually in the morning (Wobus 1964, Fjelds  2004). The clutch of Red-necked Grebes is normally completed in 3–10 days (Vlug 2002a).

1. Egg-laying interval in *P. g. grisegena*

Cramp *et al.* (1977) wrote that the eggs of Red-necked Grebes are laid daily, but Harrison (1975) stated that the egg-laying interval between successive eggs is 2 days. Wobus (1964) always found an interval of exactly 2 days, even in cases of great disturbance. Kloskowski (1999) noted that the eggs appeared in the nests at 1-2 day intervals.

2. Egg-laying interval in *P. g. holboellii*

Baicich and Harrison (1997) stated that the eggs of *holboellii* are laid at 2 day-intervals. However, De Smet

(1983) wrote that in the Turtle Mountains, Manitoba, the egg-laying interval for Red-necked Grebes frequently was less than 2 days. In this area, several instances were noted where new eggs appeared every 1 to 1.5 days. This was best illustrated by a pair on Breadon Lake that produced a 6-egg clutch in less than 6 days and produced 2 eggs in between nest checks 22.5 hours apart. In many instances, the egg-laying cycle in Turtle Mountains was reduced by at least 1 day (i.e., 4-egg clutches were laid in 5 days, 5-egg clutches in 7 days, and 6-egg clutches in 9 days). Rarely was the egg-laying interval extended beyond 2 days. In some instances where extended intervals were noted, this was followed by a spurt in egg production (2-3 eggs appearing in rapid succession). On other occasions, the entire cycle was prolonged (De Smet 1983).

Indeterminate Layer, Replacement Clutches, Replacement of Eggs in Partially Destroyed Clutches and Late Additions of Eggs

1. Indeterminate layer

Red-necked Grebes and other Podicipedidae are indeterminate layers, and they continue to lay eggs to replace those removed from the nest. A new clutch can be initiated a few days after a breeding failure (replacement clutch). Slavonian (Horned) Grebes, which repeatedly lose their clutch, may lay 50 eggs in one season (Fjelds  2004).

2. Replacement clutches

Many Red-necked Grebe pairs fail in their initial nesting attempts, but after the complete loss of a clutch, most pairs initiate at least one and up to 5 replacement clutches, generally (but not always) in a new nest (Wobus 1964, De Smet 1983, Stout and Nuechterlein 1999, Vlug 2002a). When marked pairs on Lake Osakis (Minnesota) lost their clutch, they produced a new clutch from zero to four times. Of 91 marked pairs that failed in their first attempt, 70% began a second attempt, and of the 32 that failed a second time 71% tried again. The number of pairs attempting a fourth time was much lower (39% of 23 pairs), and only four pairs tried a fifth time (three of these hatched young) (Nuechterlein *et al.* 2003).

On Pine Lake, Central Alberta, lost clutches of Red-necked Grebes were replaced as late as the second week of July. Using marked indicator eggs, Riske (1976) found at 70 nest sites observed from 13 May to 22 July 1972 that 93 clutches (and sometimes nests) were destroyed

by wind and/or abandoned, i.e. more than one clutch of some pairs was destroyed during this 10-week period; indeed, one pair had its clutch destroyed by wind at least four times in succession and laid a total of 16 eggs. Altogether only one early nest (i.e. clutch completed by mid-June) remained intact to produce young in 1972, whereas five of 20 nests initiated after mid-June were successful. This ability to re-nest reasonably successfully after mid-June following bad weather in early summer is obviously an important determinant in the survival of populations of *P. grisegena* in large lakes (Riske 1976).

In Turtle Mountain Provincial Park, Manitoba, 79 of 110 regularly observed Red-necked Grebe pairs failed in their initial nesting attempts during the investigation period of De Smet (1983); the majority (66 pairs = 83.5%) initiated at least 1 replacement clutch and 6 pairs produced at least 5 clutches during one nesting season. Among the 13 pairs that did not re-nest, 5 abandoned their nesting lakes soon after nest losses during May. The other 8 pairs that failed to re-nest were among the small percentage of pairs that started egg-laying in June, half of which lost their initial nests in July and probably failed to re-nest due to time constraints (see below) (De Smet 1983).

Kloskowski (2000) recorded 140 first and 52 replacement clutches in fish-ponds in South-East Poland in the period 1993-99. The mean date of the first egg in the first clutches was 11 May (median = 10 May), and the first replacement clutches were laid in the last ten days of May.

The percentage of pairs that re-nest following losses is high in the early nesting season and low at the end of the nesting season. Of the clutches lost prior to June, 92% were replaced, and between early and mid-June, 83% of the lost clutches were replaced. After 15 June, however, the percentages decreased sharply and almost none were replaced following losses later than 26 June. Among 7 re-nests initiated in early July, 6 were abandoned before clutch completion (Turtle Mountains, Manitoba; De Smet 1983).

Time between the destruction of a clutch and the initiation of a replacement clutch (replacement interval) is normally *c.* 7 days (Wobus 1964). The replacement intervals for Red-necked Grebes from the Turtle Mountains averaged 5.38 days but varied according to the stage of incubation during which the loss occurred. Losses incurred during the first week of incubation were replaced

in an average 4.8 days, whereas losses incurred during the second, third, or beyond the third week of incubation were replaced in average times of 5.5, 6.0, and 8.9 days, respectively (De Smet 1983).

When losses in the Turtle Mountains occurred during the first week of incubation, the laying cycle often was not interrupted, and the laying proceeded in a new nest within 1 or 2 days. When the destruction occurred near clutch completion, however, the last egg(s) were occasionally deposited on a nearby platform and were not incubated. Other pairs built a new nest for their final egg(s), and eventually supplemented these with eggs from the next laying cycle. Upon destruction of complete clutches, 4–10 days usually elapsed before the female began egg-laying again (De Smet 1983).

Only rarely is a successful replacement brood produced after the loss of *c.* 10 days old chicks (Uckermark, eastern Germany, Dittberner and Dittberner 2006).

3. Replacement of eggs in partially destroyed clutches and late additions of eggs

Replacement of eggs in partially destroyed clutches has been reported for Slavonian (Horned) (Ferguson 1977) and Red-necked Grebes. In Turtle Mountain Provincial Park, one or more eggs were added to at least 10 Red-necked Grebe clutches that incurred losses. However, continued incubation and replacement after partial clutch losses were not universal in the park. Abandonment occurred in at least 7 instances where partial clutch losses were incurred, usually when more than half of a larger clutch was suddenly decimated. When losses were more gradual, however, pairs often continued incubating even when only one egg remained.

Replacement following partial clutch losses was evident in at least 4 instances during the study of De Smet (1983). In 3 of these clutches, egg-laying began within a week after 3-5 eggs were lost, and 4 eggs were added. In the fourth instance, replacement commenced within a week after 6 or 7 eggs disappeared, but this clutch was destroyed soon after. In 6 other clutches that incurred losses of 1 or 2 eggs, however, the addition of a single egg well into incubation may not have been a deliberate attempt to replace former losses, but merely represent late additions (De Smet 1983).

Occasionally Podicipedidae add eggs to their clutch well after clutch completion. Although these late additions

are often assumed to be replacements for earlier losses, the research of De Smet (1983) indicated that this was not always the case. On 3 occasions, Red-necked Grebe pairs added a single egg 1-3 weeks after clutch completion despite no losses having occurred. Another *P. grisegena* pair with a 5-egg clutch reinitiated egg-laying about a week after completion, producing a final clutch of 8 eggs. The ultimate purpose of late additions to grebe clutches is not known. It has been speculated that these additions had a chance of contributing to overall production should most or all of the earlier eggs fail. Late additions to Red-necked Grebe clutches in the Turtle Mountains, however, were invariably deserted following partial clutch hatching or disappeared along with the remainder of the clutch (De Smet 1983).

Second Clutches and two Broods in a Season

Second clutches are clutches laid while the birds are raising some young from an earlier nest. A second clutch is an attempt to produce a second brood. Thus, a successful second clutch gives rise to a second brood.

The number of broods in a year varies greatly between the different species of grebes. Raising two or more broods per season is the rule among dabchicks *Tachybaptus*, pied-bills *Podilymbus*, and golden grebes *Rollandia*, and large young (if still tolerated on the territory) may help feed younger siblings. At the other extreme, Silvery *Podiceps occipitalis*, Junin Flightless *P. taczanowskii*, and Hooded Grebes *P. gallardoi* have only one clutch (as a rule with two eggs) per year, and often they will not even replace lost clutches (Fjeldså 2004).

In the Great Crested Grebe, the tendency to raise an extra brood is geographically highly variable. In some parts of the range second broods of this species may not occur at all, e.g. in Russia and the other countries formerly in the Soviet Union (Kuročkin 1985), but records of second broods of *cristatus* became quite common in Central and West Europe from c. 1960 onwards, with even some records of three broods (Kunz 1963, Prestt and Jefferies 1969, Leys and De Wilde 1971, Haafke 1983, Van der Poel and Ottema 1983, Kraak 1984, Van der Poel 1985, Fjeldså 2004, Rolls 2004, Vlug 2005, Berndt 2010).

Red-necked Grebes in Europe normally have one brood, and rarely two (Wobus 1961, Menzel 1971, Cramp *et al.* 1977, Melde 1978, Axelsson 1988, Dittberner 1996, Kloskowski 2001b, Vlug 2005, Dittberner and Dittberner 2006, Dietzen 2015). Of 163 breeding Red-necked Grebe

pairs in South-East Poland (period 1993-99), four attempted a second brood and two were successful (Kloskowski 2001b), and in Schleswig-Holstein (period 1969-2002) at least 36 *P. grisegena* pairs had a second clutch, and 27 of those pairs were successful in raising two broods in one season ($n = 10,349$ breeding pairs) (Vlug 2005). However, the figures in Schleswig-Holstein were undoubtedly higher than the data of Vlug (2005) suggest because multiple breeding is often difficult to detect.

In North America second clutches are also rare. In Alberta, Riske (1976) recorded two instances of a second clutch apparently being laid while the adults were accompanied by a partially grown young. In the Turtle Mountains, Manitoba, only one second clutch was recorded out of 110 pairs of Red-necked Grebes that were regularly observed (De Smet 1983).

Successful second broods of Red-necked Grebes in North America are apparently extremely rare, and Stout and Nuechterlein (1999) give only one record of successful double breeding and cite Mink and Gibson (1976). The last mentioned authors found a *P. grisegena* pair on a lake near Bottineau in North Dakota. In late May they saw a nest with seven eggs. Three chicks of this nest survived. A new nest was started on 7 July, and five eggs were present on 16 July. Unusually among grebes, incubation did not take place until the last of the five eggs was laid. The authors noticed that one of the young grebes from the first brood would incubate the eggs early in the incubation process, but it was chased from the nest by the adults when incubation was in its later stages. On 7 August all five eggs hatched. After hatching, the adults and second brood chicks left the nesting area immediately and were observed until the chicks were nearly full grown.

Peck (1999, *cited in* Sandilands 2005) reported that in 1998 a pair of Red-necked Grebes at Bronte, Ontario, apparently reared two broods.

Another record of a (possibly) successful second brood in North America is from Beaver Dam Marsh in Wisconsin in 2010. On this marsh one pair of Red-necked Grebes was discovered in 2010, and Bielefeldt (2011) saw two separate chicks of widely different hatch dates (about 55-60 days). Perhaps two nesting pairs were present, but it is also possible that the chicks resulted from a rare instance of successful double-brooding by a single pair of adults.

Red-necked Grebe pairs with second broods nest in breeding waters with an abundance of food and start their first clutch early in the season (cf. Berndt 2010 for *Podiceps cristatus*). Apparently, only early breeding on territories with abundant food allows grebe parents to overcome conflicting pressures resulting from overlapping parental investment in successive reproductive attempts (Kloskowski 2001b).

In Schleswig-Holstein, Vlug (2005) found birds with a second brood especially on newly created ponds and new natural ponds with a rich limnafauna (macro-invertebrates and small vertebrates), and in South-East Poland all pairs attempting a second brood nested on fry ponds with a high availability of tiny fish (Kloskowski 2001b).

Time appears to be an important constraint on the incidence of double-brooding (Wobus 1964, Kloskowski 2001b, Vlug 2005). Reasons for the brevity of the breeding season of *P. grisegena* remain unclear. Fish ponds stocked with tiny fish and (newly created) ponds with an abundance of arthropods and small vertebrates seem to constitute a good food supply until the end of the summer (Vlug 1996, Kloskowski 2001b). A plausible explanation supported by observations of early departures from the breeding grounds is that the timing of late broods interferes with an early move of the adults to favourable moulting areas (see 16.5.16).

The clutches of second broods are usually initiated when the young from the first broods are still dependent and usually 3-5, occasionally c. 6-7 weeks old (Wobus 1964, Kloskowski 2001b, Vlug 2002a, Dittberner and Dittberner 2006). However, the first brood young are sometimes much younger. Melde (1978) observed in Kamenz in eastern Germany in 1966, a female laying eggs in a new nest on the same days as her first brood chicks were hatching. The distance between the nests was 20 m. A few days later, the new nest was demolished by people. De Smet (1983) recorded a second clutch on Margaret Lake in Manitoba in 1981. The eggs from both clutches were laid in the same nest but laying of the second clutch commenced 1-2 days before hatching of the first. Unfortunately, this second clutch was destroyed soon after completion and the pair raised only one immature from the first clutch.

Raising young is costly to Red-necked Grebes and other Podicipedidae, and it is probable that the costs are paid through a longer inter-brood interval. Ulenaers and

Dhondt (1991) investigated the reproductive efforts of Great Crested Grebes. They calculated the reproductive effort of the first brood (the number of young hatched multiplied by the number of weeks they survived) and discovered that as the first brood reproductive effort was larger, the inter-brood interval increased significantly.

At the time when the young from the second brood hatch, the young from the first may still be partly dependent. Kloskowski (2001b) saw that in two *P. grisegena* families under observation, the first brood young were expelled from the natal territory 9-10 days after hatching of the second brood.

16.3.3 Parasitism

Intraspecific Nest (Brood) Parasitism

Cramp *et al.* (1977) and Palmer (1962) suspected that Red-necked Grebe clutches containing more than 6 eggs are laid by more than one female. However, a number of authors (e.g. Von Transehe 1965, Kevan 1970, De Smet 1983) concluded that Red-necked Grebe clutches with more than 6 eggs can be laid by one female. Von Transehe (1965) wrote that a solitary Red-necked Grebe pair on a small lake (without conspecifics) in Latvia had a clutch of 10 eggs. In all instances where 7-9 eggs constituted the complete clutch size during his study in Turtle Mountain Provincial Park, Manitoba, De Smet (1983) was reasonably certain that no dumping had occurred. A 9-egg clutch, for example, was produced by one of three pairs on Morins Lake during 1981. In this clutch, 10 eggs were laid at approximate 2-day intervals between 18 May and 4 June, but the seventh egg rolled out of the nest soon after it was laid. Daily observations revealed that this pair began continuous incubating soon after clutch initiation and allowed neither of the other Red-necked Grebe pairs onto their territory. Likewise, in other larger clutches produced during the study of De Smet (1983), egg-laying occurred at approximate 2-day intervals and no territorial breakdowns were observed. However, we must assume that large clutches sometimes and extremely large clutches always are the work of more than one female.

Although the frequency of intraspecific nest (brood) parasitism is possibly low in Red-necked Grebes, it is perhaps sometimes rather high in birds breeding in areas of great nesting density and in areas with many disturbances (see Black-necked Grebe below), but there are al-

most no observations which confirm a higher incidence of nest parasitism under such circumstances.

The observations and DNA work of Nuechterlein *et al.* (2003) suggested that intraspecific brood parasitism rates were quite low for nests of Red-necked Grebes on Lake Osakis, Minnesota. Only one of 20 eggs from eight clutches that were salvaged from females of known genotypes could not be attributed to the appropriate female. Nuechterlein *et al.* (2003) detected no increase in parasitism by birds nesting close together, but their sample sizes were small and not subjected to statistical analysis. They also had a sample of 11 eggs collected from nine clutches of genotyped females that they suspected were being parasitized, either because the clutch was unusually large or because more than one egg was laid in a 24-hour period. For these clutches, only 1 of 6 first or second-laid eggs was parasitic compared to 5 of 5 fourth-laid (or later) eggs. These results suggested that the later eggs of a clutch are more likely to be parasitic.

The ornithological literature gives a number of records of supernormal clutches, e.g. a clutch of 12 eggs on Whitefish Lake, Ontario (Wheeler 2001), and a clutch of 13 eggs on Astotin Lake, Alberta (Kevan 1970). In a nest located on a floating platform on Duck Lake, British Columbia, 25 eggs were laid in 1983 (Ohanjanian 1986). Due to the large number of eggs laid, many were knocked off or buried deeply in rotten material that had accumulated between the solid wood under-structure and the fresh material under the incubating adult. Although the nest was attended, some of the incubation was discontinuous due to the presence of fishermen nearby. This likely allowed other females the opportunity to dump eggs in the nest as the territory could not be guarded in the normal way.

Intraspecific brood parasitism or “dump-nesting” may be common in the least hostile colonial species such as Black-necked Grebes. Brood parasitism is well documented in this species and occurs in the majority of the colonies. Colonies with smaller distances among the nests show a greater rate of intraspecific brood parasitism and other disadvantages such as egg loss due to conspecifics and infanticide (Lyon and Everding 1996, Hill *et al.* 1997). Nest density might influence the frequency of brood parasitism because, when neighbours are near, Black-necked and other grebes are likely to spend significantly greater amounts of their time in ag-

gression, such as threatening, chasing, and attacking conspecifics than when neighbours are farther away. Coincident with a relatively high level of aggression and the confusion attendant with such behaviours, more opportunities may arise for a parasitic female to sneak onto a momentarily undefended nest.

Interspecific Parasitism and Mixed Clutches

Interspecific mixed clutches are only rarely found. Sometimes Red-necked Grebes lay an egg in a nest of another species. In the Uckermark, eastern Germany, two instances of Red-necked Grebe parasitism on active Coot *Fulica atra* nests were noted by Dittberner and Dittberner (1992), and one instance on an active Black-necked Grebe nest (Dittberner and Dittberner 1984). In all instances one Red-necked Grebe egg was found in a nest with eggs of the other species and none of these Red-necked Grebe eggs hatched.

