





Comparative studies of behaviour in allopatric subspecies of Grebes, Podicipedidae

Black-necked Grebe Podiceps nigricollis (Brehm 1831) and White-tufted Grebe Rollandia rolland (Quoy & Gaimard 1824)



André Konter



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Comparative studies of behaviour in allopatric subspecies of Grebes Podicipedidae

Black-necked Grebe *Podiceps nigricollis* (Brehm 1831) and White-tufted Grebe *Rollandia rolland* (Quoy & Gaimard 1824)

In the Linnaean system of taxonomy, the class Aves is further subdivided into orders, families, genera and species. According to Mayr (1970) and Campbell and Lack (1985), "to most biologists, species are groups of interbreeding natural populations that are reproductively isolated from other such groups". At a lower rank than species, subspecies or races can be defined. Different subspecies of a same species are generally distinguishable because of (often slight) morphological differences in size, in plumage coloration or in other criteria that are not sufficient to prevent interbreeding. Such subspecies are either clinal in their distribution or even geographically isolated, at least during the breeding season. In practice, we often do not have a positive proof of interbreeding and we cannot be entirely confident about the taxonomic status of the segregated populations.

Species are thought to arise predominantly through a process called the allopatric model of speciation which is initiated if an ancestral population is split (Lande 1980, Mayr 1970). In an evolutionary timeframe, the subpopulations may then develop into distinct species under the condition that their geographic isolation with no genetic exchange persists for long enough. As long as the subpopulations remain then separated, the status we confer to them is largely based on our appreciation of the morphological, behavioural and genetic differences that we observe.

The preceding theoretical considerations clarify already that a strict separation into different species or subspecies of two geographically separated populations of similar birds is not straightforward. There is not one single criterion or one measure that would trigger a sharp taxonomic separation to tell us where a subspecies ends and a species starts. We are rather in the presence of a continuum where we have to judge and weight the differences found. Especially for bird populations that are geographically completely isolated from one another, it may be largely a matter of taste whether we confer species or subspecies rank to them.

In the family of grebes Podicipedidae, the situation is not different from that in other families of birds. For some members, geographically isolated subpopulations are treated as subspecies although we are not entirely confident that the locally evolved traits are perhaps sufficient for species rank. For others, the classification into allopatric subspecies has never been really challenged. The two studies presented in continuation now investigate the courtship rituals of recognized geographical subspecies of two species of grebes.

In the case of the Black-necked or Eared Grebe *Podiceps nigricollis*, the status of the three existing subspecies in North America, Europe and Africa is so far not subject to controversy and, in literature, minimal differences between them in coloration and size have been described. Possible behavioural deviations are however less clear as there is much cross-referencing in the description of their pair bonding displays and differences may perhaps remain masked. For the American and European subpopulations, the first study focuses largely on courtship as the pair bonding behaviour is critical to speciation. It aims at clarifying the rituals used by each subspecies and at identifying possible differences.

The second species analysed is the South American White-tufted Grebe *Rollandia rolland*. Also here, we are in the presence of three recognized subspecies. There is however much discussion of whether the much larger nominate form from the Falkland Islands should have a separate species' status from that of the two continental forms. Due to the remote location of the Falkland Islands, it is partially a lack of knowledge about the behaviour of their subspecies in comparison to that of the other two subspecies that prevents progress in the discussion. This study presents the first rather exhaustive description of *Rollandia rolland rolland* from the Falkland Islands and compares its ethology, including water and platform courtship, to the knowledge published about the subspecies from the South American continent.

In the following, both studies are presented as separate papers.

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Courtship in European Black-necked Grebe *Podiceps nigricollis nigricollis* and American Eared Grebe *P. n. californicus*

A comparative study with some notes on the displays in the African Black-necked Grebe *P. n. gurneyi*

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<u>Keywords:</u> Black-necked Grebe, Eared Grebe, *nigricollis* grebe, subspecies, allopatry, courtship, display, ritual, ceremony, terminology, description of display

Abstract

The present study of courtship compares the displays of European Black-necked Grebes *Podiceps nigricollis nigricollis* to those of the North American subspecies, the Eared Grebe *P. n. californicus*. It aims primarily at clarifying uncertainties in the descriptions of the rituals that appear in literature and that partially insinuate that some displays are performed by one form and not by the other. The indications in literature are analysed in detail and lead to the establishment of a table listing areas of possible disagreement in courtship. It distinguishes basically between problems in the terminology of displays and problems in their descriptions and it lists displays possibly present in only one subspecies.

Fieldwork in Germany for the European nominate form and in Canada and in the United States for the North American subspecies allowed to draw a rather complete picture of displays and ceremonies occurring in pair bonding in both populations.

The comparative analysis first led to a partially revised terminology of courtship. A differentiation between Advertising (used in the context of mate selection and pair bonding) and Contact Calling (used to maintain or re-establish contact between partners or adults and their chicks) and a subdivision of Head Shaking as already applied for other species of grebes are introduced for nigricollis grebes. It is proposed to skip the term "Food Presentation" as a synonym for Billing or the Hunched Display. In Pivoting, four different posture adopted by the grebes were identified and they were named Low Inviting Posture, High Inviting Posture, Oblique Pivoting Posture and S-Pivoting Posture. Nestselection Display cannot generally replace the term "Inviting" as the display is performed also early in the season without apparent direct relation to nest selection. A differentiation between a Tall and a Plump Penguin Dancing introduced earlier by Fjeldså is supported. A split between Racing and Barging and a clearer differentiation between both and Parallel Swimming based on newly defined criteria are introduced. The term "Upright Rushing" is not supported as a synonym for Barging: the term is already used differently in other species of grebes. A differentiation between Pattering Retreat and the more complex Retreat Ceremony that includes a repetition of the Discovery Ceremony is proposed. The term "Weed Trick" suggests that after weed fetching Weed Dancing occurs. Therefore, Weed Presentation should be used in all cases where the dancing does not occur. Mate Guarding is considered to be behaviour and is discarded as a display; it is also differentiated from Unison Diving.

The comparative analysis of the rituals themselves identified a close relation between Pivoting and Inviting; both displays were observed to grade into one another and could likewise be followed by Weed Presentation. Generally, *nigricollis* grebes showed great variability in the way individuals of the same subspecies performed a display. However, no display was performed by only one subspecies and differences in the performances of displays between both forms seem a priori to be absent. Similarly, in the sequencing of displays no relevant differences appeared. In conclusion, the additional knowledge and confirmations resulting from this study support the present subspecies status for Eared and Black-necked Grebes.

The methodology applied did not foresee any statistical analyses which could have revealed an imbalance in the usage of different displays by the two subspecies and the calls of both forms were not analysed. A single small difference may however be crucial for a split as was the case with the Advertising call of *Aechmophorus* grebes. Future studies should consider these aspects. <u>Schlüsselwörter:</u> Schwarzhalstaucher, amerikanischer Schwarzhalstaucher, *nigricollis*-Lappentaucher, Unterart, Allopatrie, Balz, Ritual, Zeremonie, Terminologie, Beschreibung des Balzverhaltens.

Zusammenfassung

Die vorliegende Studie über das Balzverhalten vergleicht die Rituale der europäischen Schwarzhalstaucher *Podiceps nigricollis nigricollis* mit denen der nordamerikanischen Unterart *P. n. californicus.* Vorrangiges Ziel war dabei, Ungereimtheiten in den Beschreibungen der Balzparaden aus der Literatur, die Unterschiede zwischen den Unterarten suggerieren, zu beseitigen. So werden Literaturangaben detailliert untersucht, und aus ihnen ergibt sich eine Tabelle, in der mögliche Unterschiede im Balzverhalten beider Unterarten festgehalten werden. Diese Auflistung unterscheidet zwischen Unklarheiten in der angewandten Terminologie und in der Beschreibung der Vorgänge, und sie zählt Rituale auf, die vielleicht nur in einer Unterart vorkommen.

Die Feldarbeiten in Deutschland, Kanada und den USA erlaubten eine nahezu vollständige Darstellung aller Balzhandlungen der europäischen und nordamerikanischen Schwarzhalstaucher.

Die vergleichende Studie führte zuerst zu Klarstellungen in der Terminologie der Balzparaden. So wurde zwischen Advertising (Junggesellen Pose) und Contact Calling (Kontaktrufen) unterschieden. Während ersteres das Rufen nicht verpaarter Vögel auf der Suche nach einem Partner beinhaltet, wird beim Kontaktrufen das Zusammenbleiben von Partnern und ihren Nachkommen gefördert. Das Kopfschütteln wurde in die verschiedenen Arten unterteilt, die auch schon bei anderen Lappentauchern zur Anwendung kamen. Es wird vorgeschlagen, Food Presentation (Futterpräsentieren) nicht mehr als Synonym für Billing oder Hunched Display (Schnäbeln) zu benutzen. Beim Pivoting (Drehbalz) wurden vier verschiedene Haltungen der Schwarzhalstaucher identifiziert: Low Inviting Posture (niedrige Einladungshaltung), High Inviting Posture (Hohe Einladungshaltung), Oblique Pivoting Posture (schräge Drehhaltung) und S-Pivoting Posture (S-Drehhaltung). Nest-Selection Display (Nestwahlparade) kann nicht allgemein Inviting (Einladungshaltung) ersetzen, da dieses Verhalten schon früh im Jahr und losgelöst von der Nistplatzsuche auftritt. Eine Differenzierung, wie von Fjeldså vorgeschlagen, zwischen Tall und Plump Penguin Dancing (hohes und niedriges Pinguintanzen) wird unterstützt. Eine Unterscheidung zwischen Racing (Rennen) und Barging (Paralleles Aufrechtrennen) und eine deutlichere Abgrenzung zwischen beiden und Parallel Swimming (Parallel Schwimmen), welche auf neu erstellten Kriterien beruht, wird eingeführt. Upright Rushing sollte nicht als Synonym für Barging verwendet werden, da der Ausdruck schon anders für eine andere Lappentaucherart Verwendung findet. Es wird vorgeschlagen, Pattering Retreat (Fluglaufrückzug) und die zusammengesetzte Retreat Ceremony (Rückzugszeremonie), welche eine Wiederholung der Entdeckungszeremonie beinhaltet, zu unterscheiden. Der Ausdruck Weed Trick (Pflanzenbalz) legt nahe, dass nach dem Auftauchen mit Pflanzen auch Weed Dancing (Pflanzentanz) erfolgt. Deshalb sollte der Ausdruck Weed Presentation (Materialpräsentieren) in allen Fällen angewandt werden, in denen der Tanz nicht vollzogen wird. Mate Guarding (Partnerbewachung) sollte nur allgemein als Verhalten und nicht spezifisch als Balzritual betrachtet werden. Es kann somit nicht als Synonym für Unison Diving (Gemeinschaftstauchen) gelten.

Die vergleichende Analyse der Balzvorgänge selbst stellte eine enge Beziehung zwischen Pivoting und Inviting fest. Beide Rituale können ineinander übergehen und nach beiden kann gleichermaßen Materialpräsentieren erfolgen. Allgemein zeigten die Schwarzhalstaucher beider Populationen eine große Variationsbreite in der Art wie einzelne Paare ein Balzritual durchführten. Allerdings wurde kein Ritual gefunden, welches nur von einer Unterart vorgeführt worden wäre. Auch scheinen a priori keine Unterschiede in der Art der Ausführung der einzelnen Rituale zwischen beiden Unterarten zu existieren. Genauso wenig konnten relevante Unterschiede in der Reihenfolge der Balzvorgänge festgestellt werden. Zusammenfassend kann gesagt werden, dass die Resultate aus dieser Studie die heutige Unterteilung der Schwarzhalstaucher Europas und Nordamerikas in zwei Unterarten bestätigen.

Die angewandte Methodologie sah keine statistischen Analysen vor, welche vielleicht ein Ungleichgewicht in der Häufigkeit der verschiedenen Rituale zwischen beiden Populationen festgestellt hätte. Auch wurden die Rufe beider Unterarten nicht weiter untersucht. Dabei kann aber schon ein kleiner Unterschied entscheidend sein, wie das Beispiel der Balzrufe der Renntaucher *Aechmophorus sp.* zeigt. Zukünftige Studien sollten deshalb auch diese Gesichtspunkte berücksichtigen. <u>Mots-clés:</u> Grèbe à cou noir, Grèbe à cou noir américain, grèbes *nigricollis*, sous-espèce, distribution allopatrique, parades nuptiales, rituel, cérémonie, terminologie, description des parades.

Résumé

La présente étude compare les parades nuptiales des Grèbes à cou noir européens Podiceps nigricollis nigricollis à celles de la sous-espèce nord-américaine P. n. californicus. Elle vise primairement à clarifier des incertitudes dans la description des danses rituelles provenant de la littérature existante qui en partie semblent insinuer que certaines parades surviennent dans une population, mais pas dans l'autre. Les indications de la littérature sont analysées en détail et permettent l'établissement d'une table qui énumère les domaines où potentiellement des différences dans les parades nuptiales des deux sous-espèces pourraient exister. Le résultat distingue à la base les problèmes provenant de la terminologie employé et ceux résultants de la description des parades et il énumère séparément des rituels qui sont peut-être présents seulement pour une sous-espèce.

Les recherches sur le terrain en Allemagne pour la forme nominale du Grèbe à cou noir et au Canada ainsi qu'aux Etats-Unis pour la sous-espèce nord-américaine permettaient l'établissement d'un inventaire complet des parades et cérémonies nuptiales survenant dans les deux populations.

L'analyse comparative de cet inventaire menait d'abord à une révision partielle de la terminologie en la matière. Une différenciation entre Advertising (cri servant dans le contexte de la recherche d'un partenaire) et Contact Calling (cri similaire servant le maintien ou le ré-établissement du contact entre deux partenaires ou les adultes et leurs jeunes) et une subdivision de Head Shaking (secouement de tête) comme déjà appliqué à d'autres espèces de grèbes sont introduites pour les grèbes nigricollis. Il est proposé de ne plus utiliser le terme Food Presentation (offre de nourriture) comme synonyme pour Billing ou Hunched Display (se becqueter). En matière de Pivoting (pivotement), quatre attitudes différentes adoptées par les grèbes ont été identifiées: Low Inviting Posture (invitation allongée), High Inviting Posture (invitation tête haute), Oblique Pivoting Posture (pivotement avec tête avancée) et S-Pivoting Posture (pivotement avec cou en S). Nest-Selection Display (parade de sélection de nid) ne peut pas généralement remplacer le terme Inviting comme le rituel se déroule également tôt dans la saison de reproduction sans relation apparente à un processus de sélection d'une place pour la nidification. Une différenciation comme proposé par Fjeldså entre Tall et Plump Penguin Dancing (danses de pingouin basses

et élevées) est supportée. Une distinction entre Racing (course parallèle) et Barging (progression parallèle en pingouin) ainsi qu'une différenciation plus nette entre les ceux termes ainsi qu'avec Parallel Swimming (nager en parallèle) basée sur des critères nouvellement définis sont introduites. Le terme Upright Rushing (ruée verticale) ne doit pas servir de synonyme à Barging (avancer en péniche) comme il est déjà utilisé autrement pour une autre espèce de grèbe. Une distinction entre Pattering Retreat (vol de retraite) et Retreat Ceremony, une cérémonie de retraite plus complexe qui inclut une répétition de la Discovery Ceremony (cérémonie de la découverte) est proposée. Le terme Weed Trick (combine des plantes) suggère que le plongeon servant à aller chercher des débris de plantes est suivi de Weed Dancing, une danse entre les partenaires brandissant les plantes. En conséquence. Weed Presentation (présentation de plantes) devrait être utilisé dans tous les cas où la danse n'est pas présente. Mate Guarding (garde du partenaire) est considéré comme un comportement au sens large sans être une parade nuptiale qui doit être différencié d'Unison Diving (plongée commune).

L'analyse comparative des parades nuptiales ellesmêmes identifiait une relation étroite entre Pivoting et Inviting: les deux rituels pouvaient facilement s'entremêler et Weed Presentation pouvait suivre à tous les deux. Plus généralement, les Grèbes à cou noir montraient une grande variabilité dans la façon dont des individus de la même sous-espèce exécutaient une même parade. Cependant, aucun rituel ne concernait qu'une seule sous-espèce et des différences géographiques dans les performances d'une même parade sont à priori également absentes. Il en est de même dans les séquences des parades. En conclusion, les confirmations et les connaissances additionnelles résultant de la présente étude supportent bien le statut de sous-espèce pour les populations européennes et nord-américaines du Grèbe à cou noir

La méthodologie appliquée ne prévoyait pas d'analyses statistiques qui auraient permis de conclure à un usage différent des différentes parades nuptiales par les deux populations et les cris des sous-espèces n'étaient pas analysés. Or une petite différence peut déjà être cruciale pour une évaluation différente du statut taxonomique comme le montre le cri de l'Advertising des grèbes du genre *Aechmophorus*. Des études futures devraient prendre en compte ces aspects.

1 Introduction

Grebes Podicipedidae are a family of waterbirds with a worldwide distribution, except for the regions of the poles. They count 22 known species subdivided into seven genera. The Black-necked Grebe *Podiceps nigricollis* or Eared Grebe, as the species is called in North America, belongs to the genus *Podiceps*, the most numerous with a total of eight species. *Podiceps nigricollis* inhabits large parts of Europe, Asia, Africa and North America. Due to its large American population, it is the most common grebe in the world. Three subspecies are recognized:

Podiceps nigricollis nigricollis, for which the term Black-necked Grebe will be used throughout this text; it is distributed irregularly over western and central Europe and northern Asia, and more regularly from eastern Europe to central Asia.

Podiceps nigricollis californicus, called Eared Grebe here. It is found over large parts of central and western North America, from southern Canada to the southern United States.

Podiceps nigricollis gurneyi is patchily distributed over Africa south of the Sahara. In the following, the name African Black-necked Grebe is retained for it.

The Colombian Grebe Podiceps andinus was considered initially as an additional subspecies of Podiceps nigricollis and opinions about its taxonomic rank have varied (Fjeldså 1993). Fjeldså and Krabbe (1990) regarded it as an allospecies owing to its apparently more primitive characters, however more recent DNA investigations found it not to differ from the North American Eared Grebe (van Tuinen, pers. comm.). This grebe endemic to the tableland of Bogota and Ubate, Colombia, closely resembled in all plumages the Black-necked Grebe, displaying however always a chestnut fore-neck and upper breast when breeding. It was recognized as a separate species in 1959 (Meyer de Schauensee). Blake (1977) listed it under the heading Podiceps nigricollis andinus although he admitted that it could possibly be a species distinct from P. nigricollis. He reported it to have much darker and more chestnut auricular plumes than *californicus*. In addition, its wings were shorter and its bill heavier. The last official sighting of the Colombian Grebe occurred in

1977 when a census recorded three remaining pairs. Extensive search in 1981 and 1982 failed to find it (Fjeldså 1993). In July 2001, more than 500 individuals were possibly observed breeding colonially at three different locations on Lake Tota (Jiménez II & Jiménez 2005). However, the record was not confirmed. Moreover, surveys on Lake Tota between 2003 and 2006 failed to detect the presence of the grebe (Zuluaga Bonilla & Macana 2008). The species is now considered extinct (BirdLife International 2008). As no description of the courtship displays of the Colombian Grebe is available (Fjeldså 2004), this grebe could not be included in the study.

Biologically, animal individuals that actually or potentially interbreed in nature are considered to belong to a single species. For populations that are geographically isolated, this concept has its limitations. More generally however, geographical separation is a first step in speciation. In the present allopatric distribution of the three subspecies of Podiceps nigricollis, natural barriers prevent regular contacts between the populations. The Sahara in the north, the Indian Ocean in the East and the Atlantic Ocean in the west isolate gurneyi. The geographical area of californicus is delimited by the Pacific and Atlantic Oceans and nigricollis is prevented from contact with the two other subspecies by the three oceans and the Sahara.

In an evolutionary timeframe, geographic isolation may lead to genetically distinct populations and to the development of isolating mechanisms or boundaries that prevent random mating between subpopulations if they were to reunify. In the very long run, the lack of contact and genetic exchange might then lead to separate species rather than subspecies status for the subpopulations. Differences sufficient to consider a split for isolated populations of a common stem into separate species do not show up all of a sudden. They are the result of an evolutionary process that needs time. Evolutionary deviations may express in morphology, ecology or ethology. Behaviour in general and displays during pair bonding in particular are however most critical to speciation.

Together with physical character traits and ecological requirements, the comparison of displays greatly helped to organize birds into different orders and families, and to distinguish different genera that again could be more or less closely related within a family. For the interpretation of courtship rituals, it is assumed that displays evolved out of more general behaviours related to comfort or aggression that became ritualized in time and thereby changed their meaning. According to Fjeldså (1985), a simple display is more primitive than a complex one and a display that is close to an apparently non-ritualized activity is more primitive than an apparently homologous display which is stereotyped.

As in other bird families, the rituals of grebes serve mate choice and the strengthening of pair bonds and they constitute a more or less strong barrier against hybridization with other species. Courtship has a bond-forming role in which the mutual and reciprocal ceremonies function to inhibit and absorb such pair disrupting influences as aggression and fear. They are essentially appeasing displays and function mainly during that critical, transitional period coming between winter individuality and the occasion of maximum sexual cooperation at copulation (Simmons 1970).

In water courtship of grebes, differences in the rituals and even more different rituals insure that a grebe will mate with an individual of its own species or, in other words, they prevent individuals belonging to separate species from forming pairs. Generally, the plumed grebes, Horned P. auritus, Red-necked P. grisegena, Great Crested P. cistatus, Black-necked or Eared, Hooded P. gallardoi, Silvery P. occipitalis and Junín Flightless Grebe P. taczanowskii, show displays with stereotyped head shaking, upright dancing and rushing and a discovery ceremony, in which several stereotyped elements follow one another in an almost fixed sequence, but with interspecific differences (Fjeldså 1985). The situation in the subpopulations of *nigricollis* grebes is unclear in this respect. Published knowledge insinuates that differences in behavioural traits might exist, but remains silent of whether these could be meaningful in the context of species recognition. A comparative study of courtship displays is therefore needed to clarify possible differences in the rituals of the three subspecies that may have evolved so far.

Whereas little has been published about the courtship of the African Black-necked Grebe, the displays of the European Black-necked and the North-American Eared Grebe have been described in detail, especially by Prinzinger (1979),

McAllister (1958) and Palmer (1962). All three authors have however largely based their work on only one subspecies and have not themselves studied the behaviour of the others. As a consequence, their comparisons remain superficial. Later authors often either relied on the published descriptions for the subspecies in the focus of their interest or mixed up the displays listed for both subspecies. One might therefore doubt whether differences in the pair bonding activities of the subspecies are correctly reflected in more recent literature.

In colonial species, pair formation between two individuals does generally not progress without intervention of other conspecifics. In territorial species, the sudden appearance of a competitor will lead to harsh ritualized aggression often followed by physical dispute. Colonial grebes can however not constantly fight or otherwise attack potential rivals; aggression might possibly be less intense and express itself differently. For instance, in Western Aechmophorus occidentalis or Silvery Grebes, rivals of the same sex may display together and they try to convince with harmless competition rather than fight. It might not always be possible to clearly differentiate between pure courtship displays and ritualized aggression, also because many pair bonding displays arose out of ritualization of initially aggressive behaviours. However, a picture of the behavioural differences in pair bonding of *nigricollis* grebes is incomplete if it ignores all competitive interactions.

This paper aims at analysing differences in courtship in its widest meaning, i.e. including ritualised competitive behaviour, between Blacknecked and Eared Grebes. It focuses on water courtship considered as essential in speciation and only briefly describes platform courtship. The prime intention is to establish an accurate and comprehensive catalogue of courtship rituals in both subspecies. As a by-product of the clarifications, an assessment of possible areas of differentiation becomes possible. The African Black-necked Grebe is only marginally included in the analysis. On one hand, the lack of published descriptions about its courtship prohibits a meaningful comparison. On the other, at the places in Kenya and South Africa visited by the author and holding the subspecies, the grebes did hardly display.

The material and methods part of this work is followed by a summarized presentation of the published knowledge about the courtship displays and competitive interactions of all three subspecies. In continuation, the results of the fieldwork in Europe and North America are presented in a way to obtain a full picture of the behaviours of *nigricollis* and *californicus* and focusing on areas of contention that arose from literature. Finally, the appearing ethologic differences will be discussed.

2 Material and methods

Terminology: As defined by Moynihan (1955 in Nuechterlein & Storer 1982), a display or ritual is defined as a behavioural pattern or posture that is ritualized or adapted for signal function. Grebe displays are often organized into highly stereotyped sequences called ceremonies and defined as formalized interactions involving two or more birds and a combined performance or two or more displays in a predictable sequence (Smith 1977 in Nuechterlein & Storer 1982).

Published knowledge about courtship rituals: Ornithological books, species accounts and major ornithological journals in Europe, North America and South Africa were searched for descriptions of and indications about courtship displays of Podiceps nigricollis. The findings were summarized per subspecies. Some authors (Cramp & Simmons 1977, Fjeldså 2004, Bauer & Glutz 1987, Koop 2003,...) based their descriptions at least partially on material stemming from European and North American populations without clear geographical differentiation. Without an unambiguous indication about the performing subspecies, such descriptions were not retained here.

Fieldwork in Europe: All observations of European Black-necked Grebes occurred at the Nature Reserve of the Wagbachniederung, Baden-Wurttemberg, Germany, about 30 km north of Karlsruhe, elevation 95 m a.s.l.. This protected area covers about 224 ha. It developed from a former arm of the Rhine that was naturally separated from the main river some 8,000 years ago. Today the area is dominated by a big gravel pit excavated from 1973 to 1980, the sewage ponds of a former sugar factory and some surviving original reed *Phragmites australis* surfaces (Lohmann & Haarmann 1989). The sugar factory ceased activities early in the 21st century, and the reserve experienced lower water levels due to the missing sewage waters. Meanwhile, the competent authorities have put in place an alternative water provisioning system.

In spring of the years from 2001 to 2007, regular trips to the nature reserve allowed to get acquainted with the place. These were not yet organized with the intention to analyse the courtship rituals of the Black-necked Grebes. Detailed observations of displays were recorded only occasionally. From 2008 to 2011, all courtship displays were monitored. In these years, the author and one or two helpers were present at the nature reserve on 2 and 3 May 2008, on 28 and 29 March, 14, 25 and 26 April, 10 and 11 May 2009, on 2 April and from 5 to 11 April 2010 and from 19 to 23 April 2011. In total, 22 days of observation occurred. Daily fieldwork lasted between five and eight hours and generally started at around 8 a.m.

In 2008, 2009 and 2011, over 90% of the observations concerned pond 3C (N 49°15.647, E 8°31.011). It was generally not used by the grebes for breeding although some platform construction attempts were observed. All other records stemmed from pond 4B (N 49°15.694, E 8°31.190) that in 2006 exceptionally hosted a colony of six platforms. These disappeared shortly after their construction, destroyed by heavy rainfalls. In 2010, the observations were about equally spread between ponds 3C and 4B as unusually many grebes were present on pond 4B.

Access to the reserve is by walking. The courtship of the grebes was followed from the shore with Zeiss 10x25 binoculars. Digital photographs were taken with a Sigma AF 800 mm lens mounted on a Minolta Dynax 7D camera. In addition, many displays were filmed with a Sony Handycam. Tape recorded field notes complemented the observations and helped to keep track of the occurrences. A major part of the displays was performed at less than 20 m from the shore, and optical help was not always needed to follow the action closely.

To provide an idea about the size of the Blacknecked Grebe population at the Wagbachniederung, Table 1 displays the maximum numbers of grebes for different time periods as reported on the website http://www.norbert-kuehnberger. de/wagbach.htm, complemented by own counts. It appears that the numbers built up generally on ponds 3C and 4B in March and reached their

Table	1: Maximum	numbers of	Black-necke	d Grebes	recorded	at the \	Wagbachniede	erung in
	different	years based	l on records	reported	at http:/	//www.r	norbert-kuehr	berger.
	de/wagba	ch.htm and	own counts	(mårked w	vith *).			-

Year	1-15 March	16-31 March	1-10 April	11-20 April	21-30 April	1-10 May	11-20 May	21-31 May
2005	1	18	30		18	5	10	16
2006	/	/	33	50	50	/	4	/
2007	7*	30*	55*	/	15	22	/	/
2008	5	32	38	40*	/	24*	4	4
2009	5	27*	17	20	22	20	12*	/
2010	/	/	39	21	6	/	>16	>14
2011	/	/	/	/	24*	/	/	/

maximum in the first decade of April. The birds then dispersed to the ponds that are used for breeding perhaps from mid-April or early May onwards. There, they remained largely hidden for observers. The local movements explain part of the low counts in May, but the numbers may also be lower because non-breeders possibly migrate at least partially to other places. First families generally appear in late May or early June. During this field study, the numbers of grebes present fluctuated between seven and 55.

Fieldwork in North America: Eared Grebes were observed at Oak Hammock Marsh, Manitoba, on 18 May 2008, at a shallow body of water near Blaine Lake, Saskatchewan, on 24 May 2008 and at Little Manitou Lake, Saskatchewan, on 25 and 27 May 2008. In addition to the sites in Canada in 2008, the following sites in the US were visited from 14 to 27 May 2011: Upper Klamath Lake and Lake Ewauna, both in southern Oregon, Lower Klamath Refuge and Tule Lake Refuge, both in northern California. On most of the 18 days, fieldwork lasted from 7 a.m. to 5 p.m.

Oak Hammock Marsh, located some 20km north of Winnipeg, was accessed on foot. It is a wetland of international importance under the Ramsar Convention. The original marsh covered close to 470 km² near the south-western corner of Lake Winnipeg. The 36 km² of Wildlife Management Area of today comprise the persisting and partially restored prairie marsh consisting of approximately 20 km². Parts of the marsh can be easily surveyed from the elevated tracks on the dykes leading into it. About 30 grebes present close to the dyke were observed for about five hours. Little Manitou Lake is an extremely saline lake of ca. 13 km² located 51°44 N and 105°30 W, near Manitou Beach and about 100 km SE of Saskatoon. A population of 53 Eared Grebes was observed there out of a parked car from the dam-road cutting the eastern edge of the lake. The third Canadian place of observation was west of the settlement of Blaine Lake (52°49 N and 106°57 W). The body of water is cut in two by a rural road. 66 Eared Grebes were present in the southern part (another 18 in the northern part). All observations were executed from the rural road using a car as a blind.

Upper Klamath Lake is a natural water basin and the largest freshwater lake in Oregon. It has a total length of 32 km and is about 13 km wide. Observations at Upper Klamath Lake were limited to Putnam Point (elevation 1,260 m, 42°14.302 N, 121°48.460 W) located at the southern end of the lake between Moore Park and Pelican Marina where some 20 Eared Grebes were present. The elongated Lake Ewauna (elevation 1,238 m, 42°13.130 N, 121°47.299 W) is connected to Upper Klamath Lake by the Link River, the head-water of the Klamath River. Lake Ewauna is about 2 km long and 0.5 km wide. Less than 20 Eared Grebes were counted close to the city shore. Both Oregon Lakes were surveyed on foot. The bodies of water of the Klamath valley in California are known to receive each year thousands of Eared Grebes for nesting, water levels permitting. The two lakes visited there are part of the Klamath Basin National Wildlife Refuges. Tule Lake Refuge (41°52.510 N, 121°32.670 W) is an artificial water impoundment of mostly open water covering about 5,250 ha and surrounded by croplands in an altitude of 1,220 m. Lower Klamath National Wildlife Refuge (elevation 1,240 m, 41°57.367 N, 121°42.196 W) consists of a mix of shallow freshwater marshes, open water, grassy uplands and cropland covering some 18,000 ha (U.S. Fish & Wildlife Service 2008). Fieldwork in both Oregon refuges was executed using a car as a blind. The car was parked at suitable places along the auto tours leading through the refuges. It then remained immobile for periods of time up to three hours. Unit 2 of Lower Klamath Lake was in addition observed from stops along Stateline Road 161. Stopping places surveyed inside the Oregon refuges held up to 300 Eared Grebes and in both refuges, in total over 2,000 Eared Grebes were recorded.

At all North American locations, the behaviour and the displays of the grebes were followed from the shore with Zeiss 10x25 binoculars. As in Europe, they were documented by photo (Sigma AF 800 mm lens mounted on a Minolta Dynax 7D camera), video film (Sony Handycam) and immediate voice recording.

Sex recognition: As in grebes both sexes look very much alike, it was generally not possible to distinguish males from females. Bill length can however be used to sex Eared Grebes with over 90% accuracy (n=614, Jehl et al. 1998). In a few observations, this criterion was applied to sex the performing birds.

3 A few postures of *nigricollis* not directly related to courtship

Postures assumed in displays may be derived from behaviours occurring in daily life. It is therefore useful to present here a brief summary of regular bearings observed in *nigricollis*. Unless otherwise stated, the descriptions are based on the postures reported by Prinzinger (1979) for the Black-necked Grebe. To help the description, some attitudes of ornamental feathers, neck or body were clearly defined and named.

The ear tufts may be subject to lateral and vertical positioning. Vertically, they may be **fanned out** completely, **shut** or **relaxed**. In the first case, they

are most conspicuous as the area covered by the yellow tufts is maximal. In the second case, this field is minimal. Laterally, the tufts may be **depressed**, completely pressed against the head, or they may be flared out. If the tufts are laterally depressed, the naming of the vertical positioning is simply retained in the following, except that for shut, **sleeked** may also be used. If fanned out and flared out, the tufts are said to be **flared out**.

The neck may be held vertically rather straight or curved to a greater or lesser extent. If not straight, the neck may take three basic forms. First, there is the high S-form in which the lower neck is slightly bent forward and the upper neck slightly vaulted backward. Second, in the low s-form, both curvatures are more marked and the entire form described by the neck is more compressed. Third, the neck may be kind of retracted or folded with more angular curves: in this case it is said to be in z-form. A neck that is held in one line may be more or less extended. If not particularly extended, it is simply straight. It may be extended to maximum length or fully stretched. In the intermediary case, it is simply said to be extended. In all three conditions, the neck may be held vertical, it may be slightly advanced from the vertical plane or obliquely advanced, and it may slope slightly backward or be hold back. In addition to the bearing of the neck itself, the positioning of its feathers is of importance. These may be depressed, relaxed or erected. It is noteworthy that quite often not all neck feathers are in the same condition.

Finally, the grebe's body may be rather **horizontal** on the water surface. If the breast is elevated and the vent lowered, the body is **sloping**. The body may be sloping to varying degrees.

Alarm posture (Achtungshaltung): If Blacknecked Grebes are frightened or notice a possible danger, they adopt the Alarm posture with the neck very straight and vertically stretched and all feathers of head and body depressed. The bill is in the horizontal plane. The bird appears slim. At times, the grebe may raise its crest. In the Alarm posture of Wittgen (1962), the Blacknecked Grebe has the neck slightly bent back and the head advanced. In Eared Grebes, the posture itself is similar to the one described by Prinzinger. Whereas Prinzinger indicated that the European nominate may utter a weak alarm call, McAllister (1958) has not heard any vocalization in the American subspecies. **Excitement or Upset posture (Erregungshaltung)**: During courtship, especially in the context of Advertising, and in association with aggressive interactions, Black-necked Grebes may adopt the Excitement posture. While the neck is still vertical, it is held less straight, more in the high S-form, and the feathers of the body are more relaxed than in the Alarm posture. The crest and the ear tufts are more or less spread, the body is sloping. Some white may become visible on the elevated upper breast. Most often the birds excitedly swim to and fro in this posture.

Searching posture (Suchhaltung): Unpaired European individuals or birds having briefly lost eye contact with their mate may adopt the posture. All body feathers are relaxed so that the bird seems bigger. Crest, ear tufts and neck feathers are raised or spread, the neck is held vertical and the beak horizontal. The back appears a bit arched.

Air Alarm posture (Luftalarm): Black-necked Grebes observe aerial predators by holding their head obliquely turned upward. The drawing in Prinzinger shows a grebe with the neck rather protracted and the wings slightly lifted. Storer (1982) used the term Sky Jabbing for a similar posture in the Hooded Grebe.

Looking-at-the-breast (Vor-die-Brust-schauen): At times Black-necked Grebes are observed to bent their neck and lower their head in a way that their beak points at their breast, occasionally even touching it. Prinzinger did not detect the meaning of the posture. Simmons (1979) used the term Breast Touching for Great Crested Grebes that by a short rubbing of the bill in the feathers of the breast get rid of excess water. This action looks similar, but is rather a maintenance activity not to be confounded with Looking-at-the breast.

Threat postures: The threatening Black-necked Grebe has its neck extended horizontally and flat over the water surface. The ear tufts may be partially flared out and the crest is somewhat raised. If really upset, the back feathers are also raised (Wittgen 1962). In the Eared Grebe, the neck is held oblique and the body is sloping. At low intensity, the angle of the neck is 45° forward, the bill straight forward and open, the feathers of the neck are depressed and the crest is raised. The threatening grebe may be stationary or moving. With increasing intensity, the speed of the movement in the direction of the opponent increases. In high intensity, it is

supported by wing beats (McAllister 1958). The latter corresponds to the Attack posture of Wittgen (1962): his drawing represents an assaulting flat jump or pattering with beating wings.

Defence posture: Wittgen (1962) mentions the posture without further describing it. In his drawing, the bearing of the Black-necked Grebe closely resembles the Threat posture with the feathers of the mantle elevated.

Surrender posture: this posture mentioned by Wittgen (1962) was again not described. In the drawing, a defeated grebe has its bill pointing at the skies and it presents the unprotected throat, neck and breast to the opponent. A similar or corresponding posture has not been described by any other author, neither for *Podiceps nigricollis* nor for any other grebe species. It is mentioned here only to be complete, but I have never observed it in the field and I seriously doubt that it really exists.

Fjeldså (1982) noted the following characteristics of the species. Loosely flocked, Blacknecked Grebes often scud vividly to and fro, neck drawn in, plumage relaxed, sometimes lifting the folded wings slightly and tilting them forward. Generally, they often raise their crown-feathers in excitement. They may raise them so much that they bulge forward.

4 Description of courtship in literature

In literature the courtship of the African Blacknecked Grebe is hardly described. Most descriptions simply refer to publications relating to European or American populations of the species. Therefore, the subspecies *gurneyi* is only treated briefly after the summarized description of displays in European and American *nigricollis* populations. For the latter, water and platform courtship are treated separately.

4.1 Water courtship of European Black-necked and American Eared Grebes

For the European subspecies, Wittgen had already published a description of pair formation and

courtship displays in 1962. His work is rather incomplete and for many rituals, details are missing. Whereas most authors of his period were convinced that courtship in the species is greatly limited to nocturnal hours, Wittgen came to the conclusion that especially during later morning hours, courtship is intense. The intensity then drops and becomes important again more towards the evening. Wittgen noted that shortly after the birds returned from their wintering grounds, pair formation started. He speculated that even earlier, during migration or on the wintering grounds in the Mediterranean, at least some individuals could engage in courtship activities.

Franke (1969) basically limited his report to the platform courtship of Black-necked Grebes. His only indication of water courtship concerned the noisy early-season aggregations of the birds. During these gatherings, the grebes utter calls similar to those heard during copulation and he thought that they serve as a kind of pre-courtship in pair formation on a common tournament place.

Prinzinger (1974, 1979) published more detailed descriptions of courtship in Black-necked Grebes and, unless otherwise stated, the presentation below is based on his work. In his descriptions, Prinzinger included elements of courtship that he had not personally witnessed, but that were reported for the North American subspecies. These are not considered here, unless they were described later by other authors for the species in Eurasia.

For American Eared Grebes, the descriptions are based on McAllister's work of 1958, unless otherwise stated. In her introduction, she noted that all rituals are performed by either sex and the displays occur all on the open water surface in the centre of the breeding lakes, without any kind of territory being involved. According to Bent (1919), Eared Grebes are evidently mated when they arrive at their breeding grounds. McAllister did not confirm this. She noted that pair formation displays are performed rather synchronously by all Eared Grebes present. She was of the opinion that the increased use of Advertising behaviour served the synchronization of courtship.