Eggs of Great Crested *Podiceps cristatus*, Western *Aechmophorus occidentalis*, Slavonian *Podiceps auritus* and Pied-billed Grebes *Podilymbus podiceps*, Coots *Fulica atra* and Redheads *Aythya americana* (North America) were found in active nests of Red-necked Grebes (De Smet 1983, Stout and Nuechterlein 1999, Vlug 2002a, Dittberner and Dittberner 2006, Van Damme 2006).

Van Damme (2006) discovered on Duck Lake, British Columbia, that Western Grebes repeatedly laid eggs in the nests of Red-necked Grebes. On 7 July 2006 she found a Red-necked Grebe nest with three brown stained Red-necked Grebe eggs and two brown stained Western Grebe eggs suggesting that the eggs had been well incubated. A fortnight later the Red-necked Grebe pair of this nest was recorded with one Western Grebe and three *P. grisegena* chicks (see 16.5.17).

16.3.4 Clutch Size

The complete clutch size of the Red-necked Grebe is very variable. Palmer (1962) gave a range from 3 to 6, Makatsch (1974) from 3 to 7, Cramp *et al.* (1977) from 2 to 6 eggs, Stout and Nuechterlein (1999) from 1 to 9, and Vlug (2002a) from 1 to 7 eggs, but the upper limit is unclear, since larger clutches may be laid by two females. A number of authors (e.g. Von Transehe 1965, Kevan 1970, De Smet 1983) concluded that Red-necked Grebe clutches of up to 9 or 10 eggs can be laid by one female (see 16.3.3).

The largest normal clutch of the Red-necked Grebe may be three or four times as great as the smallest, a difference that transcends the variation in clutch size found in most birds (however, such a difference is also found in Great Crested and Slavonian Grebes).

The reason for the variation of the clutch size in Red-necked Grebes is not known. Factors contributing to the final clutch size are possibly the availability of food, population density, breeding strategy, inheritance, the birds' previous experience, behavioural coordination between the mates, success in establishing territories, latitude, and frequency of nest predation (*cf.* Lack 1968, Kevan 1970, Fjelds  1973*d*, Simmons 1974, Owen 1977, Perrins 1985, O'Connor 1991, Vlug 2005, Gill 2007, Kloskowski *et al.* 2012, Vlug 2012, Birkhead *et al.* 2014).

Kevan (1970) recorded that the nests on Astotin Lake (Alberta) with large clutches were usually farther than average from other nests. She suggested that this may indicate that Red-necked Grebes nesting farther from other grebes had larger territories which enabled them to feed with fewer disturbances from neighbouring pairs, and she believed that this points to the food locally available for the laying female as being the main proximate factor in determining how many eggs will form the clutch at any particular time. However, although laying eggs is never without fitness costs, females of Red-necked and other grebes show a relatively small energy investment in the eggs and do not utilize (much of) their body reserves for egg formation (the eggs are small and do not contain much yolk, see 16.3.1), and so it seems unlikely that the availability of food is an important proximate factor determining the clutch size. But the correlation between food supply and clutch size need not necessarily be direct, and it is possible that the current clutch size is correlated with the number of young most likely to survive later if the food conditions operating at laying continue at the time of hatching (Simmons 1974, Kloskowski 2003*a*). Thus, varying the number of eggs laid allows the parents to bet-hedge in an uncertain environment.

Probably, a number of female Red-necked Grebes in their second (or third) calendar year produce small clutches because they nest in less suitable habitats, have no experience and thus fewer prospects for raising young. Fjelds  (1973*d*) recorded that there is an overall positive trend between the food situation and average

clutch size in Slavonian (Horned) Grebes in Iceland and northern Norway – the fewest eggs being laid in poor lakes and pools. The smallest clutches were laid by pairs which were apparently excluded from the best sites, and then selected less suitable ones. The author concluded that the apparent tendency to lay few eggs on localities less favourable for rearing young is to a considerable degree explained, or at least much accentuated by, the exclusion of the subordinate categories (probably especially second calendar year birds) from the optimal breeding grounds. Fjelds  (1973*d*) supposed that low clutch sizes are not caused by physiological deficiencies, but that the actual mechanism is degeneration of follicles or inhibition of their full development in response to psycho-physiological mechanisms rather than inability to form them.

Kloskowski *et al.* (2012) discovered that male contribution to nest building was of primary importance in explaining the variation in clutch size in Red-necked Grebes. The authors suggested that male contribution to nest building provides the female with an indication of the male's paternal quality, the female adjusting the clutch size accordingly (see 15.3.2).

Many theories on the determination of clutch size are based on the outcomes of individual breeding seasons, rather than on lifetime reproductive success. The Red-necked Grebe probably has high annual survival rates, and one may speculate that there is a trade-off between reproductive effort and survival that maximizes lifetime success rather than success in any one breeding season. Red-necked Grebes whose clutch size corresponds to the maximum number of young they are able to feed, may end up so emaciated that their own life expectancy is reduced. So, it is possible that many birds produce a relatively small clutch because this is adaptive in the sense that it allows them to remain fit, and to go on reproducing themselves for many additional years. It may also be that they produce more competitive young in this way (*cf.* Williams 1966, Clutton-Brock 1991, Bennett and Owens 2002, Fjelds  2004, Vlug 2005, Birkhead *et al.* 2014). The mean clutch sizes of Red-necked (Ohanjian 1986) and Great Crested Grebes (Leys *et al.* 1969) making food flights are smaller than found in most other studies. This may be attributable to the greater energetic demands on the birds which must fly to forage for themselves and their chicks. By reducing the clutch size (and

number of chicks) the birds decrease these high costs of reproduction and increase their life expectancies.

Clutch Size of *Podiceps grisegena grisegena*

A warning must be given here: a number of authors not only use complete but also incomplete clutches for their calculations of the mean clutch size, which means that their data are not strictly comparable with those authors that only use complete clutch sizes in their calculations.

Bauer and Glutz von Blotzheim (1966), Makatsch (1974), Cramp *et al.* (1977) and Harrison and Castell (2002) claim that the nominate subspecies normally has a complete clutch of 4-5 eggs. However, the majority (80-90%) of the clutches in the Uckermark, eastern Germany (Dittberner 1996, Dittberner and Dittberner 2006) and in Estonia (Onno 1960) comprised 3-4 eggs (*n* = 237 clutches).

The mean clutch size of the Red-necked Grebe in the different areas in Europe and Western Asia was (*n* = number of clutches):

Area	<i>n</i>	Mean	Author
Lewitz, Mecklenburg-Vorpommern (Mecklenburg-West Pomerania)	95	3.93	Zimmermann (1987)
Uckermark, eastern Germany	193	3.41	Dittberner (1996)
Region around Leipzig, Sachsen (Saxony)	46	3.9	Höser <i>et al.</i> (1998)
Vejlerne, Denmark	413	3.02	Kjeldsen (2008)
South-eastern Poland	108	3.83	Kloskowski (2000)
Estonia	44	3.55	Onno (1960)
West Ukraine		4.09	Buchko <i>et al.</i> (1995)
Volga delta, Russia	(c.) 200	3.2	Markuze (1965)
Naurzum Lakes, Kazakhstan		3.27	Gordienko (1981)

The mean clutch size of the nominate species differs from area to area (range of regional means 3.02-4.09).

Clutch Size of *Podiceps grisegena holboellii* in North America

As in Europe, the data of mean clutch sizes of different authors are not strictly comparable (see above). Bent

(1919), Palmer (1962), Baicich and Harrison (1997) and Stout and Nuechterlein (1999) wrote that a Red-necked Grebe clutch in North America generally consists of four or five eggs. De Smet (1983) discovered that in the Turtle Mountains, Manitoba, 58% of the clutches had four or five eggs, and 22% six eggs (*n* = 100 clutches). However, Campbell *et al.* (1990) recorded that 18 % of the clutches in British Columbia consisted of two, 22% of three, 24% of four and only 13% of five eggs, which means that most clutches had 2-4 eggs (64% of 703 clutches).

The mean (complete) clutch size of the Red-necked Grebe in the different areas in North America was (*n* = number of clutches):

Area	<i>n</i>	Mean	Author
Yellowknife area, NW Territories	80	4.38	Fournier and Hines (1998)
British Columbia	703	3.50	Campbell <i>et al.</i> (1990)
Duck Lake, lake, British Columbia	55	4.07	Ohanjanian (1986)
Duck Lake, marsh, BC	57	3.25*	Ohanjanian (1986)
Astotin Lake, Alberta	77	4.62	Kevan (1970)
Pine Lake, Alberta	73	3.97	Riske (1976)
Potholes near Pine Lake, Alberta	13	5.46	Riske (1976)
Turtle Mountains, Manitoba	100	4.95	De Smet (1983)
Lake Osakis, Minnesota	111	4.3	Stout and Nuechterlein (1999)
Whitefish Lake, Ontario	214	3.7	Wheeler (2001)

* Ohanjanian (1986) suggested that the low mean clutch size of the birds breeding in the marsh near Duck Lake was perhaps partly due to the increased energy costs of foraging (food flights).

The range of regional clutch size means was 3.25-5.46. Vlug (2002a) suggested that the Red-necked Grebe in North America has on average a larger clutch size than the nominate in Europe.

Seasonal Decline in Mean Clutch Sizes

A seasonal decline in the mean clutch size of Red-necked Grebes has been widely reported (Onno 1960, Wobus 1964, Kevan 1970, Riske 1976, De Smet 1983, Ohanja-

nian 1986, Stout and Nuechterlein 1999, Dittberner and Dittberner 2006).

In the Oberlausitz, eastern Germany, the average clutch size of *P. griseigena* in April was 4.9, in May 4.0-4.3, and in June/July 2.5 to 3.3 eggs (Wobus 1964). In the Uckermark, eastern Germany, the average clutch sizes from April to early June were fairly constant (3.2-3.9 eggs, $n = 182$ clutches), but then, from the middle of June to early July, they declined sharply to 2.5-2.7 eggs ($n = 11$) (Dittberner und Dittberner 2006). The figures of Dittberner und Dittberner (2006) suggest that only breeders very late in the season (after the middle of June) lay reduced clutches. The data from the Red-necked Grebe in North America seem to confirm this opinion.

The mean complete clutch sizes for early (initiated during May or early June) and late (initiated after 15 June) Red-necked Grebes in different areas in North America was (data shown as mean \pm SD; n = number of clutches):

Area	n	Mean, SD	Author
Duck Lake, lake, British Columbia			Ohanjanian (1986)
Early clutch size	23	5.22 \pm 1.61	
Late clutch size	25	3.12 \pm 1.11	
Duck Lake, marsh, BC			Ohanjanian (1986)
Early clutch size	46	3.37 \pm 0.16	
Late clutch size	6	2.17 \pm 0.37	
Astotin Lake, Alberta			Kevan (1970)
Early clutch size	56	5.18 \pm 1.45	
Late clutch size	21	3.14 \pm 1.31	
Pine Lake, lake, Alberta			Riske (1976)
Early clutch size	27	4.85 \pm 1.04	
Late clutch size	46	3.46 \pm 0.95	
Turtle Mountains, Manitoba			De Smet (1983)
Early clutch size	86	5.13 \pm 1.22	
Late clutch size	14	3.86 \pm 1.17	
Lake Osakis, Minnesota			Stout and Nuechterlein (1999)
Early clutch size	78	4.6 \pm 1.3	
Late clutch size	33	3.5 \pm 1.1	

The reason for producing smaller late clutches in Red-necked Grebes is not known. Many species of birds in north temperate regions have seasonal variations in clutch size which may be adaptations to temporal variations in food supply. A small clutch later in the season could be the result of decreased availability to grebes of aquatic insect larvae of such groups as the dytiscid beetles, caddisflies (trichoptera), damselflies (zygoptera), and dragonflies (anisoptera). During proliferation of submergent aquatic vegetation as the summer progresses these prey organisms would become increasingly protected and the flying forms would also become unavailable to the Red-necked Grebes once they emerged as adults (Riske 1976).

It is also possible that late clutches are mainly produced by subordinate birds (especially grebes in their second or third calendar year?) which did not have the chance to obtain a territory earlier in the season, but later have the opportunity to occupy a nesting place because the dominant pairs with chicks relax their territorial defence. In response to the earlier exclusion from the breeding bird community, the subordinate grebes lay small clutches (*cf.* Fjelds  1973*d*).

Clutch Size of Replacement Clutches

After the complete loss of a clutch, most Red-necked Grebe pairs initiate at least one and up to 5 replacement clutches. In Sachsen (Saxony) the number of eggs in replacement clutches seems often smaller than in first clutches (H ser *et al.* 1998). Kloskowski (2000) wrote that the mean size of first clutches in south-eastern Poland was 3.89 \pm 0.87 ($n = 80$ clutches, range 1-6), and of replacement clutches 3.68 \pm 0.67 ($n = 28$ clutches, range 2-5). However, this difference was not significant.

In contrast to H ser *et al.* (1998) and Kloskowski (2000), De Smet (1983) recorded that replacement clutch sizes (in Turtle Mountains, Manitoba) tended to be larger than initial clutch sizes on any given date, but this tendency was not significant.

Wobus (1964) and Fjelds  (2004) discovered that early in the season Red-necked and Slavonian (Horned) Grebes laid not only large initial but also large repeat clutches, and late in the season they produced both reduced first and repeat clutches. In other words, according to these authors, the average repeat clutch is of the same size as the initial clutch, and the seasonal regression for initial clutches and re-nestings are perfectly parallel.

16.3.5 Egg Losses

Many Red-necked Grebes lose their eggs. In south-eastern Poland, 25.5% of the active nests were destroyed before hatching of any egg ($n = 196$ clutches) (Kloskowski 2000), as were 41% of the clutches on the Naurzum Lakes, Kazakhstan (Gordienko 1977). In the Uckermark, eastern Germany, 11% of the clutches were completely destroyed ($n = 205$ clutches), and among 713 eggs found there, 14.2% failed to hatch (Dittberner 1996).

Among 697 eggs found in regularly observed Red-necked Grebe clutches in Turtle Mountain Provincial Park, Manitoba, at least 550 (78.9%) failed to hatch (De Smet 1983), and of 544 nesting attempts that Nuechterlein *et al.* (2003) followed on Lake Osakis, Minnesota, 412 (76%) did not hatch one or more young. Wheeler (2001) discovered that the reproduction of the Red-necked Grebe population at Whitefish Lake, Ontario, in 1993 and 1994 was extremely low: 96% of 789 eggs failed, and only 4% (32 eggs) resulted in hatched young.

The egg losses are partially compensated by the production of replacement clutches (see 16.3.2). In south-eastern Poland, 83.4% of the breeding pairs ($n = 163$) hatched at least one egg (Kloskowski 2000), on Lake Osakis, Minnesota, 55.3% ($n = 132$) (Stout and Nuechterlein 1999), and in Turtle Mountains, Manitoba, 50.9% ($n = 114$) (De Smet 1983).

Egg Losses by Wave Action (see also 12.2.2)

Wave action during storms is a major cause of nest and egg losses in large breeding waters of Red-necked Grebes and other Podicipedidae, especially on wind exposed places without enough protective emergent growth. The damage to the nests and clutches caused by high waves can be countered to some extent by continuous and accelerated building, but these activities are often without success. Wave action not only causes egg losses, but may also kill large numbers of small chicks. Lake size and reproduction are often negatively correlated, because the destructive force of waves increases as the area of the lake grows (Vlug 1983, 2005).

Nuechterlein *et al.* (2003) studied a population of 80-100 breeding pairs of Red-necked Grebes on Lake Osakis, a large (2,537 ha), windblown lake in Minnesota. In every year of their study (1995-98), wave action caused by sporadic windstorms was responsible for the most failed nests (38% of the nest losses). After severe

windstorms, they saw that the nests were sunk or had disappeared, with the eggs sometimes located nearby on the lake bottom. The losses tended to be greatest early in the season before most new emergent growth was above the water level and able to act as a breakwater. Breeding Red-necked Grebe pairs arriving on Lake Osakis were highly attracted to several large floating Narrowleaf Cattail *Typha angustifolia* mats that had broken off and drifted away from the mainland to become "islands" snagged within rooted emergent beds. These mats provided prime nesting habitat protected from waves (and predators) that was chosen by nearly 40% of the breeding population.

Riske (1976) discovered a high negative correlation ($r = -0.85$) between the average wind-force (during May, June and July in 1970-73) and the mean numbers of larger young per *holboellii* pair on Pine Lake, Alberta. In 1971-76 the mean brood success (= percentage of Red-necked Grebe pairs raising at least one young) on this wind exposed lake was only 25% of 207 pairs, and the mean number of young raised per successful pair (= per family) was 1.37 ($n = 51$ families). In complete contrast to Pine Lake, the pothole-nesting birds (near Pine Lake) were almost immune to destruction of their nests by wind because of shelter afforded by adjacent topography and the small size of the water bodies, both of which contribute to preventing waves from being generated. The author found significant differences (at the 0.01 level) between the mean numbers of young produced per pair on Pine Lake versus the potholes near Pine Lake. In 1970-76 the mean brood success of the Red-necked Grebe on the potholes was 65% of 63 pairs, and the mean number of young raised per successful pair (= family) was 1.63 ($n = 41$ families). The potholes apparently were best suited for the production of young, whereas Red-necked Grebes that nested on lakes produced fewer young per pair as the size of water body increased ($r = 0.74$ for combined 1970-73). Riske (1976) concluded that increasing exposure to wind leads to a decrease in numbers of young per pair.

Ohanjanian (1986) studied Red-necked Grebes on Duck Lake, British Columbia, from 1982 to 1984. The population on this lake nested in the open on the lake. The nests were constructed on accumulations of submergent vegetation, principally Spiked Water Milfoil *Myriophyllum spicatum*. As the season progressed, the accumulations of Spiked Water Milfoil grew and effectively acted

as breakwaters damping the action of waves and protecting nests constructed in or behind them. Over the three years of the study of Ohanjanian (1986) complete clutches were found only in areas where accumulated milfoil was of high or medium density. Of 55 complete clutches found in milfoil on Duck Lake, 38.2% were in high density accumulations, 61.8% were in medium, and 0% were in low. All nests constructed in May of 1981-83, prior to the build-up of substantial amounts of milfoil, were lost. In 1984 milfoil did not accumulate on Duck Lake and all nesting attempts failed. Stakes driven into the substrate at fixed distances from 3 nests revealed that wind and waves could move nests. In addition, 2 nests were blown against the shore following a wind-storm in 1982.

Egg Losses by Predation (this topic is discussed in more detail in chapter 12.4.2)

Predators on eggs of Red-necked Grebes and other Podicipedidae include crows *Corvus*, gulls *Larus*, American Mink *Mustela (Neovison) vison*, Raccoons *Procyon lotor* and many other bird and mammal species.