The sequencing of the rituals here will largely follow Prinzinger (1979), except for displays not considered by this author. Prinzinger introduced the subject with the following general considerations: Courtship displays are marked by a wealth of rather rigid displays that show only little individual variation and, therefore, appear rather stereotype.

Both sexes are ambivalent in the performance of the different displays.

Unlike solitary breeding species, Black-necked Grebes do not have a well-defined courtship territory, but display on the entire water surface that is at their disposal, often in the company of conspecifics.

In time, displays gain in intensity until they suddenly cease about completely when nesting starts.

Advertising (Simmons 1954), Advertising behaviour (Junggesellen Pose): In Black-necked and Eared Grebes, the display is typical for unpaired birds in search of a partner or for paired birds having temporarily lost eye contact with the mate. In the latter case, the display is less intense. The Advertising Eared Grebe may be stationary or it swims up and down approaching other grebes with a characteristic attitude and call. The European nominate is said to be less stationary. It rather restlessly swims to and fro. During Advertising, the body plumage of the Black-necked Grebe is kept relaxed, the crest is raised, the neck fully stretched. The drawing in Prinzinger then shows a grebe with a sloping body. The neck is slightly bent forward towards one o'clock and the bill is held about horizontal. According to the drawing in McAllister, the Eared Grebe floats high on the water surface. The feathers of the entire body are fluffed making the whole bird look larger. Both crest and neck feathers are raised, the neck is extended and the bill is directed straight forward. During calling, the bill of the nominate form is slightly opened and the throat sticks out. Both sexes assume the same posture. According to McAllister, the beaks of Eared Grebes remain closed while the call is uttered.

Fjeldså (1982) distinguished between situations where a bird is calling for its partner or a young and those where the call serves to attract a future partner. He termed the first Advertising and the latter Display-calling. This naming is not followed here as Advertising is the generally accepted term in grebes, beyond *nigricollis*, for the courtship display related to the establishment of partnerships. Therefore, the term Advertising is retained for unpaired Grebes and Contact Calling is used for paired birds. In Fjeldså's Display-calling, the single Black-necked Grebe floats high on the water, the neck fully extended and vertical. It achieves extra conspicuousness by raising its neck feathers. The erect crown looks pointed as head feathers are never expanded laterally. Display-calling birds swim cautiously towards singles or pairs, stopping a little away to turn from side to side.

In the European subspecies, the Advertising call starts with a long first syllable that may be composed of up to eight clearly separable parts. Fjeldså (1982) described the call of the Blacknecked Grebe as a soft and extended whistle that may grade into contact calls used in pair and group situations. An analysis of vocal Advertising in the Eared Grebe showed that, although superficially similar, female calls are significantly higher in frequency and shorter in duration and that courting males readily distinguish calls of unpaired females from those of unpaired males. As a consequence, courting grebes already know the species and sex of their display partner upon hearing its initial spontaneous Advertising calls (Nuechterlein & Buitron 1992). Advertising by courting, unpaired Eared Grebes is loud and frequent during pair formation. Well-formed pairs Advertise less frequently (Cullen et al. 1999). Advertising is contagious and the number of calls given per bout varies considerably (Cullen 1998). Except for the copulation duet given while on the nesting platform, courtship vocalizations occur mostly on the open water (Cullen 1998).

According to the above descriptions, the postures of Advertising grebes could differ geographically. In the Eared Grebe, the Advertising bird floats high on the water surface. According to Fjeldså (1982), this is also the case in the Black-necked Grebe. Prinzinger pretended that Advertising European birds have their breasts elevated and their vents submerged. Whereas the American grebe has its bill shut while calling, the nominate subspecies opens it. During Advertising, Blacknecked Grebes appear to be always moving. Eared Grebes could be more stationary. The reaction of the display partner remains unknown in the Eared Grebe. In Europe, it assumes the same posture as the Advertising grebe. It also seems reasonable to distinguish the calls of unpaired birds from those of firmly paired grebes having momentarily lost contact with their mate and to use different terminologies for both situations. Fjeldså's (1982) proposal of naming is not followed. Advertising will be used for grebes in search of a partner and Contact Calling if an adult seeks to re-establish contact with its mate or young. As in grebes Advertising calls are species-specific, a comparison of the calls of *nigricollis* subspecies could be judicious.

Shaking (Kopfschütteln): Generally, Head both European partners are facing during Head Shaking, but Prinzinger observed the display while the partners were swimming parallel to one another, too. Both grebes remain silent during the display. Body plumage and crests are raised. The body is sloping as the breast is elevated on the water surface. The heads are turned left and right in alternation while the bill is kept horizontal. Up to 12 head turns may be performed, apparently always one partner leading. Short head waggles are interspersed. Head Shaking is generally associated with Habit Preening and Head Scratching or it is inserted in between other rituals. Regularly, Head Shaking glides into Penguin Dancing.

Fjeldså (1982) added that the head is shaken with horizontal, precise, neat jerks often in two steps and alternating to either side. Wittgen (1962) reported that prior to Head Shaking, the birds are close to one another with their necks extended low over the water surface. The crest and the ear tufts are maximally spread as in the Threat posture. When coming together, the Black-necked Grebes raise the heads and their slightly elevated breasts seem to be touching. Head-shaking then starts. With the neck extended and the bill pointing upward, the grebes sway their heads to and fro. The display progresses with steadily increasing speed. Finally, the neck is fully stretched and the head is quickly shaken horizontally.

In the Eared Grebe, Head Shaking exists as an independent display and it is also part of Penguin Dancing. As a separate display, the two birds are high on the water surface and swim along rapidly. One partner leads and is positioned slightly in front and to the side of the other. It has the body feathers raised. The necks of both grebes are fully extended and upright. The crests are raised and the neck feathers depressed. The head is turned smartly left and right, all in the horizontal plane. Six to 12 turns constitute a ceremony. Thereafter, both birds usually dive. According to Palmer (1962), Head Shaking may be interspersed with Habit Preening. A major difference between the subspecies during Head-shaking could be that Eared Grebes always swim rather side by side while Black-necked Grebes are most often facing and only occasionally side by side. The American subspecies shakes all in a horizontal plane while European birds can insert short vertical head waggles. Generally, grebes may Head Shake, waggling their heads quickly upward or swaying them slowly from side to side with their beaks either held horizontal, upward or lowered. Fjeldså (1982) added a fourth category, Bill Flicks. Head Shaking may therefore serve as a generic term for all kinds of waggling, swaying, turning, dipping and flicking head movements. When it comes to detail, a more precise terminology should be used. Referring to Simmons (1975), I propose to use Head Turning or Slow Swaying for the movements in the horizontal plane, High Head Waggling for the quick upward waggles that resemble a series of exaggerated head flicks, and Low Head Waggling for the more downward oriented head movements with a lowered bill. Bill Flicking best describes a single quick upward or slightly sideward thrust of the head.

Pumping: Wittgen (1962) reported that in Blacknecked Grebes, after Head Shaking, a series of very rapid pumping movements can follow. They consist in a sudden retraction of the neck whereby the bill each time comes into touch with the lateral breast for a short moment. This movement is repeated three to 10 times, alternating with a backward jerking of the head or Head Shaking with Habit Preening. Although Prinzinger (1979) did not mention any jerking of the head, the posture of the grebe preceding the jerking seems to correspond to Looking-at-the-breast.

Fieldwork should answer the questions of whether Pumping can be considered as a display and of whether it occurs in *californicus*, too.

Habit Preening (Huxley 1914) (Scheinputzen): In the European nominate, Head Shaking is often interrupted by Habit Preening when the neck is quickly bent towards the back. The beak remains closed while a few feathers of the folded wing are raised. The birds may Habit Preen while facing or while parallel to one another. Generally, both mates perform the display simultaneously. Habit Preening may also interrupt other rituals. Fjeldså (1982) added that Habit Preening may grade into ordinary preening. The partners then lie close and show synchronized preening of the same parts of the plumage.

McAllister described Habit Preening in the Eared Grebe as follows: courting grebes can preen vigorously in a manner not differing from ordinary comfort preening. In between, a different kind of preening may occur. Two birds drifting within a foot of each other can preen together, either bird leading, both preening the same feather at the same time. The birds are most frequently side by side, but they can end up facing. According to Palmer (1962), the stereotyped preening consists of movements by the beak mostly to the primaries and the breast feathers. It is always performed by two birds. His drawing then shows a grebe lying on its side and preening the upper breast.

The descriptions of Habit Preening for both subspecies are broadly in agreement. One could perhaps distinguish two different kinds of Habit Preening, namely the short very ritualized and stereotyped preening that may be interspersed to other rituals and the more vigorous form resembling ordinary preening. The borderline between the latter form and ordinary preening might need clarification. Perhaps the degree of synchronization or coordination between the partners could serve here.

Head Scratching (Kopfkratzen): The display has only been described for the nominate form. It appears mostly in connection to Habit Preening. It is performed by both grebes synchronously. Only one or two scratches of the head with the foot from in front occur.

This study should clarify if the display exists in the Eared Grebe.

Billing, Hunched Display (Schnäbeln): After surfacing, two Black-necked Grebes swim together and touch with their bills. Prinzinger several times observed that one bird briefly adopted a begging posture and called softly. He believed that the display corresponds to a ritualized feeding. Fjeldså (1982) termed the ritual Hunched Display or Triumph Ceremony. Members of an established pair of Black-necked Grebes move close together with expanded plumage. The necks are kinked forward and drawn in; the bill sometimes touches the water. Once breast to breast, they turn and move parallel, they partially lower their back feathers and chitter. For Eared Grebes, a similar or corresponding display was not described and, generally, food presentation was not reported during pair formation (Cullen et al. 1999).

Billing was not described separately for the Eared Grebe, but the action corresponds largely to the approach phase in its Pivoting Display (Palmer 1962). It should be checked whether the ritual exists independently from Pivoting in the American subspecies. The delivery of food during the display could be checked. It might however be of minor importance if food is really passed over as Prinzinger thought Billing to correspond to a ritualized feeding. Without regular delivery of prey, the term Food Presentation might be misleading as in other grebes it serves to describe situations where food is really passed over. It seems preferable to stick to Billing or Hunched Display in the context of the display, regardless of whether food is passed over or not.

Pivoting Display (Drehbalz): Prinzinger referred to Palmer (1962) when he described the Pivoting Display and he never observed the ritual in the European nominate. According to Fjeldså (1982), established mates sometimes touch bills on the water. Frequently, pivoting follows and the birds end up tail to tail. Sometimes, one Black-necked Grebe just surfaced from a dive and some small food object could be passed over to the mate. Fjeldså therefore lists the observation under Food Presentation. A priori, this introduction to the display recalls the Hunched Display.

Palmer (1962) described the Pivoting Display of Eared Grebes as follows. The partners approach till their beaks nearly touch, then they pivot on the water surface till their tails touch or are very close; they now perform series of half-circle rotations in unison, often interspersed with Head Shaking during the tail-contact phase. His drawing shows two grebes facing with extended necks held obliquely advanced. The ear tufts are fanned out and the crest is slightly raised. Back to back, the neck is arched forward and the head is held lower, but neither the beak nor the neck is in touch with the water.

If existing in the European nominate, the Pivoting display was not described in much detail. Prinzinger never observed it and Fjeldså (1982) only mentioned that the Hunched Display may be followed by a pivoting movement so that both grebes end up tail to tail. A more thorough analysis and a detailed description are needed. In the Eared Grebe, the occurrence of the Hunched Display as a prelude to Pivoting and the bearing of the partners while performing the display may need clarification.

Cat Display, Cat Attitude (Huxley 1914) **(Katzenpose)**: In the Cat Attitude, the wings are extended laterally in the form of a shield (Prinzinger 1979), respectively the wings are away from the body and bent, with the carpal joint tipped forward and down to almost touch the water (McAllister 1958). Whereas in Black-necked Grebes, the head may be positioned in between the shoulders or it may be extended over the water surface, the head of the Eared Grebe is drawn down to the breast. In both subspecies, the crest is erected. McAllister added that in Eared Grebes the neck and body feathers are raised and Cullen et al. (1999) reported that the tail is cocked, too.

McAllister believed that the display is rare and its function unclear. She observed the Cat Attitude in two grebes after an unmated bird had Advertised. At another occasion, a second bird swam and dove towards the Advertising Eared Grebe that adopted the Cat Attitude. The approaching bird rose into the Penguin Attitude.

In the Black-necked Grebe, the display is part of the Discovery Ceremony. It is generally followed by Penguin Dancing.

The bearing of the subspecies in the Cat Display could differ. European grebes may have their head retracted to in between the shoulders or it may be more extended forward. In American grebes, the head is drawn down to the breast and no other posture is listed. It is generally not clear when the grebes adopt the Cat Attitude.

Ghostly Penguin Display (Simmons 1975) (Steilauftauchen): The display describes the final appearance of the diving bird in the Discovery Ceremony of Black-necked and Eared Grebes. One bird is diving into the direction of its waiting partner and slowly grows out of the water at some distance, the head appearing first. The grebe surfaces in front of the Cat bird and facing away from the latter with the body in a vertical position, heavily treading water. According to Prinzinger, the neck of the European nominate is not bent forward while the Ghost grows out of the water and its raised crest is a sign of high excitement. In the Eared Grebe, the Ghost bird has its neck bent forward and its head feathers are sleeked. Upon reaching full height, the Ghost bird turns to facing, and raises head and crest (Cullen et al. 1999).

Superficially, the emergences of Black-necked and Eared Grebes during the Ghostly Penguin Display look alike. Differences appear to exist in the bending of the neck and the erection of ornamental feathers during the process of surfacing.

Bouncy Display (Fjeldså 1973), Bouncy Dive posture (Wipptauchen): In the Discovery Ceremony, prior to the final surfacing in the Ghostly Penguin posture, the diving Black-necked and Eared Grebe may appear up to four times in a singular posturing, popping up like a cork, with the neck bent back onto the back, the bill pointing towards the skies and the upper breast gently rocking or bouncing out of the water. Cullen et al. (1999) used the term Bouncy Dive posture to describe the intermittent surfacing of the diving bird. While on the surface, the grebe holds its breast elevated, the neck is held in closed s-form and pressed against the back feathers. The grebe's beak rests on the upper breast and the tail is cocked. Wittgen (1962) termed the bearing Proud posture. He thought that it is not directly related to other courtship activities and he ranged it with his introductory displays.

No differences between the subspecies are apparent in the Bouncy Display. As the descriptions provided so far are rather superficial, a more thorough presentation might be needed.

Weed Presentation (Materialpräsentieren): Just prior to platform initiation, a Black-necked Grebe may dive for weed or grasp floating weed and symbolically deposit it in front of its partner. No case of Weed Dancing (with both grebes facing in the Penguin posture and brandling the weed due to their Head Shaking) has been observed so far. Fjeldså (1982) used the term Weed-trick for the display, following Huxley (1914) who introduced this name for the ritualized weed fetching of the Great Crested Grebe. Fjeldså wrote that single Black-necked Grebes may fetch weeds from the surface or dive it up and present them to other grebes. They often swim up to other birds with erect neck and partially raised crown feathers and then drop the weed in front of a grebe or they may even attempt to throw the weeds across the other's back or breast. These then often try to avoid being covered, turning away with extended neck. This may lead to series of turning and rapid parallel rushes. Weed Presentation is less stereotyped in Eared Grebes than in other grebes. Eared Grebe pairs may dive and present aquatic plants to potential mates. This can involve repeated, alternated presentation of the same weeds by both mates (Cullen et al. 1999).

The term Weed-trick used by Fjeldså (1982) should be abandoned for *nigricollis* grebes as it serves already in the very stereotyped Weed Ceremonies of Great Crested or Western Grebes that are followed by Weed Dancing. The weed fetching of Black-necked and Eared Grebes does not show a high degree of ritualization. Otherwise, the descriptions for both subspecies are largely concordant.

Penguin Dance Ceremony, Penguin Dancing (Huxley 1914) (Pinguintanz): In the European nominate, Head Shaking while facing one another generally precedes Penguin Dancing. With growing excitement, the breast rises and the body becomes more and more sloping until both birds stand about vertical in the water. They maintain the posture by heavily paddling with their feet. While in the Penguin posture, both grebes heavily waggle their heads. All head feathers are spread while the body feathers are relaxed. Penguin Dancing regularly follows the Discovery Ceremony. The dancing may last for several seconds and up to 15 seconds. Then, the partners fall back onto the water surface and Head Shaking follows. According to Fjeldså (1982), Blacknecked Grebes only exceptionally Habit Preen while they dance. Fjeldså distinguished between a Plump (with body slightly more immerged and body feathers raised) and a Tall Penguin Dance (the entire bird appearing slimmer with the fully extended neck forming one line with the body). Bauer and Glutz (1987) insisted that while Penguin Dancing, the Black-necked Grebes do not come to breasts touching as is the case in other grebes; the mates always remain at little distance from one another. Also, they utter a series of shrill calls. Wittgen (1962) observed the display only under bad conditions. He was of the opinion that the grebes searched support on the other's breast while they protruded vertically out of the water and shook their heads.

In Eared Grebes, the dance may begin from a dive or from the surface. Two grebes tread water while face to face. Their white breasts rise out of the water and the birds seemingly stand on their tails. Their bellies are only a few inches apart. They utter a shrill chittering call and shake their heads violently from side to side. Dropping back onto the water surface, they slow their head movements and, still facing, they perform eight to 20 turns in the swimming position. Palmer (1962) added that the breasts of the dancing grebes are not touching, their crests are up, the body and neck feathers fluffed, the necks extended. The birds never hold weeds in the bill. As they settle down, they stop the calling. The Head Shaking may be followed by Habit Preening or, occasionally, by turning into the same direction and Racing.

In substance, the Penguin Dance Ceremony is performed similarly in Black-necked and in Eared Grebes. It should be checked for both subspecies to what extent a subdivision into Plump and Tall Penguin Dancing may be useful. It is not clear whether different kinds of Head Shaking may occur during Penguin Dancing. In the context of the Discovery Ceremony, Habit Preening during Penguin Dancing has only been reported for Black-necked Grebes. Also breast contact could only occur in the European nominate.

Parallel Swimming (Parallelschwimmen): Two Black-necked Grebes swim parallel to one another with their breasts raised and their vent submerged. The necks are held vertical and the crests are raised. The birds may shake their heads. In the same posture, they also chase conspecifics. According to Wittgen (1962), the display developed out of Head Shaking. He termed it Upright Swimming. In it, both birds swim away side by side with steadily increasing speed, crest and ear tufts maximally spread and the neck completely stretched. The upper part of the neck displays a conspicuous rounding whereby the bill points downward. The elevated breast and the submerged vent complete the posture. The display has not been described for the American subspecies.

The term Parallel Swimming has not been used for the American subspecies, but the display could occur in the context of Head Shaking. As according to Prinzinger's description, in Parallel Swimming the bodies of the grebes are elevated, it should be checked to what extent confusion with Racing or Barging is possible. **Racing, Barging (Rennen)**: While swimming parallel, Black-necked Grebes may rise further into the Penguin posture, and, remaining side by side, Race over the water surface. According to the drawing in Prinzinger, their necks are stretched forming one line with their upright bodies. Prinzinger did not observe Racing in isolation, but always as a prelude to the Flight display. Fjeldså (1982) termed the display Barging: he saw it as a continuation of Penguin Dancing with the birds turning parallel and moving in one direction while still upright. The display ends with a rather simultaneous dive out of the upright posture.

In Eared Grebes, Racing or Barging occurs if very occasionally the birds turn while Penguin Dancing and run a short distance on the water surface before settling down and Head Shaking. Cullen et al. (1999) mentioned Upright Barging in the context of a courting pair that is disturbed by a third bird. The pair may then barge parallel with the crests raised and the breasts elevated high. Often, Unison Diving follows and the birds may re-appear a few metres away to Penguin Dance or resume Barging.

The terms Racing and Barging are used as synonyms and the descriptions insinuate that the grebes' bodies are in a rather vertical plane corresponding broadly to the posture in Penguin Dancing. For Prinzinger, Racing is a kind of intensification of Parallel Barging and it could make sense to distinguish between two different displays. This should be investigated for the European and for the American subspecies. It should be checked in how far Racing occurs only as a prelude to the Flight Display. Fieldwork should also try to investigate if the displays can be performed by males only.