Egg losses caused by predators vary from area to area, but low breeding success of the Red-necked Grebe is rarely attributed to depredation. On Astotin Lake, Alberta, egg predation was slight in 1968 and 1969; in 1969 approximately 1.1% of the eggs laid were lost to predators ($n = 212$ nests) (Kevan 1970). In 179 regularly observed Red-necked Grebe clutches in Turtle Mountain Provincial Park, Manitoba, 197 eggs (28.3%) were depredated, 13 eggs (1.9%) were deserted after an incubating adult was killed on its nest, and 6 eggs (0.9%) were deserted after partial clutch depredation. In addition, 75 eggs (10.8%) from regularly observed clutches were listed as “probably depredated” (De Smet 1983). At Whitefish Lake, Ontario, at least 64 (= 8.1%) of 789 Red-necked Grebe eggs were lost to predators (Wheeler 2001).

Egg Losses by Competition with Great Crested Grebes
In wetlands where Red-necked and Great Crested Grebes co-occur, abandonment of nests due to aggression by Great Crested Grebes may contribute to egg losses in Red-necked Grebes (Kloskowski 2000; J J Vlugg).

Egg Losses by Intraspecific Conflicts

Egg losses are also attributed to intraspecific conflicts. Sometimes, incubating birds can be driven away from their nests by neighbouring pairs (see Fig. 97). An incu-

bating bird disturbed by a threatening neighbour could possibly knock one of its eggs into the water as it hurriedly leaves its nest. High rates of intraspecific aggression are noted where nest densities are high and are believed to contribute to many eggs being found beside active nests at these sites (Kevan 1970, De Smet 1983).

Egg Losses by Destruction or Robbing of Nests by Man

There are reports of destruction of clutches of Red-necked Grebes in fish-ponds during the removal of the littoral vegetation in the breeding season, and of robbing of nests by humans (Markuze 1965, Kloskowski 2000, Dittberner and Dittberner 2006). Although the predation of eggs by man is only of local importance, it can sometimes cause serious losses, especially in fish-ponds.

The floating nests of Red-necked Grebes are vulnerable to boating activities; the wake generated by watercraft can sometimes wash eggs off nests (Semenchuk *et al.* 2007).

Egg Losses by Inviability of Eggs

Inviability of eggs is cited as a factor contributing to egg loss (Kloskowski 1999, 2000). In south-eastern Poland, 36 of 147 eggs (= 24.5%) in 33 clutches were undeveloped or addled (Kloskowski 1999). De Smet (1983) assessed the inviability of Red-necked Grebe eggs from the Turtle Mountains, Manitoba, by determining the eventual fate of 191 eggs from 58 successful clutches. Among these, 21.5% were inviable. Egg inviability appeared to be the primary cause for egg abandonment after partial clutch hatching by Turtle Mountain Red-necked Grebes. Among 44 eggs deserted after partial clutch hatching, 18 were addled or undeveloped, 9 had died during development, 7 were probably inviable (subsequent eggs in the clutch had hatched prior to their disappearance), and only 10 (22.7%) were viable.

At Whitefish Lake, Ontario, at least 51 (= 6.5%) of 789 Red-necked Grebe eggs were inviable (Wheeler 2001).

Egg Losses by Partial Clutch Abandonment

Desertion of the nest before all the eggs have hatched is frequently observed (Stout and Nuechterlein 1999). Not only inviable but also viable eggs may be deserted. In some nests, the deserted eggs hatched but the parents showed no interest and the chicks died (south-eastern Poland, Kloskowski 2003a).



Fig. 97: An incubating bird driven away from its nest by a neighbour. Photo: T Runge (Schleswig-Holstein)

Fig. 97: Ein brütender Vogel wird von einem Nachbarn vom Nest gescheucht.

Although the disturbance of adult birds during hatching may sometimes result in abandoning viable eggs (Wobus 1964), this is often not the case, and there is some evidence that the Red-necked Grebe has evolved asynchronous hatching and partial clutch abandonment as an adaptation to cope with food scarcity at hatching (Kloskowski 2003a) (see 16.5.1).

16.4 Incubation and Hatching

16.4.1 Skulking Behaviour of the Birds in the Period After Egg-laying

Prior to breeding, Red-necked Grebes and other Podicipedidae appear quite confident and usually behave conspicuously (with the exception of birds in areas where they are persecuted). A marked change in behaviour takes place around the time of egg-laying. During and after egg-laying, the birds suddenly become shy, seeking cover at the slightest suspicion of danger, and may live very secretly, only now and then vocalizing from their hiding place in the vegetation. Although the non-incubating birds may guard their territories from vantage points at the reed-border, much of the time is now spent in the vegetation cover. In this period, especially in over-

grown marshes, an accurate estimation of the number of birds is only possible with the help of playbacks of their calls.

The skulking habits of Red-necked Grebes in the period after egg-laying are described by Bäsecke (1948), Fjeldså (1977b), Lammi (1983), Vlug (1985), and Südbeck *et al.* (2005). Bent (1919), writing about *holboellii*, stated: "It is certainly one of the shyest of the water birds. Its hearing must be very acute; for only rarely could I surprise one in the marshes, when it would disappear instantly. What few birds I saw were generally swimming at a distance, singly or in pairs, often far out on the lake, where they always dove long before I could get within gunshot range. Only once did I succeed in surprising one on its nest and get a fleeting glimpse."

16.4.2 Brood or Incubation Patch

The brood patch is a patch on the belly of an adult bird that becomes (almost) naked and vascularized before egg-laying, against which the eggs are warmed during incubation. In both sexes of the Red-necked Grebe, one large (central) brood patch is found. This patch is elongated, and often covered by short down (Palmer 1962,

Stout and Nuechterlein 1999, Fjeldså 2004, Lea and Klandorf 2002) (see Fig. 98).

16.4.3 Start of the Incubation in Relation to Laying; Incubation Duties of the Sexes and Incubation Bouts

There are reports of Red-necked and Great Crested Grebes sitting more or less continually on the empty nest-platform several days before laying the first egg (Simmons 1955, Onno 1960, Wobus 1964). The incubation typically begins with the first laid egg, occasionally later (Onno 1960, Cramp *et al.* 1977, Kuročkin 1985, Stout and Nuechterlein 1999). Unusually among Red-necked Grebes, the incubation of a clutch in North Dakota did not take place until the last of the five eggs was laid (Mink and Gibson 1976).

Although it is true that incubation normally starts with the first egg, incubation of the first-laid one or two eggs is frequently voluntarily interrupted, and these eggs may be unattended (and uncovered) for hours, causing high losses to crows and gulls in the laying periods. Also later in the breeding period the eggs may be left unattended for up to one hour, especially during warm weather (Onno 1960, Wobus 1964, Fjeldså 2004). However, as a

rule the incubation is nearly continuous after the first eggs are laid (Stout and Nuechterlein 1999), and only disturbances may violate this continuity.

Male and female share the incubation duties and take turns in incubating the eggs. There is an exceptional record in Austria of a Red-necked Grebe paired with a Great Crested Grebe, taking turns in incubation (Dvorak *et al.* 1993).

Wobus (1964) reported that both Red-necked Grebe sexes in eastern Germany take equal shares in incubation, and that early in the incubation period, the bouts last *c.* 1-2 hours (minimum 4 minutes) and during the last period the bouts may be more than 6 hours (maximum 9 hours).

As in eastern Germany, the length of the incubation bouts of the Red-necked Grebe in North America is highly variable; shorter bouts were observed during hot weather (Stout and Nuechterlein 1999). In North Dakota, the mean incubation bout was 64.3 minutes \pm 38.5 SE for males, and 60.7 minutes \pm 32.8 SE for females (Garner 1991, *cited in* Stout and Nuechterlein 1999).



Fig. 98: Grebe lowering itself on to eggs. The brood (or incubation) patch is well visible. Photo: T Runge (Schleswig-Holstein)

Fig. 98: Taucher sich auf den Eiern niederlassend. Der Brutfleck ist gut sichtbar.

Chamberlin (1977) studied a pair of Red-necked Grebes in a marshy section of Cedarville Bay, Michigan, in 1975. He observed the incubation of the eggs for more than 150 hours and saw that the male incubated 41% of the time and the female 59%. In the morning and evening the female incubated 65% of the time, whereas during the middle of the day she was on the nest only 41% of the time. During all observations before sunrise and after sunset the female was on the nest, suggesting that she performed most of the night-time incubating. From day to day each sex tended to incubate at approximately the same times. As the birds adjusted to the incubation routine, the average duration of their individual attentive periods increased. The average incubation bout lasted 87 minutes during the first week of incubation but increased to 132 minutes during the second week with a corresponding decrease in the number of bouts per day from 10 to 7. The last few days of incubation were similar to the first days of incubation in that the mean duration of the incubation bouts decreased to 78 minutes and the frequency of changeovers increased back up to 10 per day.

16.4.4 Nocturnal Egg Neglect

Nuechterlein and Buitron (2002) placed miniaturized temperature loggers in Red-necked Grebe nests on Lake Osakis, Minnesota. These loggers revealed that 16 of the 32 monitored pairs abandoned their nests for extended periods lasting 3-9 hours during at least two of the three nights that they were monitored. The authors suspect that nocturnal egg neglect is being practiced in many other Red-necked Grebe populations throughout North America and Europe. By leaving their nests at night, the birds may be decreasing their exposure to nocturnal predators that prey on adults, such as American Mink *Mustela (Neovison) vison* and Great Horned Owls *Bubo virginianus*. Slavonian (Horned) Grebes have sometimes also been observed to leave clutches unattended for several hours during the night (Fjeldså 2004).

16.4.5 Behaviour of the Incubating and Off-duty Birds, Nest-relief (Changeover) and Settling Down on the Eggs

The Incubating Bird

As already stated, once true incubation is started (often after spasmodic brooding of the first one or two eggs), the eggs are normally incubated almost continuously, except for a minute or two at nest-relief or if the birds are disturbed. The incubating bird assumes the "pork-pie" attitude while resting or sleeping on the nest. However,

the grebe is always alert to danger and regularly holds its neck straight up and turns its head (see Fig. 95). Much time is taken up with preening and arranging nest material. At intervals the incubating grebe stands up poking the bill down among the eggs or moving plant material from the rim to underneath the eggs, thereby raising eggs and relining the nest cup. Should an egg get misplaced on to the edge of the nest, it is retrieved in the typical way: the grebe rolls it back by hooking the bill under it. This habit obviously reduces loss through the birds' unavoidable clumsiness (Simmons 1955, Vlug 2002a, Fjeldså 2004).

The Off-duty Bird

The non-sitting grebe spends its time mainly in seeking for food (for itself), in preening, in resting, and in visiting the nest. When feeding, it may have to leave the territory entirely. Red-necked Grebes nesting in small lagoons near the Baltic Sea regularly fly away to exploit the richer food supply in the marine coastal environment. This environment may have large quantities of food and therefore it may even pay off to make such flights for obtaining nourishment (Simmons 1955, Vlug 2002a, Fjeldså 2004).

The off-duty bird rests in the territory, often not too far from the nest site, sometimes in the same patch of cover, but usually at the reed-border, where it may guard the territory from a vantage point.

Nest-relief (Changeover) and Settling Down on the Eggs

In the majority of cases, the nest-relief is initiated by the off-duty bird. The birds approach the nest cautiously from the open water, swimming on the surface to the nest, usually with considerable head-bobbing movements, or approaching underwater, diving from 20-30 m away (Chamberlin 1977). The off-duty bird often brings and deposits some nest material, which will be arranged by the sitting bird, and if this bird does not rise up the off-duty bird continues to bring nest material. Most addition of material during the incubation period takes place in connection with changeover at the nest (Fjeldså 2004).

Chamberlin (1977) noted that during nest-reliefs the behaviour of the returning Red-necked Grebe appeared dependent not only on the strength of its own urge to incubate but also on the incubating bird's readiness or reluctance to leave the nest. Occasionally during extremely hot weather and after unusually long incubation bouts, the mere presence of the returning bird was sufficient to

induce the incubating bird to leave the nest. Wobus (1964) wrote that at the beginning of a nest-relief, the *P. griseigena* partners often face and perform Low Head-waggles while uttering the Display-call. Chamberlin (1977) recorded that Low Head-wagging by the returning bird was the dominant component of nest-reliefs and in most cases, it induced the mate to leave the nest. This Head-shaking was part of 49 (= 68%) of the 72 nest-reliefs observed by Chamberlin (1977). During the nest-reliefs in the first week of incubation, the returning bird showed Head-shaking as many as 6 times per changeover and often the incubating bird also participated in this behaviour. By the second week Head-shaking was primarily by the returning bird and only done once or twice per nest-relief. Chamberlin (1977) recorded that seven times when the female surfaced right next to the nest and face to face with the incubating male they both raised their necks up as tall as possible, crest plumes erect, and called loudly and simultaneously. The same display occurred twice when the incubating bird left the nest at the sight of the returning mate. The birds displayed and called as they swam towards each other and turned face to face as they passed.

If Head-shaking failed (in the Red-necked Grebe pair observed by Chamberlin) the returning bird often sat next to the nest (usually to the rear of the incubating bird) and performed comfort movements or poked at the nest for several minutes. When its mate still remained on the nest the returning bird made brief nest building actions. Twice the off-duty bird simply “gave up” after these attempts and left for a while; once the female jumped onto the nest forcing the male off (Chamberlin 1977). Wobus (1964) also recorded that, if the incubating bird does not leave, the partner may jump on the nest and pushes the incubating bird down.

Only a little time after the beginning of the final visit, the sitting grebe gets up, waddles down from the nest, and flops off into the water; it often preens, body-shakes, and flaps its wings as it goes (Simmons 1955; J J Vlug). Chamberlin (1977) noted that after each nest relief the departing bird spent 3-20 minutes (mean = 8) preening before it swam out through the vegetation to forage in the channel. Sometimes it very soon returns to add material to the nest before leaving again.

The relieving grebe almost immediately gets up on to the nest, after a moment of apparent hesitation, with a sudden leap. Often the nest starts to sway heavily (Simmons

1955, Vlug 2002a). Simmons (1955) described the nest settling phases of the Great Crested Grebe, but the Red-necked grebe shows exactly the same behaviour: standing on the near rim, the grebe arranges the nest material and gradually advances, with its feet well apart on the edge of the central depression, until directly over the eggs. It may poke its bill down among them. Finally, it heaves up its body, the head resting back on the shoulders, remains thus very full-chested for a very brief second, and then, opening its brood-patch, settles down on the eggs. The large brood-patch is exposed by the sudden parting of the thick white under-feathers (see Fig. 98). The grebe starts to shuffle its body from side to side as it lowers itself and this movement reaches its peak when the eggs are contacted. The bird settles, breast first, hind end raised a little with the feathers fluffed, and the wings droop slightly for a second, showing both white patches, before being flicked abruptly to a close (Simmons 1955; see photographs in Wobus 1964, pp. 74-5, and in Spillner 1970, p. 274) (see Fig. 96, 98 and 99).

16.4.6 Egg-turning

Many authors report egg-turning in Podicipedidae. It has been asserted that one function is to prevent diffusion pathways from being clogged by nest debris (Board *et al.* 1984). There are many observations of Red-necked Grebes standing up, curving the neck down and poking the bill down among the eggs, but Wobus (1964) wrote that real egg-turning is not confirmed by experiments with marked eggs. However, field observations of incubating Red-necked Grebes indicate that individual eggs are rotated completely at least once daily during early- to mid-incubation (Brua *et al.* 1996).

In an experiment with late-stage, pre-pipping embryos of Black-necked (Eared) Grebes, Brua *et al.* (1996) showed that these embryos vocalized more when turned than when at rest. According to the authors, grebe embryos that are about to hatch may signal their parents to turn the eggs, because positioning a piped egg upside down may suffocate the embryo in the sodden nest-material. Pre-pipped grebe embryos may vocalize more frequently when turned as a signal to their parents that they are viable and will soon hatch.

16.4.7 Egg-covering

From the onset of sustained incubation, the sitting grebe will quickly cover the eggs with nest material so that they



Fig. 99: A grebe inspecting nest and clutch. Note the large feet. Photo: T Runge (Schleswig-Holstein)

Fig. 99: Ein Taucher Nest und Gelege kontrollierend. Beachte die großen Füße.

are completely hidden from view at times. There is a misconception about this habit in Red-necked Grebes and other Podicipedidae: the eggs are not covered over when the bird leaves the nest for routine purposes but only after it has been alarmed by some enemy (Simmons 1955, Wobus 1964, Stout and Nuechterlein 1999, Fjeldså 2004). Simmons (1955) stated: "When disturbed the bird gets quickly up and, if it has time, covers the eggs over with very rapid right and left movements of the bill before flopping into the water. It may then dive right away, to lurk furtively about with neck awash, displacement-preening intermittently, or stay partly submerged in hiding near the nest – depending on the proximity of the predator. If, for some reason, the eggs have not been covered (for instance, the bird may have had virtually no warning but found the foe almost on it), one of the grebes will sometimes come back, if it can, specially to cover them before leaving again." Returning to the nest after a disturbance, the bird quickly uncovers the eggs, with rapid flicking movements. These movements are shown even if the bird had not covered the eggs when leaving the nest. This illustrates the "instinctive" nature of the behaviour (Fjeldså 2004).

The fact that the eggs are not covered when the bird leaves voluntarily suggests that its primary function is to conceal the eggs. A nest with covered eggs may resemble a random accumulation of plant debris (Simmons 1955, Wobus 1964, Fjeldså 2004).

It has been suggested that the egg-covering may slow the cooling of eggs when not incubated (Schiermann 1927) but given the high humidity of the nest material the effect may actually be the opposite if the weather is windy and cold. However, covering will prevent overheating of eggs through evaporative cooling during intense sunshine (Fjeldså 2004).

16.4.8 Incubation and Hatching Periods, and Hardiness of Eggs against Temperature Stress

The incubation period is the time required by embryos to develop in freshly laid eggs that receive normal attention by incubating parents. The incubation period is defined as the interval between the laying of the last egg of a clutch and hatching of that egg, whereas the hatching

period refers to the length of time required for any egg to hatch (De Smet 1983, Vlug 2002a, Gill 2007). There are not many data on the incubation period as defined above because the last laid eggs are frequently abandoned or disappear before hatching (De Smet 1983, Stout and Nuechterlein 1999, Kloskowski 2003a). In the ornithological literature incubation and hatching periods are often confounded, and frequently authors do not make clear which they are giving. This is unfortunate because these periods may be different.