Barge-dive Display: Two Black-necked Grebes may barge parallel for several metres, then dive in unison directly from the upright posture. For a moment the neck is kinked strongly so that the middle is arched high, the head low with sleeked feathers, before they dive. The birds come up several metres away, still together to repeat the Barging. They may then gradually loose contact or start other diving activities. The display was described by Fjeldså (1982), but not by Prinzinger. Wittgen (1962) reported that after Upright Swimming, the grebes sink back onto the water surface and a series of dives can follow. Koop (2003) mentioned that Parallel Rushing may sometimes end in a series of possibly synchronized dives. For North America, Cullen et al. (1999) indicated that Parallel Barging Eared Grebes may dive in unison and reappear to resume the Barging without specifically naming this display.

Fjeldså (1982) described the Barge-dive Display as a further development of Parallel Barging in Blacknecked Grebes. Cullen et al. (1999) did not specifically name a possibly corresponding display in Eared Grebes. It should be checked in the field whether both subspecies perform the ritual in a similar manner and whether Fjeldså (1982) and Wittgen (1962) meant the same display. It seems clear that the term Barge-dive Display involves a repetition of Barging and Diving. It should not be confounded with Parallel Barging that may end with a single dive in unison by the partners.

Flight Display, Splattering (Fluglauf/-balz): In Black-necked Grebes, the Flight Display follows Parallel Swimming that grades into Racing. During the Flight Display, both partners fly side by side just over the water surface while their paddling feet remain in touch with the water surface. After having covered some distance together, the grebes may not alight simultaneously, and often only one bird takes wings. The flight distance may however be over 50 m. Fjeldså (1982) used the term Splattering to describe a similar action when in aggressive situations two Black-necked Grebes swim together as for Penguin Dancing. Then they turn parallel and after a short rush start to flap wings. They splatter precisely as during flight, and may alight and fly 50 m low over the water. Settling again, they submerge directly from the forward gliding. No display including flight was reported for the Eared Grebe.

It should be investigated whether the Flight Display is absent from North America. The term Splattering may lack clarity as it simply insinuates the splashing of water. Also, Splattering could simply correspond to the Pattering Retreat discussed below. In this case, the term Splattering could be skipped. The contextual evidence for the display should be analysed further.

Discovery Ceremony (Huxley 1914) (Entdeckungszeremonie): This ceremony incorporates several displays. According to Prinzinger, it starts with one Black-necked Grebe diving just below the water surface (Ripple Diving, i.e. the dive is so shallow that it produces ripples on the water surface) in the direction of its partner. It surfaces in the Ghostly Penguin Display in front of the latter who adopts the Cat Attitude until surfacing is completed. The Cat bird then rises into the Penguin posture. Both grebes now move in the direction of each other until their breasts touch. They Penguin Dance for a while and sink back onto the water surface. Further courtship may follow. In Prinzinger's description, it remains unclear at what moment in time the surface bird adopts the Cat Display. Fjeldså (1982) gave the following chronological order for the different elements of the display in Europe. A bird swimming about some distance away from others display-calls. The surface bird, facing to where its partner disappeared, performs a Cat Display, raising its plumage fully, wings tilted rear-edge up and half spread. The neck is partially raised, head feathers are flared laterally. Fjeldså did not notice Ripple Diving suggesting that the Ghost bird could dive deeper than reported by Prinzinger. Within 1-5 m of the Cat bird, the approaching grebe exposes itself briefly. Emerging up to six times, it partly encircles the surface bird. During the typical exposure, the diving bird pops like a ball in the Bouncy posture, the breast elevated, sometimes holding the head rather high. After a few seconds at most, the bird dives again. It finally emerges in the Ghostly Penguin Display, oriented usually away from the Cat bird. The Ghost bird rises gradually with vertical body, but the neck arched forward with sleeked head feathers. The neck is however soon extended and the bird shoots right up in the water like in a Tall Penguin Dance, revolving and Barging towards the display partner. Fully elevated in the water, the Ghost bird expands its head feathers. Its partner extends its neck, puts its wings down and begins to tread water, too. Both move together and show a complete Tall Penguin Dance. The display often ends with Parallel Barging over a long distance. Complete Discovery Ceremonies are usually only seen in the beginning of the pair formation.

McAllister did not consider this ceremony in the Eared Grebe under a separate heading as she thought it to be an incomplete form of Penguin Dancing. According to Cullen et al. (1999), the ceremony starts with one bird Advertising repeatedly and approaching until in visual contact. One grebe then adopts the Cat Display, the other dives repeatedly towards the first bird, resurfacing periodically in the Bouncy Dive posture. The Cat bird swivels to face the approaching bird. After 3-10 appearances in the Bouncy Display, the diving grebe finally emerges with a shrill trill in the Ghostly Penguin posture. It turns to facing, then both grebes approach and raise breast-tobreast as they mutually tread water in a vigorous Penguin Dance, with slow Head Turning followed by Head Shaking and Habit Preening of side or back feathers. As Penguin Dancing subsides, Habit Preening predominates as the pair swims off side-by-side.

In the Discovery Ceremony, it is not clear to what extent the dive of the Ghost bird is shallow (Ripple Diving). At what moment in time does the surface bird perform the Cat Display and for how long is the posture maintained? These questions of detail should be investigated for both subspecies.

Retreat Ceremony: For the Eared Grebe, McAllister mentioned that rarely one bird in a pair flaps over the water a little way and then adopts the Cat Attitude turning to face its mate. Cullen et al. (1999) reported that birds sometimes separate themselves from courting groups by conspicuously pattering away across the water surface with wings flapping, to adopt then the Cat Display or to Advertise. Cullen et al. (1999) applied the term Retreat Ceremony to the pattering only, unlike other authors where the ceremony includes the pattering and at a minimum the subsequent adoption of the Cat Attitude. The Retreat Ceremony has not been reported for the European nominate.

The Retreat Ceremony was apparently not observed in Europe and it could be rather occasional in North America. The descriptions by McAllister (1958) and Cullen et al. (1999) differ. Whereas according to McAllister the retreating grebe adopts the Cat Attitude (as in Great Crested Grebes), Cullen et al. used the term for the pattering retreat alone. This is misleading. It would be best to apply the term Retreat Ceremony only if the retreating grebe thereafter adopts the Cat Attitude. The term **Pattering Retreat** could serve for the conspicuous pattering away alone.

Mate Guarding/Unison Diving: Cullen et al. (1999) used the term Mate Guarding for the rather synchronous dives of Eared Grebe pairs in which mates follow each other. Prior to nest establishment, the display is rather common. In the context of Barging, Cullen et al. named

the synchronized dives Unison Diving. In the literature about Black-necked Grebes, this simultaneous diving was not considered as a separate courtship display.

Mate Guarding has not been described for the European nominate. More generally, the term Mate Guarding does not directly imply the existence of a display. It could be seen as a simple behaviour that occurs in about all situations where two mates of a pair remain together to prevent rivals from disrupting the pair bond. According to Cullen et al. (1999), the term Mate Guarding would apply to a synchronized dive of a pair. This would mean that the term is applied with two different meanings which is confusing. Therefore, it is proposed to use **Unison diving** in all cases of synchronized dives. As concerns mate guarding (in its original meaning), it is questionable whether the behaviour should be regarded as ritualized.

Inviting (Pose), Soliciting, Nest-selection Display (Einladungshaltung): The Inviting considered here is performed on the open water surface by well-established pairs of Black-necked Grebes. It is thought to occur only later in the pre-nesting season when nest building becomes imminent. For this reason, Prinzinger associated the ritual with platform courtship. With head feathers sleeked, the head held low so that bill and throat touch the water surface and the neck slightly retracted, a grebe, according to Prinzinger usually the female, utters soft calls. It pivots to and fro and to the sides in front of the partner. In Prinzinger's monograph, the mate has meanwhile adopted the Alarm posture (Achtungshaltung) in the back of the inviting grebe: all feathers of the body, neck and head are sleeked, the neck is extended vertically and the bill is kept horizontal. The grebe appears rather slim. Occasionally, the crest may be raised as can be seen in the drawing of the Alarm posture by Wittgen (1962). In his earlier article, Prinzinger did not mention a special posture that is adopted by the grebe in the back of the inviting bird. His drawing shows a rather relaxed grebe that has its neck drawn back. It may occasionally preen. The inviting grebe may now dive for weed and deposit it in front of its partner. Both grebes may also dive simultaneously and surface with weed that is then simply dropped.

For the Eared Grebe, McAllister used the term Soliciting. The grebe's body is low on the water surface, the neck is held forward with the head and bill on the water surface. The neck is not unduly extended and the crest is down. The soliciting bird may call and its mate may answer with the same call. Cullen et al. (1999) used the term Nest-selection Display. In it, the pair swims in consort, one or both giving a pre-copulatory whirring call with the head lowered, the crest fully flattened. The bearing of this Inviting-on-water is almost identical to later inviting on the platform.

The circumstances and timely occurrence of Inviting on the open water surface should be investigated. The outcome could show in how far the display is performed without direct relation to platform initiation and whether the term Nest-selection Display (Cullen et al. 1999) may always be appropriate. Differences in the ritual between Eared and Black-necked Grebes and a possible relation with Pivoting could be blurred by the superficial descriptions for both subspecies. Further work on the display may pay off.

Arrangement of displays: Prinzinger ends its description about water courtship by stating that simple displays such as Advertising, Head Shaking, Habit Preening and Head Scratching may occur in isolation. Other displays are generally integrated into more complex ceremonies. Especially at the peak of water courtship, the ceremonies become ever longer and more complex. They start with simple rituals such as Head Shaking and end with more elaborate displays, for example the Discovery Ceremony or the Flight Display.

4.2 Platform courtship

According to Prinzinger, the courtship as described so far and except for Inviting on the open water surface is mostly performed by Blacknecked Grebes that are not yet definitively paired for the season. They serve primarily to reduce the aggressiveness of the partners so that they can get acquainted to one another. The displays following now are directly related to nest-site selection, platform building and copulation. Whether Inviting away from a platform should be part of water or platform courtship is debatable. Prinzinger and McAllister (1958) put it with platform courtship. Here, it is provisionally considered to be part of the water courtship.

McAllister (1958) reported that for initial platform building, almost any place might be chosen, but some floating algae or reeds must be present. Even places totally unsuitable for final nesting may be selected. The building activity by one pair of Eared Grebes may attract others that are driven away. A same platform may be used in turns by more pairs. McAllister (1958) thought that all platform construction is the work of females. According to Cullen et al. (1999), platforms are usually built by both sexes. Ceremonial Building is mentioned neither for European, nor for North American populations.

Otherwise, descriptions of platform rituals are generally limited to the behaviour of the birds on the platform and after mounting. The behaviour of the grebe in the water before mounting has not been classified as ritualized. In both subspecies, this grebe swims about in the back, occasionally also to the side of the Rearing and Inviting partner on the platform, and shows continued feather care with fast movements of its head to the back or, while lying on the side, to the belly (Franke 1969).

(Aufforderungshaltung): Rearing posture According to Prinzinger (1979), female Blacknecked Grebes show the display shortly before copulating. During Rearing, the grebe remains standing upright on the platform, the neck is bent forward and down, the head is thrown one or a few times laterally while Wing Quivering with closed wings occurs. It then settles down to invite. Franke (1969) reported Rearing to occur directly after a Black-necked Grebe jumps out of the water onto the rim of the platform where it remains upright and shows Wing Quivering. McAllister (1958) and Palmer (1962) pretended Rearing not to be known in Eared Grebes, however before lying down, the female remains standing with closed wings on the rim of the platform for a few seconds. In contrast, Cullen et al. (1999) describe Rearing in the same manner as in the European nominate. The Rearing Eared Grebe gives a whirring call.

A final confirmation for the occurrence of Rearing in Eared Grebes could be provided.

Inviting: In Prinzinger's monograph about Blacknecked Grebes, Inviting on the platform follows Rearing. The female generally sinks down with the belly onto the platform, neck and head horizontally protruding beyond the rim and held close to the water surface. In this posture, it turns its head to the left and to the right and calls. In the Eared Grebe, the posture is similar, and the bird has its head and neck feathers flattened (McAllister 1958). The whirring call of the Rearing posture is repeated (Cullen et al. 1999).

No differencies in Inviting on a platform appear to exist in both subspecies.

Mounting: If ready for Mounting, the male Blacknecked Grebe in the water raises all ornamental feathers (Franke 1969). It then jumps upright onto the lower back of the female and utters a thrilling copulation call. After mounting from the rear, the Eared Grebe drums alternately with the feet onto the back of the inviting partner while calling. According to Prinzinger, the female generally ceases calling when hearing the copulation call of the mate. However, Franke (1969) reported that both grebes utter an own series of tones lasting some eight seconds while copulation occurs. In the Eared Grebe, the female does not join in the call (McAllister 1958). In regular Mounting with the male on top, generally cloacal contact is established whereas in Reverse Mounting, the contact is usually not made.

A more detailed presentation of the behaviour of the grebe in the water just prior to mounting could complete the descriptions.

Post-copula, Post-copulatory or Post-courtship Display: After copulation, the male Black-necked Grebe runs upright over the back and head of the inviting grebe and jumps onto the nest rim or into the adjacent water where it lands with stamping feet. Both birds are now upright with their bodies turned in about the same direction. The necks are fully stretched vertically (Franke 1969). The heads are turned slowly and synchronously, alternating between left and right turns. Then, both grebes return into the water for bathing and preening. At times, the Head Turning may be followed by a single Habit Preening movement (Franke 1969). According to McAllister (1958), the male Eared Grebe lands in the escape bathing position with the body upright, crest and head up, and begins Head Shaking with its back to the female that raises her head for Head Shaking, too. Cullen et al. (1999) simply state post-copulatory Head Turning to occur after dismounting.

Franke (1969) reported that Mounting is repeated very often. He also noticed that other Black-necked Grebes may disturb the pairs that are preparing for copulation. At some platforms, other grebes regularly gathered and interfered in the courtship of the owners. The context of the disturbances remained unclear, and it was not known whether rivalry or an inclination for disturbing was at the origin.

Comparing the pre-copula displays of grebes, little difference exists between species in general and between *nigricollis* subspecies in particular. After jumping simultaneously with both feet onto the platform, a *nigricollis* grebe may, either first Rear and then Invite, or it may directly assume the Inviting posture. Its partner will finally jump onto its lower back for copulation. After a few seconds, it dismounts over the head of the extended grebe, jumps into the water and both engage in a Postcopula Display that is more species specific. Therefore, more detailed descriptions of the behaviour immediately after dismounting of particularly Eared, but also Black-necked Grebes might be useful.

4.3 Some notes about the courtship of African Blacknecked Grebes

In "The Birds of Africa", Brown et al. (1982) refer primarily to Cramp and Simmons (1977) to describe the courtship of their Black-necked Grebe (Fig. 1). The authors then state that the displays are not fully described in Africa and repeat in a few lines an account from Clark (1977). Broekhuysen and Frost (1968a, 1968b) reproduce only observations dealing with the nesting behaviour of the African Black-necked Grebe. It remains that at the end hardly any displays truly observed in Africa have found their way into the ornithological literature.

Head Shaking: according to Clark (1977), the partners face each other, shaking their heads repeatedly horizontally. Then bending the necks, each one lowers its head, first to one side than to the other. The description resembles a kind of nodding or of bowing by the grebes.

Racing, Barging: Clark (1977) reported that after Head-shaking, two mates could glide across the water side by side, the heads raised and the white breasts conspicuous. This kind of Racing may be disturbed by other birds and the pair may then splash dive.

Table 2: Problems with and differences in displays and their terminology of Black-necked
and Eared Grebes (1 with name of subspecies performing the display, *californicus*
= Eared, *nigricollis* = Black-necked Grebe).

Display	Terminology	Description of displays	Displays in one subspecies only ¹	Remarks
Advertising	Difference Advertising and Contact Calling	<i>nigricollis</i> generally not stationary		Reaction/reply of possible partner unclear
Pumping			nigricollis	Apparently performed in the context of Head Shaking
Head Shaking	In both subspecies, no o between different kinds	clear differentiation s of Head Shaking		Proposed to distinguish between the different forms of Head- shaking
Habit Preening		Two forms of Habit Preening could exist		
Head Scratching			nigricollis	
Billing, Hunched Display		Does feeding occur?	nigricollis	
Pivoting Display		Bearing of the displaying grebes	californicus	Does <i>nigricollis</i> use the display? Does the Hunched Display regularly serve as an introduction?
Cat Display		Positioning of head in both subspecies		At what point in time in a display is the Cat Attitude adopted?
Ghostly Penguin		Check bending of neck for nigricollis		
Bouncy Display, Bouncy Dive posture		The descriptions for both subspecies could be more precise		
Penguin Dance Ceremony		Occurrence of Habit Preening in <i>califor-</i> <i>nicus,</i> occurrence of breast contact in both subspecies		Need for differentiating between Tall and Plump Penguin Dance; check for breast contact during the display
Weed Presen- tation	Also termed Weed- trick			
Parallel Swimming			nigricollis	In the context of Head Shaking, a kind of parallel swimming occurs in <i>californicus</i>
Racing, Barging	Unclear whether there is one single or two different displays	Clearer description of the display in <i>nigri-</i> <i>collis</i> and in <i>californicus</i> needed		A comparative review of all parallel movements is needed. In how far is the display performed by two or more male grebes only?
Barge-dive Display		Different descriptions by Wittgen (1962) and Fjeldså (1982) for <i>nigricollis</i>	nigricollis californicus?	
Flight Display, Splattering	Are both terms synon- ymous?		nigricollis	Further analysis needed

Display	Terminology	Description of displays	Displays in one subspecies only ¹	Remarks
Discovery Ceremony		Occurrence of Ripple Diving		Relation between adoption of Cat Display and progress of diving grebe
Retreat Ceremony	,	Slight differences in the descriptions	californicus	
Mate Guarding, Unison Diving	Vague terminology	Context of dives and ritualization	nigricollis? californicus	Outside of Barging, it is unclear whether this is a ritual or a normal behaviour
Inviting (Pose)	Can Soliciting and Nest-selection Display be used as synonyms?			As the inviting grebe pivots on the water surface, is there a relation with Pivoting?
Rearing				Check for Rearing in californicus
Mounting		Behaviour of water bird just prior to mounting		
Post-copula Display		Vague description for <i>californicus</i>		



Figure 1: African Black-necked Grebe at Strandfontein, South Africa (2005).

With that few indications about the water courtship displays of the African Black-necked Grebes any comparison with the two other subspecies of *P. nigricollis* is impossible, and in the following, *P. n. gurneyi* will no longer be considered.

4.4 Synopsis: Areas of disagreement in displays of the European and American subspecies

The above descriptions of courtship in the *Podiceps nigricollis* subspecies *nigricollis* and *californicus* reveal problems and differences that broadly fall into three categories: problems with the terminology applied, differences and uncertainties in the descriptions of the displays and displays listed for one subspecies, but not for the other. Table 2 lists the rituals where uncertainties appear and gives an overview of existing problems according to the three categories.

5 Aggression in literature

Although it is generally assumed that *nigricollis* grebes are little aggressive against conspecifics, aggression is not completely absent; especially during pair formation agonistic interactions pop up now and then. Besides threatening, attack, pursuit and fight, aggression often occurs in the context of courtship displays. The rituals seem to be performed in a way that they could serve simultaneously the confirmation of the pair bond and the chasing of rivals. In this sense, one might question whether they are not actually courtship. In literature, the common practice has been to separate the descriptions of ritual pair bonding and agonistic behaviour. It holds however true that many courtship displays find their origins in aggressive interactions.

5.1 Aggression in the Blacknecked Grebe

For the European nominate, Prinzinger (1974, 1979) mentioned Threatening, Splash Diving (Spritztauchen), Attack, Fight and Pursuit.

During Threatening, the neck of the grebe is held more or less obliquely forward and the neck feathers are depressed. The bill is slightly opened and points at the opponent. The crest is raised. In high intensity threatening, the grebe may thus swim at the opponent and it may repeatedly utter a threat call. Threatening occurs regularly inside a colony, but also during courtship if unwanted conspecifics appear. Pike (1919 in Prinzinger 1979) described a threatening posture with the wings spread that could correspond to the Cat Display, but seems to be shown rather seldom during courtship.

The Threat posture by one Black-necked Grebe can be replied by the Defence posture. According to the drawing, the latter corresponds to a Threat posture with the back feathers about completely lifted. The opponents remain immobile and facing at short distance, in a tensioned situation causing uneasiness to both. Sudden unexpected and vigorous preening (displacement feather care) by both may end the situation (Wittgen 1962).

At times, Black-necked Grebes kick water backward with their feet while immersing (Splash Diving). It may serve to irritate opponents, especially during pursuit.

Prinzinger described three different forms of attack. At low intensity, a Black-necked Grebe swims in Threatening Posture more or less rapidly, perhaps also beating its wings, in the direction of a rival (Threat Swimming / Drohschwimmen) that may escape. At times, the attack is quickly superseded by mutual Head Shaking. At higher intensity, the attack may be launched under water (Diving Attack / Angriffstauchen). The opponent shows signs of unrest and mostly escapes either by diving, quick swimming or pattering flight. More seldom, Black-necked Grebes may attack with a pattering flight over the water surface (Pattering Attack / Drohanflug).

Aggressive threatening and attacks are especially regular during pair formation. Wittgen (1962) witnessed "heavy fighting" on the open water surface that was most intense during the periods where courtship activity culminated. In contrast, real fight was not observed by Prinzinger and he classified it as exceptional.

Wittgen (1962) also noted that the Black-necked Grebes are permanently alarmed. He thought that courtship attracted solitary birds enormously and they profited from the emotion of the displaying pair that forgets about its surroundings. Single birds may launch rather unobserved attacks.

After two mates chased a trouble-maker, they may turn to facing and engage in Head Shaking.

5.2 Aggression in the Eared Grebe

According to McAllister (1958), single birds can approach pairs and Advertise. The Advertising may be ignored for a while, but then one partner can rush in a threat posture at the troublemaker. Early in the season, partnerships do not necessarily last for long. The number of partner changes drops off rapidly in time and a few days before nesting behaviour starts, the pairs are definitive. McAllister thought that generally during courtship and on the open water, threat was rare. Depending on the intensity, the bird could be stationary in the Threat posture, move slowly towards the opponent or dash at him with wing beats. The threatened bird escaped by diving; it could be followed a short distance. McAllister reported that threat was always successful in driving the other bird away and that instead of the stationary fighting in Great Crested Grebes, attack-escape sequences were regular in Eared Grebes. She did not observe breast to breast contacts. McAllister (1958) thought that Head Shaking may serve as a threatening posture.

Cullen (1998) and Cullen et al. (1999) reported that hostility in Eared Grebes is most common during pairing and colony establishment. Eared Grebes frequently dash across the water surface towards rivals or attack from under water. Escaping birds dive or skitter across the surface. Cullen et al. (1999) mentioned that a courting pair interrupted by a third bird may use Upright Barging with the crests raised. This is often followed by Unison Diving and the birds may appear again a few metres away to Penguin Dance or resume Upright Barging.

6 The findings of the study

In the following, the findings of the fieldwork in Germany and North America are presented per display. For each ritual, a description per subspecies is provided and a comparison follows.

6.1 Advertising and Contact Calling

In the Wagbachniederung, Advertising was observed in a posture close to what Prinzinger called the Excitement or Upset Posture (Erregungshaltung). In most observations, Advertising Blacknecked Grebes floated singly and high on the water surface. The neck was held rather vertical or slightly leaned forward while calling. The crest was raised halfway and the ear tufts were fanned out, but not laterally. The short neck and occiput feathers were spread, making the neck appear thicker and giving extra conspicuousness to the bird (Fjeldså 1982). The back feathers were relaxed, the wings occasionally slightly raised. The flanks were fluffy, the tail was generally held about horizontal. In a few observations, the calling Black-necked Grebe had its tail cocked, in others it was extended horizontally. The vent of the bird could either be immerged or not. With a full and rather vertical extension of the neck, the breast was often slightly raised and the body was sloping. With each call in a bout of Advertising, the grebe slightly elevated and again retracted its head by stretching and relaxing the neck in a kind of pumping movement. While the head was thus moved upward, the throat bulged out and the bill was opened. In intense Advertising or repetition of Advertising, the neck was often fully extended and obliquely advanced, the crest raised further and the tail depressed. Immediately after calling, the bird remained alert, with its neck often held slightly backward from a vertical position, the crest still raised, the ear tufts relaxed and the neck and mantle feathers depressed. Greater alertness seemed to be the rule if the Advertising occurred closer to other grebes that could possibly react aggressively at the caller.

In some observations, the entire bearing of the calling grebe seemed more relaxed: the neck described an elongated S-form in a vertical plane, the crest was hardly erect and the neck feathers were not raised. This was for instance the case if during feeding dives the partners momentarily lost track of each other. Circumstantial evidence indicated that in these cases a rather firm pair bond may already have existed.

In the Wagbachniederung, early in the season, the Advertising grebe remained largely stationary in some distance of conspecifics. If unsuccessful, the bird could move further into the direction of other Black-necked Grebes, either using swimming, more seldom diving. Then it could repeat the Advertising. The calling bird could move hesitantly or cautiously towards others, stopping at some distance and rotating slightly on the water surface. I guess that this corresponds to Prinzinger's eager swimming to and fro by the Advertising grebe.

If successful, Advertising was followed either by a Discovery Ceremony or by a swimming or diving approach ending in a Hunched Display. In one case, the Advertising grebe was joined by a conspecific arriving with a low pattering flight over some 30 m; both engaged in Head Shaking. In no observation, the approach after Advertising was immediately followed by Penguin Dancing.

In a number of observations later in the season, the Advertising Black-necked Grebe, upon receiving an answer, swam quickly towards the second bird while repeating the calling on its way. Upon coming together, both grebes then quickly engaged in an often rather short courtship ritual, in many observations a simple Hunched Display. Advertising Eared Grebes did so in quite variable postures that did not differ in substance from those seen in the European nominate form. They had their necks elevated and held rather straight (Fig. 2) or slightly advanced (Fig. 3). The neck feathers and the crest were raised, the ear tufts relaxed or fanned out. The mantle feathers were mostly depressed; the wings could be shut (Fig. 2) or slightly lifted (Fig. 3). At times during intense calling, the neck was fully stretched and obliquely advanced. The grebe's body could remain in a completely horizontal plane or the breast was slightly elevated in a way that the body was sloping. The head was jerked up, the bill was opened and the throat bulged out during Advertising. The degree to which the crest was raised could change during calling. When a bout of Advertising ended, the posture of the grebe relaxed.

Often the calls consisted of a series of three successive whistles that was repeated several times after short interruptions. Individual series could be longer, too. Once, seven whistles in a row were recorded. Less than three whistles were only recorded at Tule Lake and Lower Klamath



Figure 2: Eared Grebe Advertising with beak hardly opened and mantle depressed, Little Manitou Lake, Saskatchewan (2009).



Figure 3: Eared Grebe Advertising with beak opened and wings slightly lifted, near Blaine Lake, Saskatchewan (2009).

Lake if the grebe interrupted the calling to snatch a Phantom Midge *Chaoborus crystillinus* that were floating all over on the water surface.

Especially at Tule Lake and Lower Klamath Lake, with hundreds of Eared Grebes around, Advertising birds were uncertain about their chances of success. They remained prudent as they risked aggression by conspecifics in their immediate vicinity. An unexpected surfacing by a feeding grebe or a pair feigning to swim slowly in the direction of the advertiser were enough for the latter to start some scratching or preening action or even to dive away. Advertising grebes in some distance of others could be stationary. More generally, they moved forward during calling, sometimes preening in between before repeating the Advertising. Some birds were observed to move over long distances while Advertising again and again and passing many conspecifics.

If the Advertising received a positive response, the Eared Grebes could engage in a Discovery Ceremony, in a Hunched Display, in Inviting or in a diving approach followed by immediate Penguin Dancing. The observations did not allow making a clear distinction between Advertising Eared Grebes that were firmly paired and solitary birds still in search of a partner. It seemed however that grebes really without a mate were more likely to have their vent immersed and their tail depressed, at least if calling close to conspecifics. Other Advertising grebes could float high on the water surface with the neck more relaxed and their tail cocked.

Differences in the postures of Advertising between Black-necked and Eared Grebes could not be established. In contrast to Eared Grebes, Black-necked Grebes were not observed to engage in immediate Penguin Dancing after Advertising followed by a diving approach.

6.2 Different kinds of Head Shaking, Pumping

As explained earlier, in the following Head Shaking will be used as a generic term for all kinds of head movements. **Head Turning** or **Slow Swaying, High Head Waggling, Low Head** **Waggling** and **Bill Flicking** will then stand for the kind of Head Shaking that is performed. During Head Turning, the head may be held more or less elevated. In High Head Turning, the neck of the grebe is rather fully stretched whereas in Low Head Turning it is lowered and rather retracted and the shaking of the head recalls the swinging of a pendulum. Pumping differs from all forms of Head Shaking described in that it consists in a kind of nodding movement of the head.

In the Wagbachniederung, Black-necked Grebes engaged in Head Shaking were mostly facing with their heads raised. Their necks were held rather fully extended upright or, if the grebes were more or less in breast contact, they were slightly bent backward and displayed a kind of elongated S-form. This helped to avoid collision of the heads. Their crests were raised, their ear tufts spread and the bill was held slightly below horizontal. From facing, the head appeared pear-shaped. Feathers of the neck could be raised and this was especially conspicuous with the upper hind neck and the lower front neck. Flank and back feathers were either relaxed or sometimes also raised. The tails were mostly cocked and both partners floated high on the water surface. The grebes generally used Head Turning (or Slow Swaying), gently moving their heads rather synchronously to the left and to the right with hardly noticeable interruptions while facing and before changing the direction of the head movements. Often, the bodies were slightly moved into the opposite direction of the head. High Head Turning could be interrupted by a body-shake that was generally a sign for the near end of the display. If the display was prolonged, it was mostly interspersed with vigorous High Head Waggling, a shaking of the head with the bill pointing to the sky, and Habit Preening. More seldom single Bill Flicks were observed. Performed in isolation or as a final step in a ceremony, Head Shaking mostly ended with both Black-necked Grebes starting synchronous Head Scratching or Habit Preening that then developed into regular preening. With increasing duration and excitement in a Head Shaking display, the grebes could lift their back feathers, occasionally even slightly their wings, and the display could develop into Plump Penguin Dancing. During Head Shaking, the male generally held its head higher than the female.

Black-necked Grebes coming together for a Hunched Display started with fast Low Head Turning with their heads lowered and their necks protracted. The ritual could end quickly if not developing into regular Slow Swaying with elevated head. During the slow Head Turning while Penguin Dancing, the necks of the Blacknecked Grebes could be less extended. High Head Waggling or Habit preening, occasionally even Bill-flicks could occur in between. The waggling and preening was often performed in alternation by both birds and could continue after the grebes' bodies were again in the horizontal plane.

Head Shaking could be interrupted and one or both grebes rotated on the water surface from facing each other to facing into the same direction. With their necks held rather upright, both could kind of proudly overlook the water surface in a kind of very Slow Swaying. They could now even start Parallel Swimming and continue the slow Head Turning that was however more irregular and the partners were generally not in unison when looking left and right. On other occasions, the Head Shaking was followed by an Inviting or Pivoting Display.

Especially early in the season, it was not always clear to what extent Head Shaking grebes were paired. Some displays were very short and appeared more as a displacement activity in a possibly more aggressive context. Low Head Waggling was observed rather seldom. It seemed to be used exceptionally by two Black-necked Grebes swimming together and that afterwards separated quickly, perhaps because they had mistaken the pairing status or the sex of the other. Also, displaying pairs could be disturbed by a third Black-necked Grebe that could immediately attack one of the partners or it could try to join into the Slow Swaying of the mates. In the latter case, it risked to be attacked and short pursuits could follow.

In a few observations, the High Head Turning ended with Pumping and the grebes jerked their heads up and down three or four times. Often, no further rituals followed or the birds only hesitantly tried to continue their courtship. Pumping was occasionally seen prior to Head Turning if two grebes appeared undecided of whether to engage or not in the display. During Head Shaking (Fig. 5), North American Eared Grebes frequently changed their positions from facing to looking in a same direction while continuing the display, either side by side, occasionally even one behind the other. While side by side, Slow Swaying with the vertical neck more in S-form seemed to be the rule; more seldom the necks were fully stretched. During facing, Eared Grebes were mostly with breasts touching. As a consequence, the necks then were bent backward in S-form. The crests were erect, the ear tufts flared out, the neck feathers up, the tail most often cocked and the flanks fluffy. The back feathers could be more or less lifted. In intense performances the wings were often partially raised. The Head Turning in a horizontal plane was regularly interspersed with High Head Waggling and Habit Preening. It often ended with Head Scratching that could quickly develop into heavy preening. In some observations, the display started with the heads held rather low, the necks describing a more depressed s-form. The heads were then soon lifted.

During Parallel Swimming, Eared Grebes were regularly observed to use Slow Swaying. Often one grebe was slightly advanced and seemed to lead. The birds had their heads elevated and the feathers of the mantle were depressed. During Penguin Dancing, Head Turning, Head Waggling and Habit Preening could occur. Bill-flicks were more exceptional.

Head Shaking was seen to serve as a prelude to the Pivoting Display, too. At one occasion, after Head Shaking, the Eared Grebes rotated to come parallel to one another and one partner, possibly the male showed Wing Quivering (a kind of wing rubbing with folded wings). In the Hunched Display, the heads were held rather low and Low Head Shaking was performed. Pumping seemed to be used in situations where the grebes hesitated of whether to start a ritual or not.

In substance, no differences in Head Shaking between European and American *nigricollis* grebes were observed. Performed in isolation, Head Turning appeared to serve in three different situations: as a form of greeting between established partners, to prudently approach a possible mate and to appease another grebe in an aggressive context. Concerning Pumping (Wittgen 1962), the present study found no evidence to consider it as a display on its own. The few observations in Blacknecked and Eared Grebes were always related to situations where the grebes appeared hesitant about whether to engage in a ritual or to continue courtship after Head Shaking. It might be more a behaviour, perhaps a kind of displacement activity helping to bridge situations of uneasiness.

6.3 Habit Preening and occurrence of Head Scratching in both subspecies

In the Wagbachniederung, Habit Preening occurred mostly in combination with Head Shaking, also during Penguin Dancing. Generally, it appeared to be less ritualized than for instance in the Great Crested Grebe P. cristatus that, with an elegant backward arching of its neck, shortly lifts a mantle feather with the beak for the batting of an eyelash. In Black-necked Grebes, the Habit Preening was generally more vigorous and it could concern the flanks, the back, the breast or even the rump. It could resemble a short intense rubbing of the feathers with the beak. The display by two grebes was seldom synchronous, at times performed in alternation, at others only one partner showed Habit Preening. Occasionally, Habit Preening ended a Head Shaking sequence.

More regularly a ritual ended with Head Scratching after which another courtship could follow. For instance, after scratching in the Hunched Display, the Head Shaking was not resumed, but a kind of more or less synchronous Habit Preening (Fig. 4) different from the first and difficult to tell apart from real feather care followed. This appeared to be a ritualized action that then graded into ordinary preening, the partners first getting out of time and then both doing their own business. Also, if the scratching interrupted high Head Shaking, Parallel Swimming or a Pivoting/Inviting Display the preceding ritual generally ended for good. Both grebes started the scratching more or less simultaneously and their action was quite synchronous. While still close together, the grebes suddenly lowered their heads to the water surface, drew in their neck and pushed their head sideward. Their ear tufts remained spread, the crest raised. They advanced a foot and lifted it out of the water to vigorously scratch their tufts or their occiput feathers with one toe. While scratching, the grebe



Figure 4: Synchronous Preening of two Black-necked Grebes (2009).

had its chin on the water surface, the beak at times even dipping in. The foot not used for scratching was held in a way to outbalance the scratching movement.

Outside of other displays, Head Scratching or Habit Preening was often used by single grebes or pairs if approached by one or two conspecifics. It appeared as a kind of displacement activity, in pairs often performed simultaneously by both grebes if the intention of the stranger was unclear. Both rituals were also used at relief after hostile interactions.

In Eared Grebes, Habit Preening was used similarly to the nominate species. Head Shaking was often interspersed with Habit Preening. Most often, the preening was vigorous and short. In a few observations, the action appeared elegant and fast (Fig. 5), closer to that of other *Podiceps* species and consisting of a brief contact between the bill and a feather of the mantle. Prolonged synchronous Habit Preening was recorded, too. During this, the pairs frequently rotated on the water surface and came from facing to parallel to one another. Head Scratching was not reported for the American subspecies in literature, probably simply because it was not recognized as a display. It was observed regularly during fieldwork in Canada and the USA (Fig. 6). Head Scratching was seen in the context of the Hunched Display, as an interruption to Head Shaking and in the final stages of Parallel Swimming or of a Pivoting/Inviting Display.

In an aggressive context, both Habit Preening and Head Scratching were used as a displacement activity. If encountering a strange grebe, Eared Grebes could briefly Head Scratch or Habit Preen and then continue their way. Also following a pursuit, a pair could stop and engage in Head Scratching that could be followed by Habit Preening.

In conclusion, the existence of Head Scratching in Eared Grebes was confirmed and no differences in Habit Preening and Head Scratching between the subspecies were detected. Three different kinds of ritualized preening appear to exist in *nigricollis* grebes:


Figure 5: Eared Grebe pair engaged in Head Shaking with Habit Preening, Little Manitou Lake, Saskatchewan (2009).



Figure 6: Eared Grebes in Head Scratching with bills dipped in, Lower Klamath Lake, California (2011).

the short and vigorous Habit Preening that can involve different parts of the plumage and that is also observed in other species of grebes,

the Head Scratching,

the prolonged synchronous Habit Preening so far not reported from other grebe species and that should perhaps be termed Synchronous Preening to avoid confusion.

6.4 Billing or Hunched Display and observations with respect to Food Presentation

Prinzinger's description of Billing appears to correspond to the Bill Touching of Koop (2003). With Hunched Display, Fjeldså (1982) chose a better term that insinuates a ritual going beyond a mere touching of bills.

In the Wagbachniederung, the display was initiated by a grebe Advertising. The mate kinked its neck forward with the head held low, the crest slightly raised and the ear tufts spread. The wings were lifted to varying degrees. The bird faced into the direction of the first Black-necked Grebe that was progressing in its direction. The latter could either swim quickly, often in a similar bearing as the waiting grebe or it could dive and surface just in front of its mate. Upon meeting, both adopted the Hunched posture and chittering calls were uttered. Both grebes performed a rather short Billing consisting in just two or three fast and Low Head Turns. During these, their beaks were close to touching. In over 60 observations of Billing, no case of prey delivery was observed in the Black-necked Grebes. Most often, Head Scratching, in rare cases Habit Preening followed.

If an Advertising grebe chose a diving approach, the partner could occasionally adopt a Cat Attitude. Possibly in this case, it expected its mate to engage in a Discovery Ceremony. The diving bird did however not pop up in the Bouncy or Penguin posture, but emerged just in front of the waiting grebe in the Hunched posture and both performed the Hunched Display. During a swimming approach, both partners could repeatedly Advertise. In a few observations, both grebes swam to join and perform the Billing. In one case, both grebes dived and met halfway for the short Low Head Turning that was continued with elevated heads and interspersed with Habit Preening.

Especially early in the season, the Low Head Turning of the Hunched Display could be continued with elevated heads. This could end either with Habit Preening or Head Scratching. If the High Head Turning was particularly intense, it could grade into Plump Penguin Dancing with the wings and mantle feathers partially lifted. Also other displays, for instance Parallel Swimming or Barging or Pivoting or Inviting followed by Weed fetching could succeed. Later in the season, often only Low Head Turning that ended quickly with Head Scratching occurred. Thereafter, both grebes could engage in some comfort activity or one or both dived.