The normal hatching period (for each egg) in Podicipedidae is three or just over three weeks, with little variation between the species, except a record of 18 days for the Silvery Grebe (Housse 1948, cited in Fjelds  2004). Fjelds  (2004) gives *c.* 23 days for Australasian Little, 20-21 for (Common) Little, 21 for Least, 21-27 for Pied-billed, 22-23 for New Zealand, 23-24 for Slavonian (Horned), 25-29 for Great Crested, 20-24 for Black-necked, and 22-24 days for Western Grebes.

Incubation and Hatching Periods in the Nominate Race

In the nominate race *griseigena*, incubation/hatching periods are reported of 20-23 days (Cramp *et al.* 1977), 21-24 days (Fjelds  2004), 22 days (Hortling, cited in Makatsch 1974), 23-24 days ($n = 2$ eggs) (Onno 1960), 23 days (in an incubator, *c.* 39.5  C) (Heinroth 1922), on average 25 days (Gordienko 1981), and exceptionally 27 days (Wobus 1964, Kuro kin 1985, Kloskowski 1999).

The incubation period in 41 clutches in south-eastern Poland in which the last-laid egg survived to hatching, ranged from 21 to 27 days with a mean of 24.0 ± 1.35 (SD) (Kloskowski 1999).

Incubation and Hatching Periods in *P. g. holboellii*

The ‘‘period of incubation’’ proved to be 22 or 23 days for eggs of *P. g. holboellii* which Bent (1919) hatched out in incubators. Kevan (1970) reported that in nests under observation on Astotin Lake, Alberta, the ‘‘incubation period’’ began with the first egg and continued for 23 days, and the ‘‘incubation periods’’ for 12 nests from British Columbia were also short, between 22 and 23 days (Campbell *et al.* 1990).

Hatching periods calculated by De Smet (1983) for 140 eggs from 52 successful clutches in Turtle Mountain Provincial Park, Manitoba, averaged 29.1 days (SD = 2.85). A modified incubation period (including hatching periods for the last-hatched egg from all successful nests),

averaged 29.0 days (SD = 3.06). Due to high rates of disappearance and desertion of eggs, however, the last egg hatched in only 11 nests. The average incubation period for these 11 nests was 27.6 days (SD = 2.76). De Smet (1983) concluded that the average incubation period for Red-necked Grebes in the Turtle Mountains was 28-29 days and considerably longer than that cited in the literature. However, Stout and Nuechterlein (1999) reported longer periods for 38 Minnesota clutches: 28.5 days \pm 2.3 SD (range 25-33, $n = 44$ eggs).

Variability of Incubation and Hatching Periods; Hardiness of Eggs Against Temperature Stress

The results from an incubator (22-23 days) represent the minimum time in which the eggs could hatch, because under natural conditions cold weather and disturbance by man and predators may protract the incubation and hatching periods. The variability of incubation and hatching periods may relate to local differences in mammalian predation pressure and nocturnal incubation abandonment patterns. As already stated (see 16.4.4), Nuechterlein and Buitron (2002) placed miniaturized temperature loggers in Red-necked Grebe nests on Lake Osakis, Minnesota, and discovered that many pairs abandoned their nests for extended periods during the night. They found that the incubation period increased if the eggs were often cooled by this nightly nest-abandonment. Extended incubation periods lasting 30 or more days were observed. The temperatures of the abandoned eggs usually dropped rapidly to below 30  C within 15-25 minutes and after this often approached or fell below 20  C. Yet the nesting success remained high, and the embryos appeared to be tolerant of this cooling. The authors suggested that Red-necked Grebes pre-emptively leave their nests at night to avoid predation on their eggs or themselves (Nuechterlein and Buitron 2002).

Not only the above mentioned study of Nuechterlein and Buitron (2002) but also other studies suggest that eggs are very hardy and able to survive low temperatures. Kloskowski (2003a) and Stout and Nuechterlein (1999) discovered that deserted eggs occasionally hatched 24 hours after the nest was abandoned by the parents, but the chicks were neglected and did not survive. The hardiness of embryos in eggs is clearly very different from the vulnerability of newly-hatched young, which are very susceptible to draughts and chilling.

Prolonged Incubation of Inviabile Eggs in Red-necked Grebes

Addled or infertile eggs may be incubated for over 1 month (De Smet 1983, Stout and Nuechterlein 1999, North America). Kloskowski (1999, south-eastern Poland) reported on non-viable eggs in 7 clutches being incubated for 34-36 days before abandoned.

16.4.9 Hatching

Hatching is to break through and emerge from the egg. Also, speaking of the egg, to break open as a result of the efforts of the embryo.

Hatching Intervals

As a consequence of the fact that the incubation typically begins with the first laid egg, hatching in Podicipedidae is asynchronous, but intervals vary greatly. The eggs in Red-necked Grebe nests usually hatch at two day intervals (Wobus 1964, Kevan 1970), occasionally daily intervals (Kevan 1970). However, Mink and Gibson (1976) observed a 5-egg clutch that hatched within a single day, and McAllister (1963) noted one instance where an entire 6-egg Red-necked Grebe clutch hatched within two days.

De Smet (1983) discovered that in the Turtle Mountains, Manitoba, the average hatching interval between successive eggs of Red-necked Grebe eggs increased from 1.1 days between the first two eggs, to 1.7 and 1.8 days from the second to the fourth egg, and to 1.9 days between successive eggs beyond the fourth egg. The first eggs within a clutch often hatched on the same day or at one day intervals. In some clutches in the Turtle Mountains, the first three eggs were found peeping simultaneously and on one occasion, the first 4 eggs hatched within a day and a half. De Smet (1983) noted that successive eggs rarely hatched at intervals exceeding two days. A number of authors attributed the difference in average hatching intervals before and after the second egg to discontinuous incubation prior to laying of the second egg (Simmons 1955, Wobus 1964, De Smet 1983).

Hatching-call, Peeping of Chicks in the Eggs

The chick breaks through the inner shell membrane and starts to peep loudly from inside the egg before hatching (McAllister 1963, Fjeldså 1977b). This Hatching-call ("Schlüpf laut" of Wobus 1964) is a short, sharp "jip" (or "iejp" or "pieh") (Wobus 1964). It is first given, at intervals of 1-2 seconds, for up to 2 days before and during

hatching. It is homologous to the "Squeak" of *Podiceps cristatus* (Cramp *et al.* 1977).

Heinroth (1922) suggested that the embryonic vocalizations are possibly an attempt to prevent the adult birds from deserting the nest before all young have hatched. A number of experiments are consistent with this hypothesis. Brua *et al.* (1996) investigated the vocal response of Black-necked (Eared) Grebe embryos to egg cooling and egg turning. They discovered that experimentally cooled late-stage, pre-pipping embryos vocalized more (more bouts of calls) than embryos exposed to normal incubation temperatures. The authors also showed that the embryos vocalized more when turned than when at rest. The embryonic vocalizations probably are multifunctional, but care-soliciting is one of their functions (see also 16.4.6).

Two other experiments revealed that embryonic vocalizations cause changes in the behaviour of adult Black-necked Grebes during late incubation (Brua 1996). In the first of these experiments a vocalizing egg was substituted in 14 nests, two days before the first egg in those nests was to begin vocalizing. In the second experiment, the incubation period was extended by two days; at that time a vocalizing egg was substituted in 15 nests. In response to the placement of peeping eggs in their clutch, the parents reduced the amount of rising and resettling and the time off the nest (while incubating), and increased the frequency of nest building, egg turning, and the time spent near the nest when not incubating. Parents also brought food to the nest in response to embryonic vocalizations (Brua 1996). So it seems very likely that embryonic vocalizations have a care-soliciting function.

Egg Tooth and Hatching Muscle

The embryo develops two structures, the egg tooth and the hatching muscle *Musculus complexus*, that aid the final escape from the egg. The hatching muscle in grebes is grossly similar in its morphology to the muscle in the chicken. However, in grebes the segments are much wider than long, and they extend farther laterally (Fisher 1961). The massive development of the muscle is transitory, the muscle is not. Fisher (1961) believed that the hatching muscle represents all or part of the caput portion of *M. cucullaris*.

The bill of grebes is tipped at hatching with a relatively large chalk-white egg tooth. Most of the development is on the upper mandible, but a small flat plate also appears

on the tip of the lower mandible. The tooth does not drop off, but gradually flattens and disappears on the surface (McAllister 1963).

Shell-breaking and Emergence

Pipping (= cracking the shell) is done by pecking with the tip of the bill armed with egg tooth material on both the upper and lower mandibles. Because of the position of the grebe chick in the egg, the pip hole is always at the blunt end about one third of the distance from pole to pole. After pipping the bill is extended out the hole and levered back so that the upper mandible strikes the unbroken shell and makes a path through it. The whole bird turns only slightly in the shell during this process. When the broken path through the shell has reached 90° in a counter clockwise direction from the pip hole, the whole neck of the bird comes into play. The neck is curved in a complete circle around the blunt end of the egg, and with the help of the legs it levers against the blunt end of the shell. The shell splits cleanly 90° clockwise from the pip hole, and the blunt end cap is bent back shattering the remainder of the circumference of the circle (McAllister 1963).

Rapid Hatching

Hatching of each egg is rapid, taking less than half an hour to a few hours after the first pipping of the egg (50-120 minutes in an incubator) (Heinroth 1922, Wobus 1964, Fjeldså 1977b, Stout and Nuechterlein 1999). This rapid hatching is said to be an adaptation to prevent drowning in the sometimes very wet nest-cup (Heinroth 1922, Fjeldså 1977b). However, although the nest of grebes is always completely saturated, it seldom has standing water at the end of incubation (McAllister 1963, Wobus 1964).

Parental Assistance and Disposal of Eggshells

Hatching of the whole clutch normally spans several days, during which period one adult is almost constantly with the young. In response to the peeping of the chicks in the eggs, the adult birds reduce the amount of rising and resettling and increase the intensity of sideways-throwing of the nest material.

The tiny hatchling grebe does not remain under the sitting adult, but, as soon as it is able, still wet, it climbs up on to its parent's back, where it is brooded under the humeral feathers and wings of the adult, which raises the wings slightly in a characteristic brooding position (Fjeldså 1977b, Stout and Nuechterlein 1999). If the brooding bird

is disturbed, it may cover a small chick over with nest material together with the remaining eggs (Vlug 2002a).

Eggshells may be pushed over the nest side, or the birds grasp them in the bill and drop them several metres from the nest. Some small pieces of the eggshell usually remain in the nest-cup (Wobus 1964, Stout and Nuechterlein 1999).

16.5 Young Birds

16.5.1 Nest Desertion and Partial Clutch Abandonment

The young grebes leave the nest on the parent's back shortly after all the eggs are hatched. The family initially moves to nearby open water, but on larger lakes the adults may swim a considerable distance from the nest, brooding the chicks on their back.

Often viable (and pipped) eggs are deserted. As already stated (see 16.3.5), in some nests, the deserted eggs hatched but the parents showed no interest and the chicks died, and there is some evidence that the Red-necked Grebe has evolved asynchronous hatching and partial clutch abandonment as an adaptation to cope with food scarcity at hatching, the advantage for survival thus being placed on the first-hatched young (Kloskowski 2003a). In fish-ponds in south-east Poland, in 38 of 54 pairs (= 70.4%) broods were reduced by last-laid egg abandonment (30 pairs) and/or starvation (37 pairs). The abandonment of the last-laid eggs was independent of clutch size, current brood size and date of nesting attempt. The only factor affecting the probability of egg abandonment was the current brood rearing conditions indicated by occurrence of chick starvation. Desertion of the last-laid egg reduces the brood before substantial resources are invested in marginal offspring at the expense of inclusive fitness of all family members (Kloskowski 2003a). This mechanism for controlling the size of the brood in critical conditions presumably operates largely through the adult's own feeding rates, or the hunger level of the newly hatched chicks (Simmons 1974, Kloskowski 2003a).

16.5.2 Occurrence of Young Birds (Hatching Dates)

Caused by a high incidence of nest destruction in some lakes, especially by wind and waves, hatching dates between different areas may vary and can be extended throughout a number of months.

Hatching Dates in Europe

Small *P. grisegena* young occur from mid-May (Central Europe) or early June (Finland) to mid-July, or still later (Fjeldså 1977b). In Schleswig-Holstein 18.3% of the broods hatched in May, 64.8% in June, 16.4% in July and 0.5% in early August ($n = 213$ families in the period 1970-73) (Scholl 1974). There is a very early record of a brood near Achterwehr, Schleswig-Holstein hatching in mid-April 1989 (Vlug 1993). At the other extreme is an observation of A Rüger (*cited in* Vlug 1996), who saw a pair with 3 chicks of *c.* 1 week old near Rantzau, Schleswig-Holstein on 26 August 1995.

Hatching Dates in North America

Due to high rates of nest destruction and re-nesting, hatching initiation dates for Red-necked Grebe clutches in the Turtle Mountains, Manitoba, extended throughout June and July. Evidence from infrequently observed pairs indicated that hatching occasionally extended into August, as the first egg from a 5-egg clutch was peeping on 29 July 1981 and another pair carried 2 recently-hatched chicks on 11 August 1981. During 1980 and 1981, peak hatching occurred in late June and early July (De Smet 1983).

Although clutch initiation dates were similar for both Duck Lake, British Columbia, and an adjacent marsh (British Columbia), the dates when first eggs hatched were markedly different (see also 16.3.2). Many partial and complete clutches were destroyed by wind and wave action on the lake in May, but contemporary nests incubated in the marsh behind the dyke remained intact due to the shelter provided by the emergent vegetation and the dyke itself. The first eggs in the marsh hatched during the last week of May while the nests on Duck Lake did so 5 weeks later in the first week of July in both 1982 and 1983. All clutches in the marsh had hatched by mid-July, however in the lake hatching continued until mid-August (Ohanjanian 1986).

16.5.3 Condition at Hatching, Development of Plumage and Bare Parts of Young Birds

Condition at Hatching

Podicipedidae have semi-precocial (Stout and Nuechterlein 1999) or sub-precocial young (like rails, cranes and divers) (Gill 2007). The newly-hatched young of the nominate *grisegena* average 98 mm in total length, weighing 17-23 g (Fjeldså 1977b). At hatching, the yolk sac is completely internal, and the aperture is barely visible; the chicks have their eyes open, and they are active,

able to climb, beg, eat, dive feebly in case of need, swim (but for only a few minutes) and stretch within an hour after emerging from the egg (McAllister 1963, Fjeldså 1977b, Stout and Nuechterlein 1999). However, their ability to regulate their body temperature seems poorly developed at first, and they need the warmth from the parents' feathers.

Plumage and Bare Parts at Hatching

The small young of Podicipedidae are covered with dense, but very short, straight down – actually the fine, terminal barbs of the still undeveloped feathers (Fjeldså 1977b). At hatching, each down feather is enclosed in a thin silvery sheath. McAllister (1963) observed that the feathers of the newly-hatched chicks expanded first on the belly, then the breast, then the back and finally the head. The back feathers were fully expanded after three to four hours under the brooder; the head feathers took a further two hours. She reported that in the incubator with its higher temperature drying was completed quickly, but the feathers expanded at the same rate as in the brooder (McAllister 1963). The sheaths break simply as a result of drying, not by activities of the birds; the chicks do not preen and are not preened by the parents.

The chicks of Podicipedidae have a highly characteristic, striped pattern (although nearly obliterated in the North American *Aechmophorus*). Although this pattern shows some individual variation, particularly on the cheeks and throat, there are clear-cut differences between the species (Fjeldså 1977b). The newly-hatched chicks of the Red-necked Grebe have white down on head and neck, with bold black stripes and blotches. The upperparts are nearly black, with faint brownish stripes on the back; the underparts are white, and the flanks are speckled dark grey (Stout and Nuechterlein 1999) (see 3.2.3 for more details).

The bill of Red-necked and other grebes is tipped at hatching with a relatively large chalk-white egg tooth. Most of the development is on the upper mandible. This egg tooth gradually disappears during the first two weeks rather than breaking off (Stout and Nuechterlein 1999). The bill of the chicks of *P. grisegena* is pink or buffish-pink with a white tip, and with two vertical black bands around both mandibles, one near the base and one near the tip. The legs and feet are greyish, and the iris is brown or olive-brown (Fjeldså 1977b, Harrison and Castell 2002) (see 3.2.3 for more details).

On each side of the face of the newly-hatched Red-necked Grebe, between bill and eye (on the lore) is a large oval of bare skin. There is also a vestigial, bare crown patch (Fjeldså 1977b, Harrison and Castell 2002).

Red-necked Grebe chicks closely resemble hatchlings of Slavonian (Horned) and Great Crested Grebes, but there are some differences (see 4.2.6).

Development of Plumage and Bare Parts of Downy Young and Juveniles

The feathers of young Red-necked and other grebes emerge slowly from the fourth week of life, and the striped pattern is gradually obliterated as the soft, down-like distal part of the barbs disintegrates through abrasion. The ventral plumage becomes feather-like first, but on the whole the growth is fairly slow, the growth of the wings is particularly retarded (Fjeldså 1977b). There is no clear-cut distinction between downy and juvenile plumages. Red-necked Grebes retain the downy pattern on the face in their juvenile plumage, until the post-juvenile moult, and large young are very characteristic due to the rufous colour of the foreneck and two very prominent, slanting black bands remaining on the side of the head (Fjeldså 1977b) (see 3.2.4 for details). The post-juvenile moult of *Podiceps grisegena* is from September to late January, some birds are nearly finished in November, and others are just starting in that period (Cramp *et al.* 1977). Even in January some individuals still show remnants of the dark juvenile head stripes.

The iris of the juvenile has a clearly visible yellow outer ring, not becoming completely dark brown before the summer of the second calendar year (Walser and Barthel 1994). The bill of the juvenile Red-necked Grebe averages paler and shows more extensively yellow than the adult in non-breeding dress; it is yellow at the base, dark greenish-brown at the tip and along the edge of the culmen, and greenish-yellow in between (Cramp *et al.* 1977). The lower part of the bare patch on the lores remains naked when the young Red-necked Grebes grow larger. These bare flushing areas fill in with feathers after about six or seven weeks.