In Black-necked Grebes, the Hunched Display could develop out of an aggressive context, too. In these cases, it possibly served as a Triumph Ceremony. A pair could engage in it either upon being approached by conspecifics or immediately after a pursuit. The partners joined for a Hunched display during which they quickly rotated from facing to side by side.

In Eared Grebes, the general unfolding of the display went as follows: after Advertising by one or both birds, one partner remained stationary and adopted the Hunched posture while the other approached either by swimming or diving. The grebes then met with their necks kinked and their heads low (Fig. 8). Upon joining, the partners were often heard to utter low calls and their bills seemed to touch. In most occurrences, the Low Head Shaking, if any, was hardly noticeable and the mates rather immediately engaged in Head Scratching followed by Habit Preening and Slow Swaying that occasionally lasted for longer. In a few observations, two or three quick Low Head Turns were seen before Head Scratching occurred. Courtship often ended either with real preening, the birds diving and continuing their feeding, both swimming together into a same direction or they simply separated again.

In a few observations, the calling partners were at greater distance from one another. Then both could move to join. In one case, one partner covered a major part of the separating distance by pattering over the water surface. It stopped at 1-2 m from the second grebe, and then both



Figure 7: Black-necked Grebes lifting their heads for High Head Shaking after a Hunched Display (2009).



Figure 8: Eared Grebes in Hunched Display with Low Head Turning, Tule Lake, California (2011).

swam together with heads low. Occasionally, the response of the second grebe to the Advertising consisted in that it adopted a Hunched posture that was soon changed into a Cat Posture. Even though the diving grebe could now surface once or twice in a normal bearing on its way, upon meeting, the Hunched Display was performed. In one observation, a partner adopted the Cat Attitude while the other surfaced in the Bouncy posture just 2 m away. The latter dived again and surfaced for a Hunched Display followed immediately by High Head Turning and Habit Preening.

At times, after meeting in the Hunched Posture, neither Head Scratching nor Habit Preening followed, but the partners turned parallel either for Parallel Swimming, Racing or even Barging. Also Pivoting and Inviting were observed to follow. In rare cases, two grebes upon meeting turned parallel to one another before adopting the Hunched posture and performing short Low Head Turning that was followed either by Head Scratching or Habit Preening or both. In a diving approach, the Billing could immediately be followed by Penguin Dancing.

Regularly the Hunched Display was performed after attack and pursuit of a third grebe or a second pair. The partners then turned to facing in the Hunched posture and showed a short low Head Shaking followed by Head Scratching and preening. Sometimes, the partners were not strictly facing, but more turned towards the opponents.

Except for a perhaps less noticeable Low Head Shaking in Eared Grebes, no difference in the circumstances or the performances of the Hunched Display between both subspecies were detected. The study confirmed the existence of the Hunched Display for North American populations.

6.5 Pivoting and Inviting pose on the open water surface

During fieldwork in the Wagbachniederung, it appeared that the Pivoting and the Inviting displays were not easily dissociated in the nominate form. Similarly, the American subspecies provided many examples in which both displays either alternated or where an interrelation of Pivoting and Inviting was obvious. Therefore, both displays will be discussed together. In literature the posture of the pivoting grebe is not described and relies entirely on Palmer's (1962) drawing of two grebes facing with extended necks held obliquely advanced. In principle, this posture could simply correspond to the bearing of the partners before the first Pivoting occurs. This study allowed defining four basic postures used by *nigricollis* grebes independently of the subspecies. The first bearing corresponds to Palmer's (1962) drawing (Oblique Pivoting posture). In the second posture, the grebe's neck is bent in S-form in the vertical plane, the ear tufts are sleeked (S-Pivoting posture, Fig. 9); the neck can be more (Fig. 10) or less retracted. If extended, the posture recalls a seahorse. The third bearing fits with the ordinary Inviting posture in which the grebe has its necks lowered to the extent that its chin rests on the water surface (Low Inviting posture, Fig. 11). The fourth bearing differs from the third in that the grebe's head is slightly lifted with the neck kinked forward. The posture is comparable to that of the grebe inviting on a platforms when it lifts the head (High Inviting posture, Fig. 11).

A Black-necked or Eared Grebe adopting an Inviting posture could pivot on the water surface with its partner either doing alike or remaining preening in its back without pivoting. In order to avoid confusion between the Pivoting and Inviting displays, the following principles were established and will be followed:

Under Pivoting Display are included all observations where two grebes rotate on the water surface more or less tail to tail, independently of the birds' bearing;

If Pivoting Display is used without indication of the grebes' bearing, one of both "Pivoting" postures is meant;

If rotating in an "Inviting" posture, Pivoting Display with Inviting is used;

If only one grebe pivots in one of both Inviting postures, we are in presence of an Inviting display.

Pivoting Displays

The Pivoting Display as described by Palmer (1962), but not directly observed by Prinzinger, occurred regularly in the Wagbachniederung and the display is well performed by the European nominate. Pivoting frequently followed a prolonged Hunched Display with regular Head Shaking as already mentioned by Fjeldså (1982).





Figure 9: Black-necked Grebes Pivoting with necks in high S-form (2010).



Figure 10: Black-necked Grebes Pivoting with necks in retracted s-form (2009).

The display was also added to the Discovery Ceremony after Penguin Dancing and Head Shaking. In most observations, Head Shaking immediately preceded Pivoting. In a few cases the display was started by two grebes after preening for a while.

Two Black-necked Grebes engaged in High Head Turning could discontinue their display. Their necks not fully extended vertically described about an arc in the vertical plane. The head was held slightly advanced quite above shoulder height (S-Pivoting posture, Fig. 9). The posture was rather stiff. Just prior to Pivoting, ornamental feathers became more and more sleeked and the crest depressed. The lateral spreading of the short black head feathers below the ear tufts gave to the head a swollen appearance. The feathers of the neck were raised and those of the mantle could initially be partially raised. During Pivoting, a rotating movement of the body on the water surface, the birds could maintain their rigid bearing or simply retract their neck a bit further (Fig. 10). Rather seldom, they adopted the Oblique Pivoting Posture of Palmer (1962) neither before the display was started nor in the display itself. They could rather opt for one of the Inviting posture, flat on the water surface with the neck advanced and lowered either with the head at shoulder height or with the chin on the water surface (Pivoting Display with Inviting, Fig. 11).

Both partners did not necessarily adopt or maintain the same posture for the entire display and the bearing of the grebes could alternate between the different postures defined. It occurred that both mates did not show the same posture simultaneously. The speed of the pivoting and its amplitude could vary greatly between two displays and even between two partners in one display. The mates came to lie vent to vent after the first pivoting. They could now have increased the distances to each other to a varying degree, from tails close to touching to a distance of over one metre in some observations. The partners mostly remained quite stationary for differing durations before again describing a greater arc on the water surface. As their Pivoting was not necessarily synchronous, their bodies were not always at an angle of 180° to each other. In some observations, the grebes came even to be about parallel to one another before again increasing the angle. The display generally ended with one and then the other grebe diving. In a number of observations, the diving simply meant an interruption of the Pivoting and the surfacing grebes resumed the ritual. The diving could also initiate Weed Presentation, even if no Inviting posture was involved in the Pivoting. In a few cases, the relaxing of the posture was immediately followed by preening. A Pivoting display performed after intense preening was often rather short, with less rotation by the partners and often without a final dive, but rather resuming of comfort activities.

The Pivoting Display was observed quite often at Blaine Lake and at Little Manitou Lake, less frequently at the Klamath valley refuges. It was preceded either by the Hunched Display, Penguin Dancing, Head Shaking or Habit Preening. The display could also be integrated into those performed in continuation of a Discovery Ceremony. Generally, High Head Turning performed in isolation or as part of a ceremony preceded. Most often, the Eared Grebes pivoted on the water surface in the S-Pivoting posture (Fig. 12). During Pivoting, the birds could however alternate their bearings. Only exceptionally, the Oblique Pivoting posture was observed, neither during the initiation of the display, nor later, and Pivoting with both partners in the High Inviting posture was rare. It was not observed with both partners in the Low Inviting Posture. During the display in the S-Pivoting posture, the crest was depressed, the ear tufts were sleeked and the feathers of the neck were lifted. The mantle feathers could be raised.

The distance between two pivoting birds was quite variable as was the speed of rotation. While rotating and after having been tail to tail, the grebes could again come to lie more side by side. In the Oblique Pivoting and Inviting postures, the partners could turn their heads slowly to the sides as in slow Head Turning. The display often ended with preening or with one or both grebes diving. If only one partner dived, the Pivoting display was occasionally continued after it surfaced again. The diving could also start Weed Presentation. In a few observations, the display followed a short pursuit between two pairs and the performing partners adopted the Oblique Pivoting posture.

Inviting on the open water surface

At the Wagbachniederung, the display was present early in the season and it was performed with



Figure 11: Black-necked Grebes Pivoting in high (left) and low Inviting Postures (2009).



Figure 12: Pair of Eared Grebes in early phase of Pivoting, Tule Lake, California (2011).

increasing frequency in time. It often followed the Hunched Display or Head Shaking performed in isolation. It could be added to the Discovery Ceremony or it occurred simply after two mates were loafing together. Occasionally, the display was performed after one or two conspecifics approached a pair. In rare cases, a grebe adopted the Inviting posture after Advertising. Then, it generally waited for the arrival of the partner and immediately dived.

Inviting was initiated by one Black-necked Grebe that either first rotated its back towards the partner and then adopted the Low Inviting posture, in rarer cases also the High Inviting posture, or that first adopted an Inviting posture and then pivoted. In the Low Inviting posture (Fig. 13), the body of the grebe was extended flat over the water surface, the back and tail feathers were depressed, the flanks appeared fluffy. The neck was generally extended or slightly retracted with the chin close to or on the water surface. The grebe in the Low Inviting posture was often heard to utter soft calls. It could change for the High Inviting posture with the head held slightly higher and the neck kinked in the middle. In both bearings, the ornamental feathers were sleeked. The Inviting bird could remain about motionless for some time, possibly alternating between the Low and High Inviting postures, slightly swaving its head now and then so as if spearing for its partner. Similar as in Inviting on a platform, the mate remained in the back of the Inviting grebe where it could heavily preen and scratch or move to and fro. It was occasionally observed to swim into the back of its partner where it stretched the neck forward and advanced its head over the rump of the Inviting grebe. In a few observations, it lowered its beak directly to the region of the other's vent as if smelling, a behaviour that could be repeated once or twice (Fig. 13). The Inviting grebe often pivoted to varying degrees on the water surface, occasionally performing a 180° or even a 360° rotation in one or several stages. After some time, the Inviting grebe could dive and this could end the display. If its partner adopted the Inviting posture prior to the surfacing of the diving bird, the display could continue with inversed roles. The Inviting grebe could also simply give up its rigid posture and perform some stretching exercises of body, wings or legs



Figure 13: Female Black-necked Grebe Inviting while the male appears to smell at its vent (2009).



Figure 14: Eared Grebe: Inviting on the open water surface, Tule Lake, California (2011).

or it could simply start preening and scratching. In some observations, the scratching grebe dived and the Inviting grebe gave up its posture after a short hesitation. In a few cases, the partners started Parallel Swimming after the Inviting display. Often, the diving grebe reappeared with weeds and Weed Presentation followed.

Early in the season, the Inviting Display was always performed at some distance from the shore and often no Weed Presentation or other behaviour insinuating any kind of nest site selection followed. Later, weed fetching succeeded regularly. Thereafter, both Black-necked Grebes regularly swam towards emerging vegetation or the display itself could already occur close to it. There, the birds could perform Ceremonial Building without that real platform building succeeded. Once a basic platform became visible, more pairs could show interest in the place. One means among others to claim the property was then to invite in front of it.

In the North American subspecies, Inviting did not markedly differ: Eared Grebes invited with ornamental feathers sleeked, the neck stretched or kinked forward and with the head held more or less low so that the chin could touch the water surface (Low Inviting posture, Fig. 14). The position of the head was often corrected in accordance with wave action. The inviting bird could raise its head slightly and move it unnoticeably to one side or the other to look back over its shoulder (High Inviting posture). Its mate generally remained preening in its back. As the inviting grebe could rotate, it occurred that the partners came side by side or even that the preening partner was in front of the displaying partner. On a few occurrences, the inviting Eared Grebe was observed to lift its mantle feathers. The reason remained unknown; one possibility is that this replaced the wing quivering in Rearing on a real platform. Two birds could alternate in Inviting, especially if interspersed with diving. Also, the preening grebe could move to the back of the inviting grebe and extend its neck over the latter's vent, just as prior to mounting on a real platform. At no location simultaneous Low Inviting by two Eared Grebes was recorded.

Inviting could simply follow comfort activities. Occasionally, one grebe invited on the open water surface after Parallel Swimming. Quite often, it served as a response to Advertising. The advertiser then most often dived and surfaced behind the inviting grebe. Sometimes it swam to there and started preening. In one occurrence, the long lasting advertising by a male grebe moving forward was answered by a female swimming in its direction. Thereupon, the male adopted the Low Inviting posture. The female dived and surfaced in front of the male where it adopted the Inviting posture, too. The male however abandoned it and started preening. The female slightly rotated on the water surface, finally both scratched their heads and the display ended. If Inviting followed Advertising, the diving grebe could surface in the Hunched posture whereupon both mates immediately showed Head Scratching. Displaying pairs could alternate between Inviting and Pivoting. More often, Inviting simply followed Pivoting. The display ended either by the grebes preening or by at least one partner diving. The dive of the Inviting grebe could also lead to Weed Presentation and both grebes thereafter alternated in Inviting and weed fetching. This could be followed by directed swimming towards emergent vegetation. Eared Grebes also invited already inside vegetation suited for nesting. Again, the partners could alternate the Inviting that could be followed by Ceremonial Building or real platform construction. Access of foreign grebes to a started platform was often prevented by adopting the Inviting Pose in front of it.

Fieldwork revealed no fundamental differences in Pivoting or Inviting between Black-necked and Eared Grebes. About all forms of the displays were observed in both species, however with a priori different frequencies. It could for instance be that Pivoting in an Inviting posture is more common in the European nominate form and that Inviting after Advertising is more frequent in North American populations.

Inviting, Soliciting and Nest Selection Display

The Inviting as understood here is generally only performed by one partner at a time. If during a sequence both grebes adopt the posture, it is always in alternation and not simultaneously as in the Pivoting Display with Inviting. Prinzinger did not list Inviting on the open water surface under water courtship, but placed it at the start of platform courtship and Cullen et al. (1999) named the display Nest-selection. McAllister (1958) used Soliciting. We may therefore ask whether the three terms can be used as synonyms or whether we have two or even three different rituals, perhaps subdivided between water and platform courtship.

Inviting, Soliciting and Nest Selection Display were performed in a similar manner on the water surface. If we look for a differentiation, we have to analyse the different circumstances under which the ritual occurred. Early observations in Europe and North America indicated that Inviting occurred mostly in isolation whereas later in the season, it was mostly followed by Weed Presentation, directed swimming towards emerging vegetation or both. It appeared that the Inviting posture was regularly adopted outside of a context pointing at imminent nest selection. In addition, early in the season, the display was regularly performed on the open water surface away from any vegetation whereas it occurred later often inside vegetated areas or close to places where nest building was at least possible. After directed swimming towards or if Inviting already inside vegetation, quite regularly Ceremonial Building followed

The display on the open water surface developed from Inviting on a real platform. Initially, it may simply have served to express a wish of nest selection. However, the findings of this study provided some evidence that its meaning may have evolved further to serve two functions. Whereas occurrences earlier in the season may simply serve pair bond confirmation, later performances that are followed by behaviours related to nest site selection or platform building can be seen as transitional to platform courtship. These later displays may be regarded as Nest Selection Displays. However this term cannot generally replace the term Inviting that should be used for describing all occurrences not involving directed swimming or weed fetching. Soliciting may serve as a synonym to Inviting.

Whereas the Inviting display has definitely to be placed with water courtship, it is a matter of taste of whether the Nest Selection Display belongs to water or platform courtship. It is in fact a transition between both.

6.6 The Discovery Ceremony and its composing elements

Advertising, Cat Attitude, Bouncy Display and Ghostly Penguin are the composing elements of the Discovery Ceremony proper. It is initiated by the Advertising call of one *nigricollis* grebe. If receiving a positive reply, one partner dives at the encounter of the other. It emerges on its way in the Bouncy Posture while the other adopts the Cat Display. It finally surfaces growing out of the water in the Upright Penguin posture.

In the Wagbachniederung, mostly both partners Advertised, but the initiating Black-necked Grebe remained often undetected. One grebe observed to call was often isolated from others. Regularly it had to repeat the Advertising before receiving a reply. In most observations, the apparent initiator of the calling thereafter also started the diving (Ghost bird). Its partner (surface bird or Cat bird) was less active. It remained turned into the direction of the diving grebe, perhaps raising its back feathers and lifting its wings slightly without really opening them. Its head lowered to shoulder height, often also slightly more elevated without that the neck was much stretched, it observed its mate's progression under water. At times, it even speared below water. Ripple Diving was not recorded during the approach of the Ghost bird, but cannot be excluded. On its way towards the surface bird, the diving grebe made one or several intermittent appearances in the Bouncy Posture (Fig. 15). During these, it floated high on the water surface with slightly sloping body and protruding breast. The tail remained well above the water surface and was cocked. The lower neck was folded back onto the mantle, the upper neck was kinked forward and the chin rested on the breast All ornamental feathers were sleeked Generally, the hind neck rested completely on the bird's back and the beak touched the upper breast. Occasionally, the folding of the neck was not so tight and the s-form that it described was more open, the bird's chin did not rest on the breast and the head was held rather high. The Bouncy grebe did generally not directly face its partner. It dived again after maybe two or three seconds of exposure, swinging its head and neck forward and down, the body following. Exceptionally, the Ghost bird only briefly emerged its head after the first dive, so as to orient itself before resuming



Figure 15: Bouncy Posture of a Black-necked Grebe directly in front of the Cat bird (2011).

its progression under water. A maximum of three appearances in the Bouncy Display were recorded before the final emergence of the diver in the Ghostly Penguin. These could happen in a straight line towards the surface bird or with some zigzagging en route. In most cases, the last appearance in the Bouncy display was close to the surface bird (50 cm to 3 m away).

Meanwhile, the Cat bird waited and rotated slightly on the water surface to remain always turned towards its progressing mate. It further lifted its wings. They first came to form a kind of tent over its back with the white tips of the secondaries becoming visible before the lateral unfolding for the full Cat display occurred. Simultaneously, the grebe could retract its neck and advance its head slightly with ornamental feathers fully spread; the crest was erect and the ear tufts were fanned out maximally. Often, the head was held rather high. In many observations, the Cat Display of the Black-necked Grebe was not performed with full spreading of the wings. Then, it resembled to the Swan Display of the Red-necked Grebe. In addition, the point in time when the surface bird adopted the Cat Attitude was variable. Occasionally, it already performed a full spreading of the wings immediately after the Ghost bird's Advertising. In many observations, the Cat Display was only adopted with the partner's last appearance in the Bouncy Posture.

After this penultimate exposure of the diver, its final dive often apparently passed below the Cat bird that simultaneously lifted its head and folded its wings away. In no case, the surface bird was still in a complete Cat Attitude when the Ghost surfaced, but it generally kept its wings slightly lifted. Its crest was still raised and its ear tufts spread (Fig. 16). It rotated on the water surface to keep track of the diving partner that now broke the water surface for its final appearance. It often emerged with a call at an increased distance of up to three metres. It did so with its body in a vertical plane, its back turned at the Cat bird, its neck and head kinked forward and the head feathers sleeked (Fig. 16). At maximum height, it initiated an elegant pivoting to facing with a lateral jerking movement of its head. At the same time, it elevated its head and spread its ornamental feathers. The neck was now extended vertically. As the lower neck feathers were depressed, the



Figure 16: Black-necked Grebe performing the Ghostly Penguin in front of the Cat bird (2010).

neck looked very slim, especially in comparison to the spheroid body that often achieved extra volume due to the lifting of the back feathers. Falling slightly back from the culminating point maintained during the rotation, the Ghost bird heavily treaded water and remained in a Tall Penguin Dance posture. In most observations, it started to proceed thus in the direction of the surface bird that adopted the Penguin posture itself and either was stationary and waited or moved at the other's encounter, Head Waggling on its way. The surface bird appeared sometimes impatient and rose its body already prior to the partner's rotation. Occasionally, the Ghost bird Penguin Danced on the place and the Cat bird covered the full separating distance. Rarely, the surface bird remained stationary, without rising into a Penguin posture, Head-shaking and Head Waggling. At times, it also adopted a kind of low Plump Penguin posture with the breast raised and the mantle feathers lifted.