16.5.4 Functions of the Striped Pattern of Grebe Chicks

The striped pattern of Podicipedidae chicks is assumed to have a concealing function (somatolysis). This explanation may be satisfactory for the primitive pattern types (*Rollandia*, *Podilymbus*, *Tachybaptus*), but Fjeldså

(1977b) doubted whether it is solely sufficient for all the grebe species. Due to the efficient protection by the parents, and the inaccessible habitats, the selection for crypsis (concealment) might seem relaxed. Since the stripes of some species (such as *Podiceps grisegena*) are highly contrasting, following the contours of head and neck rather than disrupting them, and arranged so as to reinforce the conspicuity of the patches of bare skin, also phaneric functions (conspicuous colouration) seem to have evolved (Fjeldså 1977b).

16.5.5 Functions of the Bare Lore and Crown Patches

The blood vessels in the bare patches on the lores and the crown can be enlarged and contracted so that the colour changes (Fjeldså 1977a, Stout and Nuechterlein 1999). If the chick is subject to aggression, the colour of the bare skin flushes at intervals from pink to red. The naked skin varies from pale grey or flesh pink, when begging for food, to red, when the chick is full. It is possible that these colour changes have a signalling effect which is intensified by the striped pattern of down, and appease the adults' aggression (Fjeldså 1977a, b, 2004) and stimulate their willingness to feed the chicks (Wobus 1964, Storer 1967).

As already stated, the bare crown patch of the small chicks of Red-necked Grebes is vestigial, and possibly not as important as the naked lores. Whether *Podiceps grisegena* chicks can vary the colour of the loreal and crown patch independently is unknown, but the Great Crested Grebe and Silvery Grebe *P. occipitalis* chicks do, and this suggests a possible divergence in signal function (Nuechterlein 1985). Experiments on the functions of the bare crown patch of downy Western Grebe *Aechmophorus occidentalis* chicks suggest that this functions as a generalized distress signal indicating to the parents that a particular member of the brood is in need of immediate attention (Nuechterlein 1985).

16.5.6 Regulation of the Body Temperature and Life on the Back of the Parents

As already stated (see 16.5.3), the newly-hatched chicks are able to dive feebly and swim in case of need, but they do not voluntarily stay long in the water, because their ability to regulate their body temperature seems poorly developed at first, and they need the warmth from the parents' feathers. McAllister (1963) wrote that the first down of Podicipedidae is short and so thin that the skin

can be seen without ruffling the feathers. When in the water more than a few minutes, the young bird becomes chilled, and as the down gets wet, the bird sinks lower and lower in the water. If it does not get out quickly, it drowns.

Chicks hatched from incubators crawl forward with rapid (swimming) movements of the legs, and endeavour to find warm cracks, e.g. between the fingers of the caretaker (Heinroth and Heinroth 1928). McAllister (1963) studied many young Podicipedidae in the laboratory and during the course of this study about forty chicks were lost as a result of cold. Draught was fatal even when the birds were huddled under an infra-red heater. Most deaths occurred when the birds were between 36 and 48 hours old, but they were possible during the whole first week, and a severe draught killed chicks up to twelve days. The birds refused to eat a few hours after being chilled, became listless and drowsy, and died in about twelve hours with laboured breathing and continuous soft cheeping. All were autopsied, and they showed congested (abnormally full of blood) and haemorrhaged (escape of blood from ruptured blood vessels)

lungs. No birds which died of other causes showed these symptoms (McAllister 1963). Until the thermoregulation ability of Podicipedidae chicks develops in the second week, they do not stay long in water voluntarily (Fjeldså 2004).

This susceptibility to chilling is the main reason for continuous brooding during the first time after hatching. As already stated (see 16.4.9), the newly-hatched grebe does not remain under the sitting adult, but, as soon as it is able, still wet, it climbs up on to its parent's back, where it is brooded under the humeral feathers and wings of the adult, which raises the wings slightly in a characteristic brooding position (Fjeldså 1977b, Stout and Nuechterlein 1999) (see Fig. 13 and 100). The chick climbs up on to the warm "brooding chamber" as soon as possible because to stay under the parent any longer than necessary would increase the chance of being squashed (Vlug 2002a).

Back-brooding is nearly continuous during the first week after hatching. It occurs mostly on the nest while eggs remain and later on the water. During the carrying



Fig. 100: Adult Red-necked Grebe with three downy young. The susceptibility to chilling is the main reason for nearly continuous back-brooding during the first week after hatching. Photo: T Runge (Schleswig-Holstein)

Fig. 100: Adlerer Rothalstaucher mit drei Dunenjungten. Die Empfindlichkeit gegen Abkühlung ist die Hauptursache dafür, dass während der ersten Woche nach dem Schlüpfen die Küken fast ununterbrochen auf dem Rücken getragen werden.

stage, the down of the chicks gets thicker and also waterproof, and by day 10 the ability to regulate their body temperature is apparently better developed and the Red-necked Grebe chicks spend more than half of the day on the water. Back-brooding occurs until the *P. griseogena* chicks are 10-17 days old (De Smet 1983, Stout and Nuechterlein 1999), but individual young may secure occasional rides on the adult's back (not under the wings) until it is 3 weeks old. De Smet (1983) saw a 20-day-old Red-necked Grebe chick that scrambled onto its parent's back after the adult issued a warning call.

The presence of young under the wings of an adult grebe is normally revealed by its rounded profile, caused by the slightly lifted wings. However, when there is danger in the offing, the parents press their wings down so that it is not easy to see that they are carrying young (Wobus 1964). The heads of the chicks often peep out from the feathers of the adult, but if it is cold, the young remain completely hidden.

Carrying also may help to reduce the vulnerability of the young to predators. The Alarm-call, a short, sharp and

irregularly spaced tick, results in back-brooded chicks hiding their heads beneath the back feathers of the adult and being silent, and in swimming chicks diving (Stout and Nuechterlein 1999; cf. Nuechterlein 1988). Birds carrying chicks normally stay on the water surface as much as possible. If spooked to dive the young are sometimes lucky to remain under the wings but more often they are lost and pop up to the surface, like corks (Wobus 1964, Fjeldså 2004).

The parents carry the chicks in turn, while the other brings food, changing over duties at intervals, although during rest periods they may share the young between them. The non-brooding parent gives the food directly to the young (see Fig. 101), or more rarely, gives it to the brooding parent, which then feeds the young. The chicks have well-developed overtaking and climbing responses. The adult birds also show special behaviour to invite the young to climb up. Small chicks are assisted aboard by the parent's placing its feet out sideways close to the surface of the water and thus providing a "gang-plank" for them. At change-over, the young are deliberately "shed" by the carrying parent who rises in the water and shakes



Fig. 101: A downy young on the back of one of the parents is fed by the other parent with a female Three-spined Stickleback *Gasterosteus aculeatus*. Photo: T Runge (Schleswig-Holstein)

Fig. 101: Ein Dunenjunge auf dem Rücken des einen Altvogels wird von dem anderen Altvogel mit einem Weibchen des Dreistacheligen Stichlings *Gasterosteus aculeatus* gefüttert.

itself or flaps the wings. This often stimulates immediate defecation of the chicks, and then they climb back on the other parent. Re-boarding is discouraged by the adult's rotating as the chick tries to ascend, or by its swimming or diving away or rolling over to preen its belly (Simmons 1968, Stout and Nuechterlein 1999, Fjeldså 2004).

Low temperatures and heavy, prolonged rainfall cause high mortality in small chicks in the back-brooding period, especially in lakes with food scarcity. If food is scarce, both parents have to bring food simultaneously and the chicks are often unable to shelter under the parent's wings. It is probable that the combination of weather conditions and food scarcity causes high mortality among small chicks (Vlug 2005; cf. Ulenaers and Dhondt 1994).

16.5.7 Defecation

Chicks usually defecate into the water when shaken off the parent's back or while scrambling to get out of the water (Stout and Nuechterlein 1999, Vlug 2002a). However, for the first four days or so, the young grebe, like a nestling passerine, produces its faecal droppings enclosed in a sac, depositing them on the parent's back (Simmons 1989).

16.5.8. Recognizing the Parents

The parents know their young individually, and attend to them carefully, but show aggression towards foreign young. The chicks, on the other hand, may follow any fairly large moving object until several days old. They do not recognize their parents individually until they are at least one or two weeks old (Fjeldså 1977b, Vlug 1998). Chicks which are left unattended in the water after a territorial combat, and then approach the wrong adults, are often harassed violently and may even be killed (Fjeldså 2004). It was observed in Schleswig-Holstein that after a conflict between a pair of Red-necked Grebes and an adult Great Crested Grebe, the adult Red-necked Grebes flew away; their 5-day-old chick fell off its parent's back into the water and tried to climb onto the back of the Great Crested Grebe, which pecked it (Vlug 1998).

16.5.9 Diet of Chicks

During the first one or two weeks, the parents of Red-necked Grebe chicks provide small prey items (insect larvae and other aquatic arthropods, fish fry and small

tadpoles), but switch to larger prey as soon as the young can handle them. Not rarely, invertebrates decrease in importance and are replaced by small fish (Wobus 1964, Vlug 2002a, Nuechterlein *et al.* 2003, Fjeldså 2004, Kloskowski 2004).

Kloskowski (2004) studied 32 *P. grisegena* pairs with chicks in fish-ponds in south-eastern Poland and recorded the delivery of 13,239 food items to the chicks. Invertebrates were an important prey item given to the young in the first two weeks after hatching: means 79.4% in the first and 61.4% in the second week in terms of numbers, and 51.4% and 33.5% respectively in terms of biomass. However, the estimated percentage of invertebrate prey in the food brought to the chicks decreased steadily: in the eighth week invertebrates constituted on average only 14.4% of the food by numbers and starting from the fifth week their biomass contribution did not exceed 6%. The percentage of tadpoles was relatively stable over the entire dependence period in terms of numbers (range 7.1-14.9%) and during the first five weeks following hatching in terms of delivered biomass (10.0-18.9%). Contrary to those trends, the abundance of aquatic invertebrates and amphibian larvae in the ponds increased over the breeding season in the two study years.

The author found, that the most numerous invertebrates in stomachs of dead Red-necked Grebe chicks were larval dragonflies Anisoptera, which were found in 9 stomachs, adult beetles Coleoptera (in 7 stomachs), adult "true bugs" Heteroptera (mainly water boatmen Corixidae; in 5 stomachs), and large caddis flies Trichoptera larvae (in 4 stomachs). Adult dragon- and damselflies Odonata dominated in 2 stomachs; in fact, grebes were often observed pursuing insects over water, mainly adult Odonata and "water striders" Gerridae.

Kloskowski (2004) discovered that the percentage of delivered fish increased with the age of the chicks. Already in the second week after brood hatching fish was the most important prey item in the chick diet, making up 50.6% of the estimated consumed biomass. In their last week of parental attendance 11 broods were fed solely with fish. The mean estimated length of fish delivered by the parents increased as the chicks got older. Most of fish brought to the young grebes was small, the largest fish prey did not exceed a length of 15 cm. The growing predominance of fish in the diet of young Red-necked

Grebes was not caused by a lack of alternative prey (see above) and it appears that it is a preferred prey item, when suitable relative to the ingesting capabilities of the chicks.

On fishless ponds and lakes, aquatic insects, crustaceans, leeches Hirudinea and tadpoles provide the primary food for young (and adult) Red-necked Grebes (Stout and Nuechterlein 1999, Kloskowski 2011). Amphibians made up the majority of the biomass of food delivered to *Podiceps grisegena* broods observed on carp-free ponds and were the second most important prey on ponds with young-of-the-year carp (0+ ponds). Also, amphibians featured prominently in the food of young grebes on ponds with 1-year-old carp (1+ ponds) (27.4–38.1%). Premetamorphic stages predominated (more than 90% in all broods) (fish-ponds in south-eastern Poland, Kloskowski 2011).

Red-necked Grebes on Lake Osakis, Minnesota, feed invertebrates to newly hatched chicks but primarily feed minnows (small Cyprinidae) to young birds that are over two weeks old (Nuechterlein *et al.* 2003).

Diet of Chicks and Food flights (this topic is treated in more detail in 14.3.12)

Red-necked Grebes nesting on lagoons and other shallow wetlands near the Baltic Sea make food flights to the adjacent sea. The adult grebes obtain (almost) all their own food from the sea and not from the lagoon, but the chicks are partly fed with prey from the breeding water and partly with fish from the Baltic Sea. The amount of food that is flown in gets larger as the young grow. The adult birds feed their larger chicks with relatively large fish such as Butterfish *Pholis gunnellus* (up to a length of 15 cm), Sand Goby *Pomatoschistus (Gobius) minutus*, Common Goby *P. microps*, sand lances or sand eels Ammodytidae and Snakeblenny *Lumpenus lampraeformis* (Nielsen and Tofft 1987, Vlуг 1993, 2009).

In North America food flights are recorded only at Creston in British Columbia (Ohanjanian 1986, 1989). A number of Red-necked Grebes here nested in a marsh behind a man-made dyke, and other grebes bred on an adjacent lake (Duck Lake). The birds that nested in the marsh (“fliers”) obtained a part of their chicks’ diet locally, and a part from Duck Lake: they flew up to 2.5 km to the lake to forage for their young and themselves. These “fliers” took no small fish (≤ 50 mm) from the lake, whereas the birds nesting on Duck Lake did.

Red-necked Grebe chicks at Creston were fed both invertebrates (primarily larvae of dragonflies and damselflies Odonata) and fish. The importance of odonates decreased as the chicks aged. Parents behind the dyke began to fly fish back from Duck Lake when the young were in their second week. The proportion of the diet that was flown in increased as the chicks grew. Yellow Perch *Perca flavescens* was the preferred prey species.

Feather-eating (this topic is treated in more detail in 14.8)

Red-necked Grebes and other Podicipedidae eat large quantities of their own feathers. Intact feathers are not actively pulled out of the plumage, but only ingested after they are shed during moult or loosened during preening. Many feathers are eaten during preening sessions; they are sometimes dabbled in the water, to be moistened and then swallowed. The feathers are often picked up off the surface of the water. Parent Red-necked and other grebes will give them to the chicks from the day of hatching, even before these receive their first real feed. The young birds actively beg for them (Wetmore 1924, McAllister 1963, Wobus 1964, Piersma and Van Eerden 1989, Simmons 1989, Stout and Nuechterlein 1999).

16.5.10 Feeding

All prey items are given alive to the chicks. Grebes do not tear their prey into small pieces and chicks have to swallow the prey whole. Choking on large fish by younger chicks is a risk forcing parents to select for smaller prey. Especially in the first weeks after brood hatching, parents have to select for small prey. This selection can be also carried out by chicks themselves by rejection of too large fish.

The adult carries only a single item of food at a time in the tip of the bill, and swims towards the chicks, sometimes diving en route. So, food provisioning is a serious work constraint (Simmons 1955, Fjelds  2004). Difficulties in delivering the daily demand of food in form of numerous small prey items rather than a few relatively large fishes may result in a high mortality of young in the early chick stage. Increasing fish prey size is likely to reflect an active selection of larger prey by adults for growing chicks. The chick’s bill gape size increases with growth, allowing swallowing of larger prey like fish, and the latter has higher calorific value than invertebrates or small amphibians.

When the parent approaches with food, it gives a soft, rapidly repeated Grunting-call, which stimulates the back-brooded chicks to emerge from the feathers of the brooding adult and beg. Repeated bouts are given until chicks learn to respond (Stout and Nuechterlein 1999). At first the chicks receive food while sitting on one parent (the carrying parent, see Fig. 101), though, even during the first few days of life, they will at times scramble on to the nest or into the water to get closer to the feeding parent when they are particularly hungry (see Fig. 102). From the age of four or five days, the chicks always receive food while they are on the water surface, which allows both parents to dive (Wobus 1964). The adult, with ruffled-up crest, holds the food down so it is taken at the water-level, and the chick has to take it, for at no age is food placed into its mouth. The chick snatches the food from the parent's bill with a sideways jerk of the head, manipulates it in its bill, and swallows it whole (Simmons 1955, Wobus 1964, Stout and Nuechterlein 1999). At first the chicks do not usually follow the hunting bird but remain at one spot, often with the other adult, and wait for the feeding adult to return with food. Later, when they are larger, they tend to accompany the

parents more often. In their second week, the chicks will often peer underwater and watch the food searching by the adult bird, and occasionally it will dive towards it to receive the prey underwater. In this way, a gradual transition is possible towards independent feeding by the young (Fjeldså 2004).

The frequency of food deliveries to the chicks depends on many factors such as the age of the chicks, availability and size of the prey items, feeding skills of the parents, brood size, sibling competition, weather, and competition with other breeding pairs. Kloskowski (2001a) observed 17 two- and three- chick broods of Red-necked Grebes in fish-ponds in southeast Poland. He recorded that in the back-brooding stage a chick received food c. 6-9 times per hour, or a biomass of c. 2-3 g per hour.

16.5.11 Begging

A hungry chick peeps with its mouth somewhat open and has a pronounced Begging Posture. In the simple Begging Posture the neck is stretched forward, the head and open mouth are angled upward, and the bill is



Fig. 102: A downy young on the water surface is fed with a male Three-spined Stickleback *Gasterosteus aculeatus*. Photo: T Runge (Schleswig-Holstein)

Fig. 102: Ein Dunenjunge auf der Wasseroberfläche wird mit einem Männchen des Dreistachligen Stichlings *Gasterosteus aculeatus* gefüttert.

pointing at the adult (McAllister 1963, Stout and Nuechterlein 1999, Vlug 2002a). Large Red-necked Grebe chicks often beg persistently and show a high intensity Begging Posture. It is similar to that of the Great Crested Grebe. At extremes the body is mainly submerged, with the head and neck sticking sharply up out of the water, bill open showing the red interior. The chicks peep vociferously. Particularly when approaching or retreating from an adult, their legs kick out laterally to make a very noticeable disturbance on the surface. In spite of the vigour of the leg actions, they move only slowly, except that they are very quick in turning away once they have received food (Simmons 1955, McAllister 1963, Wobus 1964, Vlug 2002a, Fjeldså 2004).

Fjeldså (2004) wrote that this high intensity Begging Posture may function in assuring continuous attentiveness of the parents, but these often reject the young, which finally give up and start diving on their own. It is unclear if the parents are just irritated by the continuous demand behaviour (from young that should be well capable of catching their own food) or mistake the Begging Posture with threat (Forward-display) – which is quite possible because of the general similarity of postures, and obliteration of the patches of bare facial skin.

The Begging and Contact-call

The Begging and contact-call (“Wiebern” of Wobus 1964) of Red-necked Grebe chicks is a persisting “bibibibibibi” (Wobus 1964) or “zipp zipp...” (Bergmann *et al.* 2008), similar in structure and rhythm to the song of the Chiffchaff *Phylloscopus collybita*. On seeing an adult coming with food the chicks utter a louder version of this call, described by Bergmann *et al.* (2008) as a rapidly alternating “ti ti tü ti tü...”. Chicks from just under one week old to more than eight weeks give the Begging- and contact-call very frequently.

When the young are 6-7 weeks old, but still dependent, they not only use the Begging- and contact-call, but also begin to utter a soft “ga” which may later develop into a soft “gagaga” with only a slight “jip” component (Wobus 1964, Cramp *et al.* 1977).

Red-necked Grebe Chicks Begging for Food and Stealing it from Adults Who are not Their Parents

There are reports of Red-necked Grebe chicks begging for food and stealing it from adults who are not their parents. These reports are only from highly populated breeding waters from which the adults undertake food

flights, i.e. lagoons and ponds adjacent to the Baltic Sea in Germany (J J Vlug), and a marsh adjacent to Duck Lake in British Columbia (Ohanjanian 1986) (see 16.5.9). As the young in those waters grew they were left alone by the adults for longer periods of time and they became more mobile. They often entered neighbouring territories while the owners were absent during foraging trips. Chicks five weeks of age and older made continuous attempts to steal fish from incoming adults who were not their parents. Ohanjanian (1986) wrote that out of 630 fish flown back, 15 were stolen successfully. The fish was quickly grabbed from the adult’s bill as it landed and swallowed. The adult would then realize the mistake and attempted to attack the thief. It appeared that the incoming birds were momentarily distracted by the landing as they failed to distinguish their own chicks for several seconds. When the mistake was detected, pursuit was immediate, however the food was lost to the young of the foraging bird, and the stealing young always escaped unharmed. This intraspecific kleptoparasitism was never observed when food items were brought to the young by swimming, nor was it observed in other wetlands than those mentioned above. It appears to be a consequence of flying food in to an area of high brood density (Ohanjanian 1986).

16.5.12 Sibling Competition

During the back-brooding period, the advantages of size and strength given to the first-hatched grebe young by asynchronous hatching (see 16.4.9) are enhanced by the establishment of a dominance hierarchy within the brood (see Simmons 1974 for *Podiceps cristatus* and Nuechterlein 1981c for *Aechmophorus occidentalis*).

Sibling rivalry probably contributes to many of the Red-necked Grebe chick losses (De Smet 1983, Kloskowski 2001a). In at least one instance, Wobus (1964) attributed mortality of a young Red-necked Grebe to starvation resulting from two siblings repeatedly attacking it during feeding sessions. Hansford (*cited in* De Smet 1983) studied the feeding ecology of a Red-necked Grebe population in Alberta during 1980 and concluded that sibling rivalry was a major factor contributing to reduced productivity in this population.

Within the Turtle Mountains, Manitoba, De Smet (1983) frequently observed Red-necked Grebe chick-chick and parent-chick interactions during feeding sessions. In one instance where mortality through sibling rivalry was sus-

pected, one parent left about a week after the young had hatched, leaving its mate to care for 2 chicks. An observation of the 8-10 day old chicks revealed much sibling rivalry, resulting in the oldest chick obtaining most of the food procured during an entire feeding session. An hour-long observation 3 days later revealed much the same trend, as the smallest chick obtained only 1 of 53 food items brought by the adult and was pecked or chased by its older sibling or parent whenever it got near the feeding parent. For 15 minutes after the feeding session, the smallest chick attempted to climb onto its parent's back but was prevented by attacks from both the adult and the older immature. Twice when it did manage to climb aboard, it was immediately shaken off and pecked by the adult. Resting on the parent's back is probably of crucial importance in surviving violent windstorms, a major source of chick mortality among grebes (Nuechterlein 1981c).

Kloskowski (2001a) collected data on the distribution of food and parental aggression within the brood from 17 *grisegena* breeding pairs that raised 2 or 3 chicks to independence at fish-ponds in south-eastern Poland. All 17 broods established dominance hierarchies, equivalent to hatching hierarchies, reinforced by pecking. The feeding hierarchy reflected dominance order in all broods. In the back-brooding stage earlier-hatched chicks received more food per hour (in terms of delivery rate: 9.15 ± 3.44 versus 5.68 ± 2.13 ; in terms of biomass: 3.42 ± 0.71 g versus 1.73 ± 0.58 g). In this period in six broods seven later-hatched chicks died.

In the back-brooding phase Red-necked Grebe chicks in south-eastern Poland were fed on the first-come-first-served basis. This policy gives advantage to competitively larger siblings and may result in the elimination of the weaker chicks. As a general rule, parents did not interfere in sibling competition for food. However, in some families suffering chick starvation, Kloskowski (2001a) saw adults pecking chicks during the early back-brooding stage. This indicates that under poor chick-rearing conditions, grebe parents may take even more active role in moderating brood reduction.

When two *grisegena* chicks were carried by an adult, the chick that either emerged from the back feathers prior to the feeding attempt or was the first to respond to the feeding attempt, was fed more frequently than the chick hidden under the feathers (Kloskowski 2003a). Feeding

experiments conducted on two live-captured Western Grebe *Aechmophorus occidentalis* pairs and their newly hatched broods showed that older chicks suppressed the responses of their younger siblings to playbacks of the parental food call. Subordinate chicks that emerged from the parent's back feathers and begged simultaneously with their older siblings were usually pecked and soon refrained from emerging until the older sibling was satiated (Nuechterlein 1981c).

Free-swimming *grisegena* chicks were more likely to be fed than their carried siblings. Older siblings took a larger proportion of prey deliveries while off the parent's back, which was not surprising, as they spent more time swimming. Sibling aggression occurred more often when both adversaries were in the water (Kloskowski 2003a).

It is believed that in Turtle Mountains, sibling rivalry contributes to higher mortality rates in larger than smaller broods (De Smet 1983). Individual mortality rates beyond 5 days of ages were 35.7% for young within 4-6 chick broods, compared to a 12.3% mortality rate within 1-3 chick broods. However, in fish-ponds of South-East Poland, chicks from the largest broods had a higher probability of survival until fledging than those from single-chick-broods (Kloskowski 2003a). Kloskowski (2003a) stated that small broods suffered from food scarcity. He observed low provisioning rates in small (reduced) broods, both prior to and after the death of the youngest chicks. This indicates that the death of the youngest chicks was caused by extrinsic food limitation rather than from despotism by dominant siblings. He argued that there are two stages of brood reduction: 1. by parental clutch abandonment (see 16.3.5 and 16.5.1) and 2. by sibling competition. Possibly, these two mechanisms are linked parental strategies, as most broods suffering starvation were already reduced by desertion of the last eggs.

Kloskowski (2001a) suggested that Red-necked Grebe parents change the within-brood investment allocation over time. In the first weeks after hatching, they allow biased food distribution and in consequence even brood reduction. After the back-brooding period, the parents show aggression to offspring, especially to the older chicks, and the within-brood hierarchy of received food is gradually reversed. The last-hatched chicks are also cared for longer than their older siblings. The parents now intervene in resource allocation and attempt to

equalize the post-fledging survival of all chicks. Parental aggression appears to be a means both for counteracting the competitive advantage of older siblings and for forcing the chicks to independence (Kloskowski 2001a).

16.5.13 Brood-division (see also 15.3.3)

A number of grebe species show brood-division: in the course of the second week after hatching the parents may separate, more or less permanently, with one or two chicks each. However, a good deal of variation is observed, from permanent division where the two subgroups go independent ways, to a loose or temporary subdivision (Fjeldså 2004).

A Red-necked Grebe pair remains together with the chicks at least through the back-brooding period, but sometimes there is a partition of the brood thereafter into two units, each in charge of a single adult (Vlug 2002a). Wobus (1964) wrote that in small ponds in the Oberlausitz, eastern Germany, where only one pair breeds, brood-division occurs very rarely, but in larger breeding waters with many pairs it has been observed frequently. As most broods in the Oberlausitz comprise two chicks, the adults will each take care of one, and the units may separate to a large extent, each occupying quite different areas of the same water. The division is such that in several pairs the male will attack the female's chick and vice versa. However, in other pairs, the two family units may rest close together without any sign of friction (Wobus 1964).

Studies of Kloskowski (cited in Simmons 1997) of *Podiceps grisegena* in south-east Poland, showed that brood-division was rare in his study population - occurring in just one family out of some ten watched for about 100 hours each and starting as soon as carrying was over, the parents soon separating to different parts of the same breeding-water. Later Kloskowski (2001a) stated that he saw brood-division in eight 2-chick *grisegena* families. However, the division was often not complete. Although the parents in four of the eight divided broods showed hostility more often to the offspring from the other family unit they (with the exception of one family) continued to provision the chicks from the other subgroup.

Brood-division is most developed in the swan grebes *Aechmophorus* and some of the *Podiceps* species. The system of brood-division may belong in a series of sustaining breeding co-adaptations (strategies) that permit

grebes to maximize their reproductive output under environmental conditions that may vary much, from lake to lake, or according to weather conditions (Fjeldså 2004). Although in theory there would seem to be no difference between the joint feeding by the parents of, say, a brood of two and the same two adults each feeding a single chick, in fact Simmons (1974) found that in some of his *Podiceps cristatus* study families there was a dramatic rise in the overall feeding rate and in the rate per chick after brood-division.

16.5.14 Second Broods (see also 15.3.3)

As already mentioned (see 16.3.2), second broods of Red-necked Grebes are rare. The clutches of second broods in the species are usually initiated when the young from the first broods are still dependent and usually 3-5, occasionally c. 6-7 weeks old. However, the first brood young are sometimes much younger. In some cases, new eggs are laid immediately before or during hatching of the first brood. It appears that the female usually incubates while the male tends the young (Fjeldså 1977a). At the time when the young from the second brood hatch, the young from the first may still be partly dependent (see also 16.3.2).

Although feeding of younger siblings by first-brood young may occur regularly in golden grebes *Rollandia*, dabchicks *Tachybaptus* and pied-bills *Podilymbus*, this has only occasionally been reported in the Red-necked Grebe (Fjeldså 2004).

The relations between the two broods in *Podiceps grisegena* are often hostile. Kloskowski (2001b) observed the behaviour of two pairs with a second-brood, one from 1994 and the other from 1999. In 1994 both broods consisted of only one (surviving) young. The first-brood young obtained 201 (75%) from 267 parental feeds recorded during the first week after hatching of the second-brood chick. The first-brood young in this family usually approached the adults when they carried food for its sibling. In consequence, the second-brood chick received food at a lower rate (5.5 per hour) than its first-brood sibling at the corresponding age (14.5 per hour). Moreover, the second-brood chick was heavily pecked by the elder sibling during the short intervals between back-brooding. Although the first-brood young approaching the adults for food was regularly chased away, the parents did not interfere with its aggression toward the sibling. In the 1999 double-brooded pair, the two

first-brood young were fed by one adult but driven away from the vicinity of the two second brood chicks. In both families, the first-brood young were expelled from the natal territory 9-10 days after hatching of the second-brood (Kloskowski 2001b).

16.5.15 Development into Independence

As already stated, the chicks are active, able to climb, beg, eat, dive feebly in case of need and swim (but for only a few minutes) within an hour after emerging from the egg. Because their ability to regulate the body temperature seems poorly developed at first, they need the warmth from the parents' feathers, and back-brooding is nearly continuous during the first week after hatching (see 16.5.6). Although from the age of *c.* 14 days onward, the chicks may leave the parents for quite a while to "go on a trip" (Wobus 1964), they are completely dependent on their parents for many weeks.

The earliest unprompted dive noted during the studies of De Smet (1983) in the Turtle Mountains was by a 5-day-old chick. By the time young Red-necked Grebes in this area were 2 weeks old, they were often observed diving during feeding sessions. These dives appeared to be exploratory, and few successful feeding dives were noted by young less than 4 weeks old. During the first month, young *grisegena* in the Turtle Mountains probably procured little of their own food except for the occasional item found on the water or picked off objects protruding from the water. Throughout their second month, immatures continued to beg for and receive food from their parents. By the age of 6-7 weeks, however, immatures that approached a feeding parent were often pecked at and driven off (De Smet 1983).

De Smet (1983) stated that young *grisegena* chicks in his study area in Manitoba were partially independent at an age of 6-7 weeks (*c.* 40-50 days). Kloskowski (2000, 2003b) observed that at fish ponds in south-eastern Poland the mean period of parental care (at least one parent feeding the young) was 47.4 ± 8.3 days (*c.* 40-55 days, $n = 33$). However, in two families under observation (each with one chick), both parents abandoned the chick within 4 weeks after hatching. At the time of desertion, the chicks weighed only 530 g and 546 g, respectively, and were not fledged. At least the chick of one of these families survived (the fate of the other chick was not determined) (Kloskowski 2003b). At the other extreme, parental provisioning occasionally continued even for as

long as 9 weeks (*c.* 65 days) (Kloskowski 2003b). It can be concluded, that in general the young depend on the parents for food for 6-8 weeks (*c.* 40-55 days) (Stout and Nuechterlein 1999). The ability to fly is often reached later, at an age of about 60 days (50-65 days) (Fjelds  1977a, b, Ohanjanian 1986, Stout and Nuechterlein 1999, Vlug 2002a).

16.5.16 Departure, Offspring Desertion and Duration of Parental Care

Adult Red-necked Grebes usually leave the breeding waters before their young and mostly they depart singly, i.e. not together with the partner (Scholl 1974, De Smet 1983, Vlug 1996, Kloskowski 2003b, Fjelds  2004).

Frequently, one member of a pair abandons its mate and still dependent young. In 17 out of 37 pairs under observation on fish-ponds in SE Poland, one of the parents deserted the family before the end of the fifth week after hatching: six adult birds departed in the third week after hatching, shortly after the transition of the chicks from a back-brooding to a free-swimming existence; three adults left their families in the fourth week and eight in the fifth. Both sexes were involved in offspring desertion: 10 females and 6 males in 16 sexed pairs (Kloskowski 2003b).

The broods (in the study area in SE Poland) that suffered desertion by one of the parents were cared for by both adults for a shorter period than broods cared for evenly by both parents (28.1 ± 2.0 days *versus* 43.0 ± 1.1 day). The remaining parents of the deserted broods did not significantly differ from adults in non-deserted broods in the duration of brood attendance (in the study area the mean period of parental care, at least one parent feeding the young, was 47.4 days). However, in two families, where the broods were reduced to one chick, the desertion of one parent was "retaliated" by its mate, i.e. both parents abandoned the unfledged chick within 4 weeks after its hatching (see above, 16.5.15). In the study area, no chick mortality was witnessed after desertion. On average, chicks in both deserted and undeserted broods made their first attempts of independent foraging in the fourth week of life (Kloskowski 2003b).

Kloskowski (2003b) discovered that offspring desertion tended to occur more frequently in broods hatched later in the breeding season. He also showed that early broods were attended longer than later broods. Overall, Red-

necked Grebe parents cared longer for larger broods and departed earlier from territories on small ponds than from territories on larger ponds.

Deserting parents rarely disappeared suddenly. Instead, 1-3 days before leaving, they terminated feeding their young and spent most of their time roosting separate from the family. Kloskowski (2003b) saw that in two cases the deserting parents abandoned the territory on large, apparently food abundant fry ponds supporting several breeding pairs, but did not leave the pond and joined floating groups of “non-breeding” individuals. These parents were occasionally recognized by their chicks that approached them and solicited food, but the deserting parents showed no reaction to the begging chicks.

A number of 2-chick broods were divided between the parents, i.e. the male favoured one chick and the female favoured the other (see 16.5.13). After the departure of one parent, the deserted chicks joined the other “sub-brood”. The aggression rate among the siblings increased in all re-amalgamated broods. However, almost no overt sibling hostility was witnessed in undivided broods in the last week before and after departure of one of the adults (Kloskowski 2003b).

The study by De Smet (1983) on Red-necked Grebes in Turtle Mountains showed that in all families under observation, one parent departed 1-3 weeks before its mate. If only a single chick was reared, the departure of the first adult often occurred before the immature was a month old. In larger broods, the initial departure generally occurred when at least some brood members were partially independent (6-7 weeks of age). Although the departure of the second adult occurred slightly earlier when smaller broods had been reared, it generally remained until the youngest members were at least 6-8 weeks of age.

During the study of De Smet (1983), departure data were collected from 11 broods. In these, the immatures generally departed at 9-10 weeks of age, although a few left before they were 2 months old, and others remained beyond 70 days. As with the adults, most immature Red-necked Grebes departed their nesting lakes singly.

Desertion by one of the grebe parents before the young are independent is surprising because the offspring require more additional care to become self-supporting. Offspring desertion at a relatively early stage of brood

rearing is likely to be at some cost to the mates continuing the care unaided or to the offspring. In the *P. grisegena* study of Kloskowski (2003b), the remaining mates increased their feeding efforts. Unilateral parental desertion is also known to occur in Great Crested Grebes (Bandorf 1982, Simmons 1997). In this species, it appears to be practised mainly by females (Simmons 1997). We must conclude that it can be a deliberate strategy, a decision, as it were, by the departing adult to “cheat” on its mate, not in order to find a better opportunity to breed with a new mate elsewhere in what remains of the season but for the sake of personal survival (Simmons 1997). The duration of parental attendance in Red-necked Grebes and other Podicipedidae is likely to be constrained by the long-lasting post-breeding (post-nuptial) moult. During this moult all the remiges and other wing-feathers, including the coverts, are shed simultaneously so that the birds are unable to fly for a longer time. Moult requires a lot of energy and the grebes try to moult intensively in a period with optimal thermal conditions, i.e. in summer (Piersma 1988a). However, as a rule this is not possible for nesting adult birds. Wing moulting and breeding of Podicipedidae typically occur at separate times during the annual cycle because these events are energetically incompatible. Apart from that, most breeding sites do not offer favourable conditions for the postnuptial moults (see 5.2.1 and 5.4). By leaving their dependent young and breeding grounds, the adults can moult in a favourable period and suitable environment and so increase their chance of survival and total long-life production (Vlug 1996, 2005).

16.5.17 Red-necked Grebes Rearing Chicks of Great Crested, Western and Clark's Grebes

There are records of interspecific mixed clutches. Whether those clutches are the result of parasitism, egg dumping, or both is unclear (Vlug 2002a). The success of parasitic eggs is usually unknown, though records exist of mixed families. Vlug (1998) observed three Red-necked Grebe pairs rearing a young Great Crested Grebe in densely populated breeding waters on the island of Fehmarn, Schleswig-Holstein, Germany. Each pair had only one foster child and no young of its own. On two neighbouring fishponds in the Barycz Valley, South-West Poland, Dziuba (2007) saw two adult Red-necked Grebes, each of them feeding a single young Great Crested Grebe. As adult grebes know their young individually and show aggression to foreign young, it is likely

that the mixed families are the result of Great Crested Grebes laying eggs in Red-necked Grebe nests. After hatching the Red-necked Grebes accepted the young Great Crested Grebe as their own.