The Penguin Dancing grebes approached until their breasts touched. They continued the dancing at close range, simultaneously performing Slow Head Turning, Head Waggling and Habit Preening. During prolonged dancing, the partners could increase the distance between themselves before moving closer again. After Penguin Dancing, both Black-necked Grebes either simultaneously or with a short time lag fell again into a horizontal plane. In about all observations, they now continued the Head Turning interspersed with Head Waggling and Habit Preening. During Head Shaking, they mostly kept the back feathers raised. The courtship could now end either with Head Scratching or Habit Preening. It could also be continued, for instance with Parallel Swimming, Barging or a Pivoting and Inviting Display followed by Weed Presentation.

In the North American subspecies, both partners were observed to repeatedly Advertise to initiate a Discovery Ceremony. It remained unknown which Eared Grebe started the Advertising, the Ghost or the surface bird. Four different stages were observed in the adoption of the Cat Attitude. At first, the surface grebe often remained alert; it held its neck rather vertical and the wings were only slightly lifted. Its ornamental head feathers were spread. The posture was followed by the adoption of a kind of Pre-cat posture with lowered head and the wings obliquely lifted, but hardly unfolded. In the next stage, the surface bird partially unfolded the wings without much lateral spreading so that they built a kind of tent over the bird's back. This corresponded to the Swan posture of the Red-necked Grebe. The bird's head could be held more or less low and retracted, the ear tufts were flared out and the crest was raised. The full Cat posture occurred with the next step when the grebe completely unfolded its wings laterally and tilted them (W-shape, Fig. 17). As in the European nominate, the point in time when the Eared Grebe adopted the Cat Display was variable. In most observations, the Pre-cat posture was adopted either with the first dive or with the first Bouncy appearance of the Ghost bird. In the course of events, the intermediate step with the wings lifted, but only slightly opened occurred. The final Cat Attitude regularly only showed up with the last Bouncy surfacing of the diving grebe close to its mate. In one observation, Advertising was answered by a second grebe about 15 m away with the Inviting posture; the calling bird dived and surfaced in the Bouncy posture after having covered half of the separating distance. Only thereupon, the Inviting grebe adopted the Cat Display.

In each ceremony, the diving grebe emerged at least twice and up to four times in the Bouncy Posture (Fig. 17), with the lower neck bent backward and the chin resting on the upper breast. The grebe's crest was flat and the ear tufts were depressed. The successive appearances were generally not in a straight line, but the distance to the Cat bird was ever shrinking. With rare exceptions, the last Bouncy surfacing was directly in front of the surface bird and the following Ghost appearance farther away.

The Cat bird abandoned its posture either immediately with the last dive or at the latest early in the final appearance of the Ghost bird (Fig. 18). The latter popped up at a variable, but generally increased distance from the surface bird. The surfacing grebe had its back turned at the partner, the neck bent forward and all ornamental feathers sleeked. Although no call was heard, in a few observations, the beak of the Ghost bird was widely opened and it is thought that it uttered a call. Standing upright on the water surface (Tall Penguin posture), it rotated to facing when reaching the culminating point, now with its neck vertically stretched and its ornamental feathers



Figure 17: Eared Grebes: Bouncy Posture in front of Cat Bird, Tule Lake, California (2011).



Figure 18: Eared Grebe in Ghostly Penguin, the partner has its wings already folded away, Little Manitou Lake, Saskatchewan (2009).

spread. Most often, the Cat bird already adopted the Penguin posture before the Ghost bird rotated. Both grebes then started to move together more or less simultaneously, Penguin Dancing, Head Shaking and Head Waggling on their way (Fig. 19). Upon coming together, the grebes Penguin Danced breast to breast, occasionally with much rotation and moving a bit apart. Their breasts were protruding, the neck was elevated in S-form and the upper neck feathers were lifted. The ear tufts were flared out and the crests were raised. The grebes could turn parallel and continue the dancing moving both side by side into the same direction. In a few occurrences, the Ghost appearance was immediately in front of the Cat bird. In these cases, the Penguin Dancing, if any, was rather short: both grebes fell quickly back onto the water surface, Head scratched and the courtship ended.

During Penguin dancing, even if lasting for quite some time, Eared Grebes were only occasionally observed to Habit Preen. Only Head Turning and occasional Head Waggling were observed. When their dancing ended, the partners continued the Head Shaking and Habit Preening. Head Scratching could now end the courtship for good or it was continued with other displays, for instance Parallel Swimming or Barging, Pivoting and Inviting and Weed Presentation. Occasionally, the weed fetching was followed by directed swimming towards the vegetation where then Ceremonial Building and further Inviting followed.

No differences between the subspecies appeared in the Discovery Ceremony.

6.7 Retreat Ceremony and Pattering Retreat

It is important to distinguish in this context from the start the retreat "flight" (Pattering Retreat) as described by Cullen et al. (1999) and discussed in this chapter from the Flight Display that is discussed later. Whereas in the first the grebes simply patter across the water surface, their feet remaining in constant touch with the wet, in the second, they may get really airborne for at least



Figure 19: Eared Grebes walking together in a Tall Penguin posture after a Discovery Ceremony, Tule Lake, California (2011).

part of the often longer distance that they cover. To avoid confusion, a distinction between the Retreat Ceremony and the Pattering Retreat is also necessary. In the Retreat Ceremony of Podicipedidae, the retreating grebe withdraws with a pattering race from an on-going display, generally from Head Shaking following a Discovery Ceremony, and adopts the Cat Attitude to perhaps initiate another Discovery Ceremony. The term Retreat Ceremony should only be used if either the preceding display is repeated or at least another ritual follows. If the action is limited to the retreat without additional courtship, the term Pattering Retreat should be used.

A Pattering Retreat was not directly observed in the Wagbachniederung. On a few occasions, a single Black-necked Grebe engaged in a pattering race away from a single or several conspecifics. After some 10 or more meters, it halted and rotated 180°, perhaps adopting a kind of Pre-cat posture. Unfortunately, in no case the retreating grebe was observed prior to its pattering. It remained unknown whether it retreated from an on-going display. While stationary, the bird was joined by a second grebe that either swam or dived towards it. Thereupon, the first grebe did neither adopt a clear Cat posture nor did any courtship follow. A complete Retreat Ceremony was not observed.

In the Eared Grebe, a Pattering Retreat was observed more often, but it seldom developed into a Retreat Ceremony. At times, the retreat across the water surface with flapping wings was performed by two birds simultaneously. At the refuges of the Klamath valley, the Head Shaking display was a few times interrupted by a Pattering Retreat of one partner. In some observations, the partners first turned parallel and seemed to engage in Parallel Swimming when suddenly one partner retreated. The second grebe then either swam or dived to join it again. The waiting bird was not observed to adopt the Cat attitude. Upon joining and except for a quick Head Scratching in one or two cases, generally no further rituals were performed. In two observations, the Head Shaking following Penguin Dancing was interrupted by a Retreat Ceremony: after the Pattering Retreat (Fig. 20), once a Ghostly Penguin and once a Hunched Display were performed. After



Figure 20: Eared Grebe in Pattering Retreat, Tule Lake, California (2011).

a Discovery Ceremony, both grebes about simultaneously interrupted the Head Shaking that followed and both pattered simultaneously away in about the same direction. After landing, both moved together and preened.

Whereas pattering occurred more or less regularly in both subspecies, mostly without that the circumstances of the retreat were clearly identified, a full Retreat Ceremony was only observed in Eared Grebes. The latter was also not previously reported in literature for the Black-necked Grebe. We may therefore conclude that it could be absent from the nominate form, but it is also extremely rare in the North American subspecies.

6.8 Penguin Dancing

Fjeldså (1982) distinguished between a Plump and a Tall Penguin Dance. While in the first, the elevation of the grebes is moderate and they show little splashing, in the second, the birds rise very high on the water surface into an Upright Penguin posture and they splash strongly. The Tall Penguin Dance follows the Discovery Ceremony. In it, the birds mostly look rather slim.

In Black-necked Grebes, Penguin Dancing was not seen in isolation. It was preceded either by Head Shaking or more commonly by the Ghostly Penguin of the Discovery Ceremony. In some rare cases, it succeeded to Parallel Swimming. Whereas in continuation of a Discovery Ceremony, both grebes performed a Tall Penguin Dancing, after Head Shaking on the water surface, a Plump Penguin Dance followed (Fig. 21). In the latter, the elevation of the grebes' bodies was less important and could not entirely reach a complete vertical position. Generally, the flank and mantle feathers were lifted and the bodies appeared very massive. In the Tall Penguin Dancing, initially the partners rose about completely out of the water and their back feathers were depressed so that their bodies looked elongated. In both forms of dancing, the neck could be stretched up vertically or slightly bent in S-form, but it was generally more extended in a Tall Penguin Dance. The ornamental and other feathers of the head were spread and the crest was raised. The neck feathers were mostly erect in a



Figure 21: Black-necked Grebes engaged in Plump Penguin Dancing following Head Shaking, with neck and mantle feathers raised (2009).

Plump Penguin Dance, but could be sleeked, at least in the lower neck, in a Tall Penguin Dance. While dancing, the Black-necked Grebes slightly rotated their bodies, perhaps a bit less in a Plump Penguin Dance, and swaved their heads alternating between left and right turns. These were often interspersed with Head Waggling or Habit Preening. Occasional Bill Flicking was only seen during Tall Penguin Dances. With lasting duration, the elevation in the Tall Penguin Dancing was lowered and in its final phase, it could grade into a kind of Plump Penguin Dancing. Whereas in a Plump Penguin Dance, the performing birds were mostly as close as breasts touching, in the tall form, the partners could come breast to breast and separate again.

In the Eared Grebe, the Tall Penguin Dancing (Fig. 22) continued the Discovery Ceremony and the Plump Penguin Dancing arose out of High Head Turning. Due to their greater elevation from the water surface in the Upright Penguin posture, the birds' bodies appeared often rather slim. The feathers of the lower neck were depressed and the necks looked fragile. If not at maximum height, the feathers of the mantle could be slightly lifted. While dancing, the grebes performed Head Turning and their bodies seemed to partially follow the sideward movements of the heads. In the Plump Penguin Dance, the mantle feathers were generally raised farther and all neck feathers were erect. The bodies appeared very rounded. In both forms of dancing, the crests were raised and the ear tufts spread. The Head Turning was interspersed with High Head Waggling, more seldom with Habit Preening of flank or back feathers. Similarly to the Black-necked Grebes, the Eared Grebes could dance breast to breast or at a little distance from one another.

On several occasions, a pair of Eared Grebes performed the Penguin Dancing after a prelude not witnessed in Black-necked Grebes. A partner could respond to an Advertising call by adopting the Pre-cat, occasionally even the Cat Attitude and remain stationary while the calling grebe dived. It surfaced again directly in front of the waiting grebe and both immediately engaged in a Tall Penguin Dance that could last for longer. The behaviour was observed rather regularly and could be seen



Figure 22: Eared Grebes engaged in Tall Penguin Dancing with Head Waggling, with lower neck feathers depressed, Tule Lake, California (2011).



Figure 23: Eared Grebe trying to cover its partner in s-pivoting posture with weeds, near Blaine Lake, Saskatchewan (2008).

as a shortened version of the Discovery Ceremony. It is proposed to name it Discovery Dancing. The display could be followed by Head Shaking, Habit Preening, Pivoting or Inviting with Weed Presentation

Based on the observations, no differences in Penguin Dancing proper were detected between *nigricollis* and *californicus*. A separation into a Plump and a Tall Penguin Dance is justified by differences in the performances and in the bearings of the grebes. Discovery Dancing was only recorded in Eared Grebes.

6.9 Weed Presentation and Ceremonial Building

In the Wagbachniederung, Weed Presentation was preceded either by the Pivoting or the Inviting display or an alternation of both. Early season performances of these displays were generally not followed by weed fetching, even if they ended with diving. Closer to platform initiation, Weed Presentation was frequent. It occurred likewise of the ponds. While one Black-necked Grebe dived for weeds, the other generally remained stationary on the water surface. The surfacing bird could immediately drop the weeds while still at some distance from its mate. More often, it swam with ornamental feathers sleeked towards it and deposited the weeds close to it. Occasionally, it attempted to place the weeds on the partner's breast or back that tried to avoid to be covered. The weed fetching and dropping could be repeated one or several times by the same bird or, more often, in alternation by both mates. The Weed Presentation could be interrupted by Inviting and Pivoting before it started anew. Each grebe could dive up to three times before the display stopped either with Head Scratching, Habit Preening, simply diving or swimming away, occasionally in the direction of emerging vegetation. Weed fetching close to vegetated areas was at times followed by Ceremonial Building. In a first step, the surfacing bird simply dropped the weeds. Before they sank, the same grebe or its partner grasped them, lifted them and deposited them with an arching of the neck either on the water surface or on some

close to the shoreline and in more central parts

emergent vegetation. The other grebe could now simply lift the same weeds and drop them on the same spot or it dived for new plant debris that it placed ceremonially. The weeds, even if held back by surface vegetation, were generally not further arranged.

Also in Eared Grebes, Weed Presentation (Fig. 23) was preceded by Inviting or Pivoting or both. The weed fetching could be performed by only one partner or by both in alternation. Up to three alternated dives with Weed Presentation by each partner were recorded. In a few observations, the surfacing Eared Grebe seemed irresolute about what to do with the plant material; it brandished the weeds once or twice with sideward turns of its elevated head and then simply dropped them while still at a bit of distance from the stationary partner. Occasionally, the same weeds were presented several times in a row to the partner before alternated diving for weed fetching started. The latter could also lift the floating weeds and both engaged in Ceremonial Building.

No differences in Weed Presentation and Ceremonial Building between both subspecies were recorded.

6.10 Parallel Swimming, Parallel Barging and Racing

The field observations in Europe and North America showed that at least three different kinds of parallel progression in one direction by two or more grebes exist and that these need clearer delimitations than those provided so far in literature. The terminology and the descriptions are revised here. Although the review suggests a subdivision in three different displays, there is much variability in the parallel movements of Black-necked and Eared Grebes.

In **Parallel Swimming**, the grebe's body remains either in a rather horizontal plane or the breast is slightly raised and the vent minimally submerged. The elevation of the body always remains below an angle of 30° and the breast remains at least partially submerged. The neck is held rather vertical, more or less stretched or in elongated S-form, and the head is slightly advanced.

In the Wagbachniederung, Parallel Swimming (Fig. 24) was generally preceded by another



Figure 24: A third Black-necked Grebe has joined a pair engaged in Parallel Swimming (2010).

ritual, often Head Shaking occurring in isolation or in succession of other displays. It sometimes followed Parallel Penguin Dancing or Parallel Barging. The Black-necked Grebes turned parallel to one another and both partners swam side by side into the same direction. Depending on their speed, their breasts could be more or less elevated. Their necks were most often held in elongated S-form. At times, the head was kinked and the bill pointed slightly downward. The crests were erect, the ear tufts flared out and the short head and neck feathers were generally raised. The mantle feathers were either depressed or relaxed. The partners had a kind of proud looking air and occasionally turned their elevated heads to the right or to the left as if overlooking the surroundings or perhaps observing the reactions of conspecifics in the vicinity. The movements of the head were rather paused and not always synchronous. They resembled slow Head Turning. In slow swimming, a pair could occasionally perform a short Head Waggling or intersperse Habit Preening. One partner, possibly the male, generally held its head higher and it could be

slightly leading. Coming to a stop with their heads still elevated, a pair could continue the Head Turning briefly while still parallel. The display often ended with one and then the other bird diving or with comfort behaviour.

In a competitive or aggressive context, a pair often chose Parallel Racing to swim at others. Occasionally, a pair used fast Parallel Swimming to perhaps chase or simply impress conspecifics. It could then swim directly in their direction or it oriented to pass close to them. The targeted grebe(s) could join into the Parallel Swimming (Fig. 24).

Eared Grebes performed Parallel Swimming in the same manner as the nominate form (Fig. 25). They then moved parallel to one another often with their necks high in S-form. Their crests were erect, their ear tufts spread and their heads appeared pear-shaped. The neck feathers could be more or less lifted. The feathers of the back were depressed or raised to varying degrees. As the breast was often slightly elevated, the body was sloping. In a few observations, the partners swam one behind the other rather than side by



Figure 25: Eared Grebe in Parallel Swimming, Lower Klamath Lake, California (2011).



Figure 26: Black-necked Grebe pairs in Racing (background) and in Parallel Barging (front) (2010).

side. The grebes regularly showed slow Head Turning while progressing. Habit Preening or Head Waggling occurred at times during slower progression. The ritual ended with Head Scratching, Habit Preening or diving. After a dive, both partners could surface together and only Head Scratch then. In one observation, Habit Preening and a new bout of Parallel Swimming followed before the courtship ended with preening. A pair disturbed by a third Eared Grebe could also use Parallel Swimming to chase it, but more commonly it engaged in Parallel Racing. The progression generally ended with Head Scratching.

In comparison to Parallel Swimming, **Racing** or **Parallel Racing** pairs initially always elevate their breasts, raise their bodies at least partially out of the water and they become sloping, occasionally even oblique (angle of elevation in the range of 45°). In addition, their necks are retracted in Z-form (Fig. 26). The drawings of both authors that used Racing (Palmer 1962, Prinzinger 1979) show two grebes progressing fast with elevated bodies leaned forward from

the vertical, but with the extended neck simply bent forward. Both may have overlooked the Z-form of the neck or they have integrated Racing and Barging in one single display. Note that the kinking of the neck in Z-form not appearing in any drawing of parallel movements in literature (Cullen et al. 1999, Fjeldså 1982, McAllister 1958, Palmer 1962, Prinzinger 1979) is essential for separating Racing and Barging. In Racing, the birds' progression is generally faster and the whirlpools created by the strong kicking of their feet are always visible. While quickly progressing parallel to one another, the birds' necks remain sharply kinked in the middle and bent forward, but the elevation of the bodies can differ markedly in different performances of Racing. During pursuits, they may remain close to horizontal. A common characteristic in all occurrences is the speed and the Z-form of the neck. Parallel Rushing or Upright Rushing (Fjeldså 2004) might possibly serve as a synonym for Racing, however both could lead to confusion if compared to the Rushing of Aechmophorus grebes. Therefore, it seems best to stick to Racing or Parallel Racing.

In the Wagbachniederung, pairs performed Parallel Racing (Fig. 26) either in isolation or more often in a competitive context. Both mates raised their bodies mostly out of the water into a more or less oblique posture and, heavily treading water, progressed in one direction. If performed in isolation, the bodies were most elevated. In a pursuit, the bodies could only be slightly elevated over the horizontal plane. The grebes' necks were retracted and the ornamental feathers were spread. While Racing side by side with some speed, the Black-necked Grebes could turn their heads not unlike Head Turning. The grebes could also change direction one or a few times on their way. The display ended with both mates falling back onto the water surface and either diving or performing Head Shaking, Head Scratching or Habit Preening. In a competitive context, a pair could target a third conspecific or another pair. At times, the second pair or the third grebe, rather than escaping, managed to get parallel to the displaying pair and to join in the ritual. After an aggressive encounter, the ritual often ended with a Hunched Display. In one observation, Racing preceded the take-off by both grebes that landed again after a short flight.