One adult Red-necked Grebe was seen feeding a Western Grebe chick for more than 20 minutes, and another pair was observed in close association with both a Red-necked Grebe chick and a Western Grebe chick at Lake Osakis, Minnesota (Stout and Nuechterlein 1999).

Van Damme (2004, 2006, 2008) made a number of interesting observations on Duck Lake, Creston Valley, British Columbia. During the 2003 breeding season she saw Western Grebe chicks on the backs of adult Red-necked Grebes or being fed by or swimming with adult Red-necked Grebes away from the nest sites. At least four families were involved. On 6 July 2003 she found a nest with 3 eggs incubated by a Red-necked Grebe. On 12 July there were two downy Western Grebe chicks resting on the back of the adult Red-necked Grebe along with one egg still in the nest. Two other Red-necked Grebes, sitting on nests, were observed each with a single Western Grebe chick.

In 2005, she recorded two mixed families each with one Western Grebe chick (Van Damme 2006). It was obvious that the Red-necked Grebes were rearing only the foster chicks and had none of their own. During the 2006 season, six pairs of Red-necked Grebes nested within, or at the periphery, of a Western Grebe colony on Duck Lake. The author discovered one nest with three Red-necked and two Western Grebe eggs. A fortnight later the Red-necked Grebe pair of this nest was recorded with one Western Grebe and three *grisegena* chicks. The Western Grebe chick was larger in size, obtained most food and gained more access to the foster parents' back than its smaller "siblings". It acted aggressively toward one of the Red-necked Grebe chicks by jabbing at it with its bill (*cf.* normal sibling competition, see 16.5.12). A week after the last chick hatched, Van Damme (2006) only saw the Western Grebe, and there were no surviving *grisegena* chicks. It seems likely that the three smaller young did not survive the competition from the larger Western Grebe chick. These observations probably explain the almost complete absence of larger Red-necked Grebe chicks in mixed families with Western or Great Crested Grebes. During the breeding season of 2000 at Duck Lake, Van Damme (2008) observed a pair of Red-necked

Grebes feeding a Clark's Grebe *Aechmophorus clarkii* chick. Again, no Red-necked Grebe chicks were seen.

There is one observation of a *Podiceps cristatus* foster parent with a *grisegena* chick: R K Berndt and T Runge saw an adult Great Crested Grebe in close association with a begging Red-necked Grebe chick of 6 weeks old at Dodauer See, Schleswig-Holstein, Germany.

Peculiar is the observation of a pair of Red-necked Grebes at Aukrug, Schleswig-Holstein. The birds were seen feeding their own young and also several times a young Coot *Fulica atra* of about three weeks old (Berndt, cited in Vlug 2002a).

At the Pfaffensee in Hessen, Germany, a pair of Red-necked Grebes lost their nest 7 times in 2008. Then the grebes "kidnapped" and frequently fed two young Coots (Hessische Gesellschaft für Ornithologie und Naturschutz 2010; S Stübing).

16.6 Demographic Factors (this topic is treated in more detail in 11.2.2)

Although there are data of brood success and family size on the breeding grounds, all that we can say about the population regulation in the Red-necked Grebe is hardly more than an educated guess because we know almost nothing about the demographic factors of the species such as annual survival or mortality rates, immigration or emigration and the number of non-breeding summering birds.

16.6.1 Age at First Breeding (this topic is treated in more detail in 11.1)

Second calendar year Red-necked Grebes attain the nuptial plumage and are usually sexually mature. There are records of Red-necked Grebes breeding successfully at this age. But in spite of that, the majority of these young birds do not breed. It is believed that they normally spend the summer away from the breeding waters.

16.6.2 Brood Success (Percentage of Pairs Raising at Least One Young) (this topic is discussed in more detail in 11.2.2)

Europe

The mean brood success (= percentage of pairs raising at least one young) of European Red-necked Grebes

is 41% ($n = 19,020$ pairs; however, the sample of Schleswig-Holstein, 14,976 pairs, is highly over-represented). The brood success varies significantly from one European area to another (range of regional means 17% to 80%), but the data obtained by different authors are often not directly comparable, since there is no consistent method of measurement. Sometimes all the birds on the breeding waters (breeders and birds that have been totally prevented from breeding) are included in the calculations and sometimes only the birds proven to have bred there. Few authors have documented how many pairs leave the breeding area early without producing any young.

North America

In North America (1969-96) on average 60% of the pairs are successful ($n = 1,125$ pairs) (Vlug 2002a, calculated from Kevan 1970, Riske 1976, De Smet 1987, Fournier and Hines 1998). Brood success in Pine Lake, Alberta (25%) (Riske 1976) was the lowest, and in the Northwest Territories, Canada (72%) (Fournier and Hines 1998) the highest of all the studied areas in North America.

Range of Annual Means of Brood Success

Everywhere in its distribution area brood success of *griseogena* not only varies between the areas, but also between the years, e.g. from 14% to 68% in the period 1969-2014 (= 46 years) in Schleswig-Holstein (J J Vlug), from 3% to 51% in the period 1989-2003 (= 15 years) in Vejlerne, Denmark (Kjeldsen 2008), and from 51% to 85% over 11 years in the Northwest Territories (Fournier and Hines 1998).

16.6.3 Brood Size (Family Size, Young per Successful Pair or Young per Family) (this topic is treated in more detail in 11.2.2)

Europe and the Western Part of Asia

The majority of the successful pairs in Europe are observed with 1 or 2 young of at least a few weeks old. In Europe the mean number of (larger but still dependent) young per successful pair (= young per family or brood size) is 1.73 ($n = 8,783$ families; the majority, 5,671 families is from Schleswig-Holstein). The mean brood size differs from area to area (range of regional means 1.11-2.80).

North America

The majority of the successful pairs (families) in North America (as in Europe) are observed with 1 or 2 young

of at least a few weeks old. In the period 1936-96 the mean number of dependent young per successful pair was 1.95 (range of regional means 1.31-2.05, $n = 1,328$ families).

Range of Annual Means of Brood Size

In the whole distribution area of the species brood size not only varies between the areas, but also between the years, e.g. from 1.33 to 2.18 in the period 1969-2014 (= 46 years) in Schleswig-Holstein (J J Vlug), and from 1.59 to 2.25 over 11 years (1986-96) in the Northwest Territories (Fournier and Hines 1998).

16.6.4 Life Span and Survivorship (these topics are treated in more detail in 11.2.2)

Chick Mortality

The majority of the successful pairs are observed with 1 or 2 young of at least a few weeks old. However, complete clutches usually consist of 3, 4 or 5 eggs (Vlug 2002a). Many factors are responsible for the difference between clutch size and brood-size. Partial clutch abandonment during hatching is frequently observed, especially in food shortage (Stout and Nuechterlein 1999, Vlug 2002a, Kloskowski 2003a). During the first days after hatching, the chicks are very vulnerable to chilling; damp, cool, and stormy weather is a major source of mortality, especially when food is scarce (Wobus 1964, Vlug 1985, Dittberner 1996, Vlug 2002a, Vlug 2005). So, it is understandable that the mortality is the highest during the first 5-10 days after hatching, and there is little mortality after the first month (De Smet 1983, Ohanjanian 1986, Stout and Nuechterlein 1999, Kloskowski 2000).

Survival Rates of Adult Birds

Although we know something about brood success, family size and chick mortality on the breeding grounds, we know almost nothing about the survival rates of the adult birds and of the young birds after leaving the breeding waters.

Some studies in particular areas involve checking to find what proportion of birds present in one year are still there the next. This method does not tell us where or when particular individuals die, nor does it separate deaths from permanent emigration (Newton 2013). The annual rates of colour-banded adults returning to Lake Osakis, Minnesota, over 5 years ranged from 61% ($n = 69$) to 100% ($n = 9$), suggesting high annual survival rates for adult Red-necked Grebes (Stout and Nuechterlein

1999). Bellebaum *et al.* (2018) estimated apparent survival of Red-necked Grebes based on a 20-year colour-ringing programme in eastern Poland ($n = 91$ colour-banded adults and 79 young). The average annual apparent survival was 0.16 in first-year females and 0.76 in adult females, or 0.18 and 0.79 for sexes pooled, respectively.

16.6.5 Life-history Features (this topic is discussed in more detail in 11.2.3)

Red-necked Grebes belong, among the Podicipedidae, to the K-strategists. The adult birds have developed behaviour patterns to increase prospects for their own survival at the breeding sites, e.g. leaving the nests for extended periods at night (by leaving their nests at night, the birds may be decreasing their exposure to nocturnal predators that prey on adults) (Nuechterlein and Buitron 2002), the defence of large territories which means that established pairs have more food available than the bare necessities (Vlug 2005), and early departures from the breeding waters to the moulting sites (Vlug 1996).

Red-necked Grebes which make food flights often have a lower than normal brood success and a smaller brood size. However, these adult birds do have large feeding areas (sea or large lake) at their disposal. The large bodies of water offer them more predictable conditions, too, so, the long-life expectancies of these grebes are high. Probably, Red-necked Grebes breeding near large bodies of water follow the strategy of living a long life with a high total lifetime reproduction, even more so than those breeding in small ponds (Vlug 2005).

17. Deutsche Zusammenfassung

Die Grundlagen unserer heutigen Kenntnisse über Verhalten und Ökologie des Rothalstauchers hat Ulrich Wobus in seiner Monographie von 1964 gelegt. Das vorliegende Heft des "Corax", als zweite Monographie über diese Art, soll den gegenwärtigen Wissensstand zusammenfassen und ist vor allem als Nachschlagewerk für Interessierte an der Biologie der Lappentaucher und anderer Wasservögel gedacht. Diese Arbeit behandelt nicht nur die Rothalstaucher aus Europa und West-Asien, sondern auch die Vögel aus Nord-Amerika und Ost-Asien.

In **Kapitel 1** werden die Familie der Lappentaucher sowie die Ornithologen vorgestellt, die sich auf diese Familie spezialisiert haben.

Kapitel 2 gibt eine Übersicht über die Geschichte der wissenschaftlichen Namensgebung und Klassifikation des Rothalstauchers (Fig. 1-5).

In **Kapitel 3** über Körpermerkmale und Taxonomie werden u.a. der Tauchapparat der Lappentaucher, ihr Skelett (Fig. 6) und ihre Muskulatur untersucht. Die Zehen mit den breiten Schwimmlappen (Fig. 7) sind eine besondere und einzigartige anatomische Struktur der Lappentaucher. Das Kapitel enthält auch eine detaillierte Beschreibung des Federkleides und der nicht befiederten Teile der Rothalstaucher aus Europa und West-Asien (Fig. 8-16 und 102).

In **Kapitel 4** werden die Unterschiede der Feldkennzeichen des europäisch-westasiatischen Rothalstauchers mit denen der nordamerikanisch-ostasiatischen Unterart (Fig. 17-20) und anderen Lappentaucherarten und Seetauchern verglichen. Rothalstaucher im Brutkleid sind unverwechselbar, aber Vögel im Ruhekleid sind, insbesondere aus größeren Entfernungen, nicht so einfach zu erkennen.

Kapitel 5 behandelt die Mauser der Alt- und Jungvögel. Bei der postnuptialen Vollmauser fallen alle Schwungfedern und andere Flügelgedern gleichzeitig aus, so dass die Rothalstaucher während mindestens 2 bis 3 Wochen flugunfähig sind.

Kapitel 6 beschreibt die Lautäußerungen der Alt- und Jungvögel. In ihren Brutgewässern machen die Rothalstaucher sehr häufig Gebrauch von ihrer Stimme. Die markanteste Lautäußerung ist der eindringliche und sehr laute Reviergesang ("uööh-Gebrüll"), der von beiden Geschlechtern geäußert wird.

Zwar sind zahlreiche äußere Merkmale des Rothalstauchers messbar, die fünf in **Kapitel 7** analysierten Parameter werden aber am häufigsten verwendet: Körper-, Flügel-, Schnabel- und Tarsuslänge und Körpergewicht. Nicht nur die zwei Unterarten des Rothalstauchers unterscheiden sich in ihrer Größe, es gibt auch Variationen zwischen Populationen innerhalb dieser Unterarten. Zusätzlich bestehen innerhalb einer Population Maßunterschiede zwischen Männchen und Weibchen.

In **Kapitel 8** werden Systematik und Stammesgeschichte (phylogenetische Entwicklung) des Rothalstauchers und seiner Verwandten untersucht. Die Lappentaucherfamilie umfasst sieben Gattungen mit 22 Arten (Fig. 21-25). Die acht *Podiceps* Arten werden in der Regel auf zwei Untergruppen verteilt. Die erste besteht aus Rothals-, Hauben- (Fig. 22-23) und Ohrentaucher (Fig. 24), die zweite aus dem Schwarzhalstaucher (Fig. 25) und vier mit ihm eng verwandten Arten.

Seetaucher und Lappentaucher ähneln sich, aber diese Ähnlichkeiten beruhen auf konvergenter Evolution. Molekulare, morphologische und oologische Analysen dagegen unterstützen vielmehr ein Schwesterngruppenverhältnis von Lappentauchern und Flamingos.

In **Kapitel 9** wird das Habitat dargestellt sowie die zwischenartliche Konkurrenz, die die Habitatwahl beeinflusst. Die wichtigsten Brutgewässer in Europa sind Binnengewässer, die in der Regel ziemlich flach sind, mindestens einige Ufervegetationszonen aufweisen und eine reiche Unterwasservegetation besitzen, in denen größere Wirbellose und kleine Wirbeltiere gedeihen. Bei zunehmender Eutrophierung verlassen die Rothalstaucher ihre Brutgewässer.

In Schleswig-Holstein und anderen mitteleuropäischen Gebieten brütet ein Großteil der Bestände an ablassbaren Fischteichen (Fotos der Brutgewässer in Schleswig-Holstein Fig. 26-33). Im Durchschnitt nutzen 33 % der Brutpaare in Schleswig-Holstein Gewässer zwischen 0,05 und 5,0 ha Größe.

Häufig werden neu angestaute, künstliche und natürliche Flachgewässer schnell von vielen Rothalstauchern angenommen; nach einigen Jahren sind aber in der Regel starke Bestandsrückgänge zu verzeichnen.

Die Habitatwahl des Rothalstauchers wird durch den Haubentaucher kaum beeinflusst. Die beiden Arten sind zwar nicht vollkommen, aber doch genügend ökologisch getrennt, um eine Konkurrenz sehr zu beschränken. Die Brutplatzwahl des Rothalstauchers kann hingegen durch Konkurrenz mit Karpfen und anderen Cypriniden erheblich beeinflusst werden. Die Karpfenfische, insbesondere die alten, großen Exemplare, konkurrieren nicht nur direkt um Nahrung, sondern können auch indirekt die Entwicklung der Nahrungstiere von Rothalstauchern beeinträchtigen.

Während des größten Teils des Jahres leben Rothalstaucher in Meeresgebieten, und nur während einer kurzen Periode, nämlich ungefähr 4 Monate, finden wir sie in ihren Brutgewässern.

Kapitel 10 gibt eine detaillierte Übersicht der Brut- und Winterverbreitung des Rothalstauchers (Fig. 34). Die Nominatform *Podiceps grisegena grisegena* (Boddaert) nistet in Europa und West-Asien, und *Podiceps grisegena holboellii* Reinhardt brütet in Nord-Amerika und Ost-Asien. Die Art kommt nicht in Mittelsibirien vor.

Im Winter werden Rothalstaucher häufig in der Ostsee, im Schwarzen Meer, im Kaspischen Meer und entlang der Küsten des Atlantischen und Pazifischen Ozeans gefunden.

Kapitel 11 diskutiert die Populationsschwankungen und demographischen Faktoren (Bruterfolg und Familiengröße) aus vielen Gebieten und Ländern des gesamten Verbreitungsgebietes.

In Schleswig-Holstein (1969-2014) brachten 38 % von 14.976 Paaren an den Brutgewässern mindestens ein Junges hoch. Die jährlichen Fluktuationen des Bruterfolges waren groß und schwankten von 14 % bis 68 % in dem Zeitraum. 52 % der erfolgreichen Paare (= Familien) hatten ein und 37 % zwei Küken.

Die Altvögel im Brutgebiet haben bestimmte Verhaltensweisen entwickelt, um ihre eigenen Aussichten auf ein langes Leben zu erhöhen, z. B. frühes Verlassen der Brutgebiete mit dem Ziel, die Mauseergebiete aufzusuchen. Rothalstaucher, die Nahrungsflüge unternehmen, zeigen häufig einen geringeren jährlichen Bruterfolg (d. h. Prozentsatz der Paare mit großen Jungen) und eine kleinere Familiengröße als Artgenossen in anderen Brutgewässern. Die Altvögel verfügen dafür über große Flächen (Meer oder großer See), an denen sie Nahrung suchen können, und die großen Gewässer bieten ihnen auch relativ gut vorhersagbare Bedingungen. Dadurch haben sie besonders große Aussichten auf ein langes Leben und eine langjährige Reproduktion.

Im Zeitraum 1985-2014 war die Zahl der Brutpaare in Schleswig-Holstein ziemlich konstant und fluktuierte zwischen ungefähr 500 und 700 Paaren. Wenn auch der Brutbestand 1969-1978 kleiner war (ca. 350 Paare), war auch er ziemlich stabil. In Schleswig-Holstein treten hohe Brutpopulationsdichten auf, was für Bestände an

der Verbreitungsgrenze ungewöhnlich ist: bis 8 Paare an einem Binnengewässer von 1 ha (= 8,0 Paare pro Hektar) und sogar bis zu 40 Paare an einem Teich von 3 ha Größe auf Fehmarn (= 13,3 Paare pro Hektar) (Fig. 32). Nirgendwo sonst im weltweiten Verbreitungsgebiet des Rothalstauchers sind solch hohe Siedlungsdichten festgestellt worden.

Thema des **Kapitels 12** sind die vielen Bedrohungen, denen die Art ausgesetzt ist. Einige Beispiele sind die Zerstörung von Gelegen und Küken, verursacht durch hohen Wellenschlag, das Sterben von vielen frisch geschlüpften Küken durch regnerisches und kühles Wetter und die Gefahren durch schlechtes Wetter während des Zuges und durch die Vereisung der Wintergewässer. Parasiten gibt es in einer verwirrenden Vielfalt; sie können sich verheerend auf Lappentaucherpopulationen auswirken. Viele der ernsthaften Bedrohungen werden durch den Menschen verursacht. Einige Beispiele sind Ök Katastrophen, Pestizide, Schwermetalle, Verlust und Degradation der Habitate, Fischernetze usw.

Kapitel 13 zeigt eine detaillierte Übersicht der Zugbewegungen. In ihrem ganzen Verbreitungsgebiet sind alle Rothalstaucher Kurz- oder Mittelstreckenzieher. In der Regel zieht die Art zwischen den Brutgebieten im Binnenland und den Wintergebieten auf dem Meer. Die Zugwege zeigen eher eine Ost-West als eine Nord-Süd Richtung. Die Vögel ziehen häufig in kleinen Trupps. Der Herbstzug beginnt mit einem Mauserzug; alle Schwungfedern werden gleichzeitig abgeworfen (Flugunfähigkeit). Nach deren Erneuerung fliegen die Vögel weiter zu den Wintergebieten. Alle bekannten Mauserplätze liegen auf dem Weg zu den Winterlebensräumen oder direkt in diesen Gebieten.

Ein Teil der Rothalstaucher verbringt den Sommer an Gewässern, die für das Brutgeschäft ungeeignet sind. Vögel, die nicht erfolgreich im Brutgeschäft waren, können an den Brutgewässern Trupps bilden (Fig. 35).

Kapitel 14 behandelt Nahrung, Nahrungserwerb, Nahrungskonsum, Methoden der Nahrungssuche (aktives Verfolgen oder Sammeln) und Nahrungsflüge des Rothalstauchers (Fig. 36-38). Die Nahrungszusammensetzung beider Unterarten wird analysiert und verglichen. Die Konkurrenz mit Haubentauchern und Karpfenfischen wird umfassend besprochen ebenso wie das Fressen von Federn und die Speiballenbildung (Fig. 39-40).

Die Hauptnahrung des Rothalstauchers (Nominatform) in den Brutgewässern besteht aus Wasserinsekten und deren Larven (z. B. Libellen und Wasserkäfer), Mollusken (Wasserschnecken), Krebstieren, Amphibien, Kleinfischen und Fischbrut.

Beim Nahrungserwerb in großen Seen und an Meeresküsten, insbesondere im Winter, kann der Fischanteil überwiegen. Die Küken des Rothalstauchers, deren Eltern Nahrungsflüge von den Brutgewässern zur Ostsee übernehmen, erhalten viele relativ große Fische wie z. B. Butterfische und Meergrundeln.

In **Kapitel 15** werden Verhaltensweisen wie das Laufen, Fliegen (Fig. 41-46), Schwimmen und Tauchen diskutiert. Ebenfalls werden die Komfortbewegungen wie z. B. Baden, Putzen der Federn (Fig. 47-49), Körperschütteln (Fig. 50), Flügelschlagen (Fig. 51-52), Strecken (Fig. 53-54), Kopfkratzen, Kehleberühren (Fig. 20) und Schlafhaltung (Fig. 55) beschrieben.

Rothalstaucher sind streitlustige Vögel, die aggressiv ihre Reviere verteidigen; in der Regel nisten die Paare daher einzeln. Sie zeigen nicht nur eine innerartliche, sondern auch eine zwischenartliche Revierverteidigung. Agonistische Verhaltensweisen, d. h. Drohverhalten, Angriff, Kampf, Verteidigung und Flucht (Fig. 56-68 und 97), werden ausführlich behandelt.

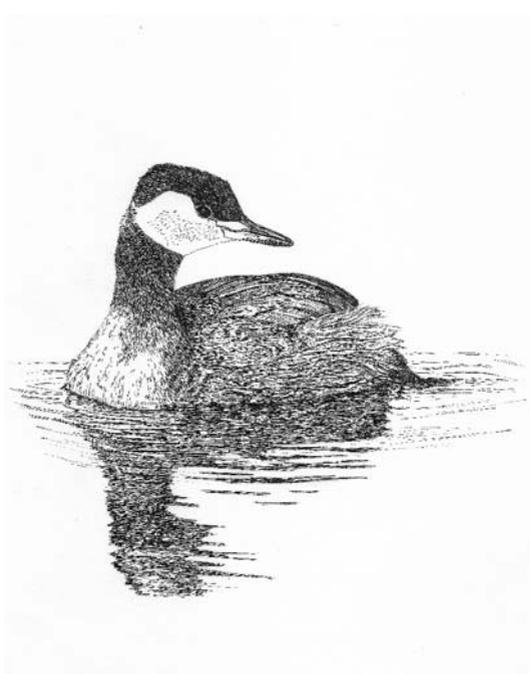
Die Wasserbalz des Rothalstauchers kann spektakulär sein, und beide Geschlechter beteiligen sich daran in einer Vielfalt von äußerst ritualisierten Verhaltensketten, die zu den komplexesten gehören, die aus der Vogelwelt bekannt sind (Fig. 69-84). Dieses Wasserbalzverhalten, die Plattform- oder Paarungsbalz, die Kopula und die Postkopulabalz (Fig. 85-91) werden detailliert besprochen und mit verwandten Arten verglichen. Die Postkopulabalz ist beim Rothalstaucher stärker ritualisiert als bei den anderen *Podiceps*-Arten.

Kapitel 16 enthält eine Übersicht über das Brutverhalten des Rothalstauchers. Weil dieses Verhalten in alle Aspekte des Lebens eindringt, ist dieses Kapitel das umfangreichste der Monographie. Das Kapitel gibt unter anderem eine Übersicht über Nestbau (Fig. 92-93) und Nistplatz (Fig. 94).

Kolonialität bei Rothals- und anderen Tauchern wird ausführlich diskutiert. Rothalstaucher brüten manchmal in hoher Dichte, z. B. an Gewässern in der Nähe der Ost-

see. Dorthin werden sie unabhängig voneinander durch besondere Umweltmerkmale angezogen (Semi-Kolonialität), und nicht durch die Präsenz von Artgenossen (echte Kolonialität), wie das z. B. beim Schwarzhalstaucher der Fall ist.

Andere Themen in diesem Kapitel sind Eier und Gelege, Brutverhalten (Fig. 95-99), Schlüpfen der Küken und Schlüpfdaten. Weiter werden die Funktionen des Streifenmusters und der nackten Stellen auf dem Scheitel (diese Stelle ist rudimentär bei Rothalstaucherküken) und in der Zügelgegend (zwischen Auge und Schnabel) der frisch geschlüpften Küken erläutert. Der Aufenthalt der Jungen auf dem Rücken der Eltern (Fig. 100), das Füttern der Küken (Fig. 101-102), das Verlassen des Restgeleges, die Konkurrenz zwischen den Geschwistern, die Aufteilung der Jungen auf Männchen und Weibchen, Zweitbruten, die Entwicklung bis zur Unabhängigkeit und das frühe Verlassen der Küken von einem Elternteil sind weitere Themen. Asynchrones Schlüpfen und Verlassen des Restgeleges stellen Anpassungen dar, um die Familiengröße bei Nahrungsmangel zu bewältigen. Außergewöhnlich sind die Beobachtungen von adulten Rothalstauchern, die Küken von Hauben-, Renn- oder Clarktauchern großziehen.



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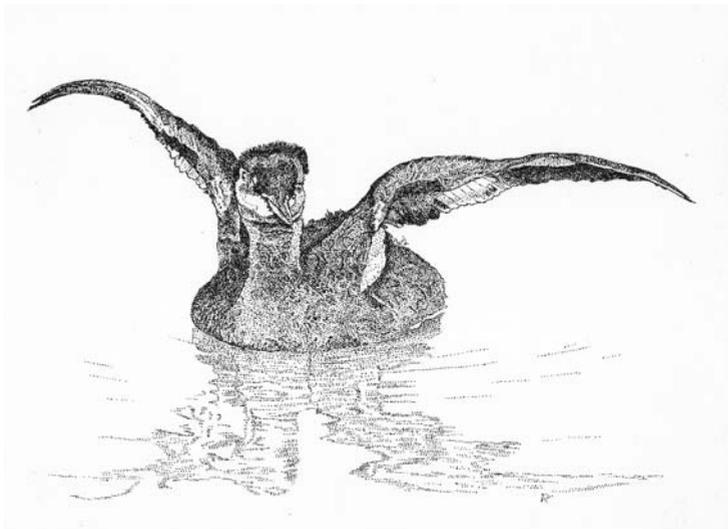
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Dank an Jan Johan (Han) Vlug

Thanks to Jan Johan (Han) Vlug

Sein vogelkundliches Leben hat Han Vlug weitgehend den Lappentauchern gewidmet. Ihn fesselten ihr Verhalten, ihre Biologie und Ökologie sowie die unterschiedlichen Anpassungsstrategien der einzelnen Arten. Begonnen hat alles mit dem Haubentaucher; ab 1965 hat er dessen Reproduktion an einigen Gewässern in Noord-Holland untersucht. Zum Vergleich besuchte er Gewässer in Masuren/Polen und in Mazedonien, die damals noch jenseits des „Eisernen Vorhangs“ lagen und schwer zu erreichen waren. In der Auswertung stellte er u.a. die Bedeutung umfangreicher Ufervegetation in großen Gewässern heraus (1979). Besonders intensiv widmete er sich über etliche Jahre den Mauserkonzentrationen im IJsselmeer, damals mit bis zu 20.000 Tauchern einer der bedeutendsten Mauserplätze Europas (1976). Ihren vorläufigen Abschluss fanden diese Studien in einer teilweise von seiner Frau illustrierten Monographie (1983), in der bereits alle Aspekte von Bestand und Verbreitung, über Biologie und Ökologie bis zum Verhalten angesprochen sind, die ihn noch heute beschäftigen.

Zu dem Zeitpunkt hatte er sich bereits dem Rothalstaucher zugewandt. Den Anstoß gab Band 1 der schleswig-holsteinischen Avifauna, wo er die damaligen Kenntnisse zu den Lappentauchern ausgebreitet fand. Der Rothalstaucher, farbenprächtig, mit einer besonders intensiven Balz, auf kleinen Gewässern lebend, in vielem ähnlich, aber doch ganz anders als der Haubentaucher, lud ihn förmlich zu Untersuchungen ein. In Schleswig-Holstein gibt es einen guten Bestand, von den Niederlanden aus relativ schnell und unkompliziert zu erreichen. Im Sommer 1980 reisten Rineke und Han Vlug an, und etwas später unternahmen wir die ersten gemeinsamen Exkursionen an Brutgewässern. Seitdem hat Han ein Archiv mit allen Brutbeständen und Reproduktionsdaten der Art von den Anfängen bis heute aufgebaut. Zurzeit hält er sich dreimal im Jahr, im Mai und Juli je zwei Wochen und zur Nachkontrolle eine Woche Anfang August, in Ostholstein auf, um Paare und Familien zu erfassen, und das seit 38 Jahren. Quartier nimmt er stets im Raum Selent, etwa im Zentrum des ostholsteinischen Verbreitungsschwerpunktes. Von dort sucht er die Brutgewässer meistens mit einem Mofa auf. Oft über anstrengend weite Strecken, in einem Sommer wie diesem nicht selten abends pitschnass ankommend.



Mit Rineke (†) und Han Vlug am Trenthorster Mühlenteich im Kreis Stormarn. – 21.7.1984.

With Rineke (†) and Han Vlug at the mill pond of Trenthorst in the district of Stormarn – 21.7.1984.



Han Vlug am Baggerteich in Westermarkelsdorf/Fehmarn, dem Gewässer, von dem die weltweit höchste Siedlungsdichte des Rothalstauers bekannt ist. – 30.7.2017. Fotos: G. Berndt.

Han Vlug at the flooded pit of Westermarkelsdorf on the island of Fehmarn. This stretch of water has the highest recorded density of Red-necked Grebe anywhere in the world.

Ab 1985 hat er wiederholt über seine Untersuchungen in Schleswig-Holstein im Corax Bilanz gezogen. Dadurch gehört der Rothalstaucher in Schleswig-Holstein (und Deutschland) zu dem am besten untersuchten Vogelarten. Hans Arbeiten sind keine reine Brutstatistik, sondern schließen Biologie und Ökologie ein. Ohne

diese Untersuchungen hätten wir nur einen Bruchteil der Kenntnisse und keinen landesweiten Überblick. Als nächstes steht sicher eine Arbeit über die Ergebnisse bis zum Jahr 2018 an.

Mit Hilfe der weltweiten Literatur zu Lappentauchern und einer Korrespondenz mit diversen Ornithologen im Ausland hat sich Han Kenntnisse angeeignet, die er insbesondere in Betrachtungen und Gedanken zur Biologie und Ökologie anwenden kann. Daraus resultiert wie von selbst die spannende und eine Untersuchung krönende Frage nach der ökologischen Einnischung der einzelnen Lappentaucher-Arten, ihren Unterschieden und Gemeinsamkeiten, ihren Interaktionen. Bei einer noch nicht publizierten Arbeit zu den Strategien des Haubentauchers konnte ich mit ihm zusammenarbeiten. Solche Fragen spielen auch in der vorliegenden Rothalstaucher-Monographie eine große Rolle. Es ist eine Ehre für die Ornithologische Arbeitsgemeinschaft, dass Han Vlug diese ein Ornithologenleben bilanzierende Studie im Corax veröffentlicht.

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Rolf K. Berndt

Ziel der Ornithologischen Arbeitsgemeinschaft (OAG) ist es, die Vogelwelt Schleswig-Holsteins und Hamburgs zu erforschen und zu ihrem Schutz beizutragen.

Schleswig-Holstein hat aufgrund seiner Lage zwischen Nord- und Mitteleuropa sowie Nord- und Ostsee eine herausragende Bedeutung im eurasisch-afrikanischen Vogelzugsystem und als Rast-, Mauser- und Überwinterungsgebiet für arktische Wat- und Wasservögel („Vogelzuglinie“ Fehmarnbelt, Wattenmeer). Die Vielzahl unterschiedlicher Lebensräume führt auch bei den Brutvögeln mit mehr als 200 Arten zu einem besonderen Reichtum.

Die Mitglieder der OAG verbindet das Interesse an der Beobachtung und Erforschung der schleswig-holsteinischen Vogelwelt. In vielen Untersuchungen und Gemeinschaftsprojekten werden gezielt Bestandserfassungen einzelner Arten oder Artengruppen durchgeführt, ökologische Zusammenhänge aufgedeckt, Wechselwirkungen zwischen Landschaft und Vogelwelt untersucht sowie langfristige Veränderungen dokumentiert. Dabei ist es häufig auch Ziel, zusammen mit anderen Verbänden zum Schutz der Natur beizutragen. Die OAG bietet aber genauso denjenigen ein Dach, die hauptsächlich Spaß an gemeinsamer Vogelbeobachtung haben und sich gerne mit Gleichgesinnten austauschen.

Derzeit sind in der OAG über 600 Einzelmitglieder sowie zahlreiche Institute, Museen und Bibliotheken im In- und Ausland vereint.

Folgende **Projekte** werden von der OAG langfristig organisiert (nähere Informationen z. B. auf der OAG-Homepage <http://www.Ornithologie-Schleswig-Holstein.de>):

- Vogelzug-Planbeobachtungen
- Wintervogelzählung
- Internationale Wasservogelzählung (monatlich September bis April) sowie Zwergschwannerfassung
- Monitoring häufiger Brutvögel in der Normallandschaft
- Brutbestandsaufnahmen und Siedlungsdichteuntersuchungen ausgewählter Arten und Lebensräume.

Daneben ist die OAG an verschiedenen Erfassungs- und Schutzprogrammen für Greifvögel (z. B. Projektgruppe Seeadlerschutz, BfN-Projekt “Rotmilan - Land zum Leben“) beteiligt. Sie arbeitet bei Bestandserfassungen eng mit der Naturschutzverwaltung des Landes und dem Dachverband Deutscher Avifaunisten (DDA) zusammen und unterstützt auch private Arbeitsvorhaben. Gelegenheitsbeobachtungen sind gleichfalls wichtige Mosaiksteine für ein Bild von der Vogelwelt Schleswig-Holsteins. Diese können Sie direkt im Meldeportal unter www.ornitho.de eingeben.

Mit einem umfangreichen **Vortragsprogramm** findet jeweils Anfang März die Jahrestagung der OAG statt. Gäste sind herzlich willkommen. Im Kieler und Lübecker OAG-Arbeitskreis stellen Mitglieder bei monatlichen Treffen Arbeitsvorhaben und -ergebnisse vor, diskutieren aktuelle Geschehnisse oder führen gemeinsame Exkursionen durch.

In Hamburg wird die OAG durch den Arbeitskreis an der Staatlichen Vogelschutzwarte vertreten.

Der aktuellen **Information** der Mitglieder dienen die Rundschreiben, die i. d. R. dreimal jährlich erscheinen, die interne Mail-Gruppe und die Homepage im Internet.

Die **Veröffentlichungen** der OAG haben weit über die Grenzen Schleswig-Holsteins und Hamburgs hinaus einen guten Ruf. Schon ihretwegen ist der Anteil der Mitglieder aus anderen Ländern hoch.

In der Zeitschrift **CORAX** werden wissenschaftliche Artikel zur Vogelwelt Schleswig- Holsteins und Hamburgs publiziert. Schwerpunkte sind die Entwicklung von Vogelarten und -gemeinschaften in Lebensräumen Schleswig-Holsteins sowie überregional interessante Arbeiten zur Biologie und Ökologie der Vögel. Der CORAX erscheint etwa zweimal im Jahr und wird den Mitgliedern kostenlos zugeschickt.

Die „**Vogelwelt Schleswig-Holsteins**“ als Buchreihe im Wachholtz-Verlag, Neumünster, ist ein langfristig angelegtes Gemeinschaftsvorhaben der OAG. Bisher sind 7 Bände (Seetaucher bis Flamingo, Greifvögel, Entenvögel I und II, Brutvogelatlas, Seltene Vogelarten und Zweiter Brutvogelatlas) sowie als Band 8 **Geschichte der Feldornithologie in Schleswig-Holstein und Hamburg** erschienen.

Mit ihren Untersuchungen, Auswertungen und Veröffentlichungen liefert die OAG wesentliche wissenschaftliche Grundlagen für den Schutz der Vögel und ihrer Lebensräume in Schleswig-Holstein.

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