In Eared Grebes, Parallel Racing was observed mostly in aggressive situations when two mates chased one or two other birds. The bodies of the chasing pair were mostly above the water surface (Fig. 27), but they could remain in a rather horizontal plane. During the race, the pursuing pair could change its direction, zigzagging in accordance with the sudden turns of the escaping conspecific. The grebes had their necks retracted or folded in a kind of Z-form with the crests raised and the ear tufts flared. Racing was occasionally performed by three or even four birds that remained rather parallel to one another. Sometimes sky jabbing preceded the start of the display. It generally ended with Head Scratching by the pursuing pair. After Racing by two pairs, both could show Inviting at some distance from one another. The performances outside of aggression often followed fast Parallel Swimming. The kinking of the neck was then perhaps less pointed and the grebes could perform slow Head Turning on their way.

In **Barging** or **Parallel Barging**, the grebes' bodies are elevated into a rather vertical position corresponding generally to a Penguin



Figure 27. Racing Eared Grebes, Tule Lake, California (2011).



Figure 28: Barging Black-necked Grebes (2007).

posture. However, the elevation on the water surface may be more limited and only the breasts may emerge. The neck is held more or less vertically extended as it is stretched to varying degrees. This description is entirely in line with the drawings in Cullen et al. (1999) and Fjeldså (1982, 2004) and both authors used the term Barging. Also Storer (1969) used the term Barging in grebes to describe a slow forward motion in the Penguin posture.

In the Wagbachniederung Black-necked Grebes engaged in Barging out of Penguin Dancing (Fig. 28). While still vertical, they rotated to face and slowly progressed into the same direction. Their elevation was generally less than in Tall Penguin Dancing, their necks remained rather vertically extended, their crests were raised and their ear tufts flared out. In slow performances of Barging, it occurred that the partners were not entirely parallel to one another. Occasionally, they were even one behind the other. Also, only one partner could perform the display; while it progressed in the Penguin posture, the second bird swam behind with only its neck elevated and it showed now and then Habit Preening. The display occurred also in continuation of Head Shaking. In a competitive context, a pair could immediately perform Barging rather than Racing. Both partners then lifted up their bodies and raised at a minimum their breasts out of the water. In all observations, the grebes held their heads rather vertical and high. Their heads were slightly kinked and their bills pointed rather downward. Their crests were raised, the ear tufts fanned out and the neck feathers were lifted. The Barging partners progressed rather parallel to one another. They did not necessarily move directly at the opponent(s), they could orient to pass close.

The speed of the Barging was variable, often slower in the absence of conspecifics in close vicinity and faster if performed in an agonistic context. Conspecifics pursued could join into the display and three or four birds finally progressed parallel to one another. Parallel Barging was not observed as a prelude to flying as indicated by Prinzinger (1979).

Eared Grebes performed Parallel Barging in continuation of Penguin Dancing or after Head Shaking following the Hunched Display. In one case, Pivoting was followed by Barging after the partners had rotated to side by side. In the Penguin posture, the Eared Grebes had their mantle feathers often raised. The birds had their crests raised and the ear tufts flared out. Their necks were vertically stretched to different degrees, the heads slightly advanced. Occasionally, the neck was less extended and formed a more sinuous s-form. The courtship could be followed by a Pivoting Display or by Head Shaking or it ended with a dive or Head Scratching and Habit Preening. In North America, Barging was not observed in an aggressive context.

All three forms of parallel progression occur in both subspecies of *nigricollis* grebes. Differences in the performances were not detected. Blacknecked Grebes could however engage more often in Barging after Penguin Dancing than Eared Grebes and the latter were not observed to engage in the display in agonistic situations. The term **Parallel Penguin Dancing** may serve as a synonym in all cases where the Barging follows Penguin Dancing. It may even be used to differentiate between occurrences after Penguin Dancing and those in an aggressive context.

6.11 Barge Diving or Barge-dive display

According to Fjeldså (2004), the Parallel Barging of Black-necked Grebes can grade into Barge Diving (also termed Barge-dive Display, Fjeldså 1982). This is especially the case after long lasting Penguin Dancing, in continuation of a Discovery Ceremony. In the Wagbachniederung, the ritual was not observed; the Barging rather ended with a final dive that could be quite synchronous and parallel. The surfacing grebes were not seen to repeat or alternate the diving or Barging or to engage in a series of synchronized dives as reported by Koop (2003). Only after Parallel Swimming, once a pair performed a series of successive dives and swims. Although both grebes progressed into the same direction, their diving was not synchronous.



Figure 29: Two Black-necked Grebes retreating with a pattering flight (2009).

After Barging, Eared Grebes could dive rather synchronously, but again neither the Barging nor the diving was observed to be repeated. In contrast, during Parallel Swimming both grebes could dive simultaneously and surface together, show Head Scratching, resume the swimming and dive anew. Such occurrences remained however rare.

This study detected Barge Diving in none of the subspecies. The display is obviously rare.

6.12 Flight Display and flying

Field observations showed that before entering the subject, there is a need for a clear definition delimiting flight from pattering over the water surface. Based on Konter (2012), I will differentiate between pattering (a grebe with flapping wings runs with paddling feet or glides over the water surface, but remains in constant contact with the wet), pattering flight (after initial pattering, a grebe gets really airborne for a distance of a few meters during which it leaves no more footprints on the water surface) and real flight (the distance covered while airborne exceeds 10 m).

During each observation period in the Wagbachniederung, Black-necked Grebes were seen either to patter over the water surface or to take wings, either sole or in twos (Fig. 29). Unfortunately, the context or the starting point of the action was seldom registered, especially if real flight followed. In most occurrences, the birds were only noticed when already in the air.

Simple pattering was used predominantly in aggressive situations likewise by the aggressing and the escaping Black-necked Grebe. The birds raised their bodies rather completely over the water surface to rush with closed or flapping wings and paddling feet. Also, a single grebe could thus patter, occasionally even using a pattering flight over quite some distance to intervene in the courtship of two conspecifics. These occurrences of flight and pattering were not considered to be courtship rituals.

If engaging in real flight, the Black-necked Grebes started with a kind of Parallel Racing with flapping wings and paddling feet. They held their necks kinked forward and all head feathers were sleeked. The birds' feet remained first in contact with the water surface and they could cover thus some distance before engaging in a quite low flight of perhaps up to 2 m above the water surface. Just prior to landing, the grebes trailed their feet behind and they alighted with a sliding glide on their breasts, often keeping their wings unfolded perhaps to help deceleration (Fig. 29). The take-off by two grebes was seldom completely synchronous and the birds generally flew one behind the other. They could alight at a little distance from each other, gliding possibly a bit further apart after landing. Thereafter, they generally swam at each other's encounter, preening and scratching on their way. They performed a bout of Head Shaking and Head Scratching upon joining. Except for a short Parallel Swimming ending with a dive, no further courtship followed. In some observations only one Black-necked Grebe flew up leaving an area with more conspecifics. It was unknown whether the flying grebe was driven away or whether it failed to take along the partner of its choice. In two occurrences, this grebe Advertised after landing.

Also in Eared Grebes, many cases of pattering or flight were recorded without that courtship was involved and these are not dealt with here. Also excluded here are the records of pattering already discussed under Pattering Retreat. From the remaining observations, only two concern a single grebe pattering into the direction of a conspecific. In the first case, it stopped 1-2 m away and both birds swam together to perform Head Scratching followed by preening. In the second, a grebe pattered over the water surface to join a conspecific and both dived together. This was not unlike occurrences in Horned Grebes P. auritus where a single bird may react to the Advertising call of the partner by flying towards it (Storer 1969). Four times a single Eared Grebe performed a similar flight retreating from a flock. In two cases repeated Advertising followed, but did not seem to provoke an answer. In another, it was soon followed by a second grebe that landed close to it and both performed Head Shaking.

In total, 16 cases of simultaneous flight by two Eared Grebes were recorded in Canada (Konter 2009a) and in the USA. In 13 occurrences, both birds taking wings and soaring to well above the water surface originated from a larger group of conspecifics. In one observation, the partners had been stationary and parallel to one another for a while. All of a sudden both raced and took off. In the Flight Display, the partners flew simul-



Figure 30: Part of a group of Eared Grebes engaged in Pattering Flights, Tule Lake, California (2011).

taneously, either in parallel or one behind the other, into the same direction and landed after 20-40 m in areas rather devoid of other grebes. They could now either simply drift apart during preening, swim together into the same direction or simply dive. In one observation, one partner adopted the Inviting Posture with its back turned at the second bird after landing; the latter joined its mate in swimming, both turned parallel and dived. In another case, the pair engaged in Parallel Swimming with Habit Preening. In two cases, the point of departure of the pairs in flight was unclear. The last record concerned two Eared Grebes moving parallel to one another on the water surface with no other conspecifics in their immediate vicinity. Suddenly both halted, lifted their necks, engaged in Racing and got airborne. They landed close together after maybe 15 m, stretched their necks vertically up, paused like this for a second, and finally swam together into the adjacent vegetation.

Observations at Tule Lake on 25 May 2011 revealed group behaviour of Eared Grebes described for the first time in Konter (2012). At a part of Tule Lake called the English Channel, the grebes engaged in mass pattering and pattering flights. They did so in consecutive waves all into a same direction. The sudden take-off by one or two grebes seemed to pull with them others in their immediate vicinity and on their way (Fig. 30). Groups of 10-30 birds pattered over a short distance (20-30 m), some briefly losing the contact to the water surface in a pattering flight. Possibly those grebes getting airborne did so to avoid collision with conspecifics that remained stationary. The Eared Grebes seemed to patter at different speeds within one wave and birds in the back were faster and often passed those in front of them. After some 2-3 minutes, the area was about empty of Eared Grebes. However, 10 minutes later most grebes had returned. The mass pattering and emptying of the area was repeated at least four times on that day. Counts on the next morning suggested that about all grebes engaged in the manoeuvres had left the place overnight. It was suggested that the "flight" manoeuvres were not displays. The group pattering by the Eared Grebes was rather comparable to the agitation or zugunruhe in Silvery

Grebes during their migration towards the final breeding grounds (Fjeldså 1982, Konter 2009b). Fjeldså termed it Pre-migratory Restlessness. It is not known to what extent the behaviour could contribute to a synchronization of onward migration and thereby favour a simultaneous colony establishment by large numbers of pairs in Eared and Silvery Grebes.

The Flight Display warrants further fieldwork before a complete comprehensive description in both subspecies is possible. Our present knowledge is not sufficient to evaluate possible differences in the performances of *nigricollis* and *californicus*.

6.13 Mate Guarding and Unison Diving

In general, mate guarding describes a behaviour by which partners in a pair guard each other to refrain rival conspecifics from disrupting the pair bond. As a consequence, they increase the percentage of daily time spent together and both mates not only display together, but frequently stay side by side for most of their feeding and loafing activity. This behaviour was obvious in European Black-necked Grebes. It was less apparent in North American Eared Grebes, possibly because due to the bigger sizes of the populations it was about impossible to follow a single pair for long. The distribution of the grebes over the water surface was however always very much in twos and this insinuated that once a pair bond of Eared Grebes was established, the partners tried to keep together. In this behaviour of both subspecies, no element of ritualization was detected. This mate guarding cannot be regarded as a courtship display and, to avoid confusion, it is also suggested not to use the term "Mate Guarding" as a synonym for Unison Diving or otherwise in the naming of courtship rituals or ceremonies.

Rather synchronous or alternating dives occurred frequently in the Wagbachniederung and in North America. The Black-necked and Eared Grebes performed them in the context of Inviting, Pivoting, Weed Presentation, Parallel Swimming or Barging. For this synchronous diving of the partners that did not lead to a series of dives, the term Unison Diving as described by Cullen et al. (1999) could be used. It has to be stressed that Unison Diving would however not be a display on its own performed in isolation, but it would describe the final phase of other rituals. Alternating dives for instance performed in the context of Weed Presentation do not fall under Unison Diving.

During fieldwork, an additional diving performance was recorded frequently. Two grebes not too far from one another could Advertise. Thereupon, one partner adopted a kind of Hunched posture, often facing away from the partner. The latter quickly swam in its direction. Just prior to meeting, sometimes low calls uttered by both were audible. Hardly together, the grebe in the Hunched Posture dived and was immediately followed by the other. The same course of events was observed in nigricollis and californicus. It appeared rather ritualized and the term Diving Display is proposed for it.

6.14 Sequence of displays

If engaging in a Discovery Ceremony, Blacknecked Grebes continued their courtship regularly with Penguin Dancing followed by Head Shaking and Habit Preening. Most pairs then added other rituals and either showed Parallel Swimming or Inviting/Pivoting or both in a row. At times, Parallel Swimming was replaced by Barging. After an alternation of Pivoting and Inviting, Weed Presentation occurred regularly. Thereafter, the courtship often ended. Occasionally, Head Scratching or a second Parallel Swimming or both displays were added. In no occurrence, the displaying partners went beyond. Discovery Ceremonies performed early in the season were generally followed by more additional displays than those seen later. These often ended after a very short Penguin Dancing and Head Shaking (Table 3).

More seldom, the Black-necked Grebes continued displaying after Head Scratching, Head Shaking and Habit Preening following a Hunched Display. If this occurred, the grebes showed great variability in the rituals used. Barging, Parallel Swimming and Penguin Dancing could succeed directly. Unison Diving or Pivoting/Inviting could then follow to Barging and Parallel Swimming whereas Barging ending with Head Shaking and Habit Preening was occasionally seen after

Table 3: Complete sequence of displays for both subspecies in the context of the Discovery Ceremony.

Sequence as observed for <i>nigricollis</i> and <i>californicus</i>
Advertising \rightarrow Bouncy Posture and Cat Display \rightarrow Ghostly Penguin \rightarrow Penguin Dancing \rightarrow Head Shaking and Habit Preening \rightarrow (Parallel Swimming or Barging) \rightarrow Pivoting/Inviting \rightarrow Weed Presentation
1. Possible continuation in <i>nigricollis</i>
\rightarrow (Head Scratching) \rightarrow (Parallel Swimming)
2. Possible continuation in <i>californicus</i>
\rightarrow (directed swimming) \rightarrow (Ceremonial Building)

 Table 4: Complete sequence of displays with Hunched Display in californicus.

Advertising \rightarrow Hunched Display \rightarrow Head Scratching \rightarrow Head Shaking and Habit Preening \rightarrow Parallel Swimming or Barging \rightarrow Pivoting/Inviting \rightarrow Weed Presentation

Penguin Dancing. After Pivoting/Inviting, diving occurred, either Unison Diving that ended the display or weed fetching that initiated Weed Presentation. A preferred sequence in the displays was not obvious.

If not disturbed by conspecifics, courting Eared Grebes could perform a continued series of displays in a row. The records showed that courtship could be especially prolonged after Advertising either in succession to the Hunched Display or in the context of the Discovery Ceremony. If after Advertising courting grebes performed the Hunched Display with Head Scratching, Head Shaking and Habit Preening, the rituals were not continued in many observations. The pairs showed however great coherence in the display that followed. The partners could turn parallel and either show Barging or Parallel Swimming. Courtship ended then in most occurrences with Unison Diving or preening. In a few cases Pivoting or Inviting followed and in two cases Weed Presentation was added on top (Table 4). If the Discovery Ceremony was performed (Advertising, Bouncy Posture and Cat Display, Ghostly Penguin), Penguin Dancing, Head Shaking and Habit Preening about always followed. Thereafter, the pairs could engage either in Parallel Swimming or in Barging. At times, Pivoting/Inviting immediately followed Habit Preening, at others it was performed after Parallel

Swimming or Barging. In slightly more than half of the observations, the courtship did then not end with diving or Habit Preening, but was continued with Weed Presentation interspersed with Inviting. In one single observation, courtship went further: after an alternation of Pivoting, Inviting and Weed Presentation, the partners swam together to emergent vegetation where they performed Ceremonial Building (Table 3).

6.15 Courtship in the context of rivalry

Shortly after their annual arrival, most Blacknecked Grebes appeared to be quite firmly paired and about the entire population moved about in twos. A few grebes remained without a partner. Their attempts to find another solitary grebe of the opposite sex or to disrupt an existing pair bond, besides provoking purely aggressive reactions, could follow a more ritualized course. Their encounters with bachelors or pairs often ended after mutual Head Scratching. Solitary grebes often advertised continuously, also in the vicinity of pairs. Now and then, they succeeded in attracting one of the partners and both engaged in a Hunched Display or even a Discovery Ceremony. In a few cases, one partner in a pair loafing close together replied positively to the Advertising call of a third grebe by adopting a Pre-cat Posture. The advertiser dived and immediately surfaced in the Ghostly Penguin without intermittent appearances in the Bouncy Posture; thereafter, both birds engaged in Penguin Dancing. At the latest at this stage, the new pair was assaulted by the initial partner and the Penguin Dancing troublemaker was driven away. Twice also, an unpaired female invited close to the male of a pair that was feeding. The attracted male swam closer, but its surfacing female immediately attacked the rival upon noticing the scene. Courtship between an unpaired and a paired grebe seldom lasted for long: the latter's regular mate generally intervened quickly. Despite being driven away, some bachelors could insist and closely follow a pair for long periods, advertise repeatedly and constantly be chased. Their pertinacity sometimes paid off and on the next day a change of partners was observed.

More commonly, a pair aware of a rival bachelor in its direct vicinity reacted by either Parallel Swimming or Racing (Fig. 31) or Barging at it, sometimes repeatedly. Mates joining after having successfully driven away conspecifics generally performed a Hunched Display in this case serving as a Triumph Ceremony that could again be followed by Parallel Swimming, Racing or Barging. The partners could also immediately show Head Scratching or preen or even engage in Inviting. Parallel Swimming, Racing or Barging by one pair was at times directed at another pair. This one could simply escape. At times, both pairs ended up in Parallel Swimming, Racing or Barging either one in front of the other or even in slightly different directions (Fig. 26).

In several observations, a pair swam about in the Hunched Posture, one grebe leading. With their heads retracted to in between the shoulders, the ear tufts spread, also laterally, and the crests raised, the grebes moved directly in the direction of other pairs or single grebes loafing at some distance. While progressing side by side, they performed quick Head Turning just as in the Hunched Display. Reaching the conspecifics, they could suddenly accelerate their speed, and, maintaining their posture or elevating their bodies for Racing, they feigned a ritualized attack. The loafing grebes generally escaped to the side. The pair could now move towards the next pair in its vicinity and repeat its provocative behaviour. This intentional swimming at conspecifics may be a kind of strength test for the pair bond.

In competitive situations with either two pairs or a pair and a third grebe, at times, the Low Inviting posture was immediately adopted by one mate. The partner adopting the bearing remained stationary with ornamental feathers sleeked and faced about into the direction of the opponent(s), avoiding however generally direct eye contact. The second grebe stayed in the back, either preening or simply waiting. The action may have signalled the strength of the pair bond.

The behaviour of unpaired Eared Grebes did not differ from that of Black-necked Grebes. They were continuously moving about and Advertising, approaching solitary grebes and pairs with care. They used Head Scratching and Head Shaking and they remained ready to either escape or engage in displays with the conspecifics they encountered. Pairs regularly used Parallel Swimming, Racing or Barging against bachelors and other pairs that could then join in the display. Two pairs could also meet in the Hunched Posture and perform quick Head Turning. In conflict situations, Inviting on the open water surface was observed several times as a kind of defensive reaction. It also occurred after aggressive encounters with conspecifics, but then the Triumph Ceremony was seen more often.

6.16 Platform courtship

Rudimentary platforms in the area where Blacknecked Grebes displayed could attract the attention of more pairs simultaneously and prior to colony establishment up to five pairs were observed aggregating around one same platform. The occupying pair preparing for copulation sometimes had to chase conspecifics that then approached. It normally left after repeated mounting and the platform was taken over without much aggression by a next pair that was loafing close feigning no interest in the place.

Platform courtship often started with one grebe Inviting in front of the platform before it hopped onto it and showed Rearing. Upright on the platform, the Black-necked Grebe had its neck extended and kinked forward, the ornamental feathers were relaxed or raised. It slightly lifted the wings and showed Wing Quivering while



Figure 31: Pair of Black-necked Grebes Racing at conspecific (2010).



Figure 32: Eared Grebe Rearing on a stone, Tule Lake, California (2011).

slightly moving its head to one side. Thereafter, it laid down flat onto the platform with the neck extended forward for Inviting. In rare cases, the grebe invited immediately after jumping onto the platform. It then reared only if its partner hesitated for too long before mounting. The latter stayed in the back of the platform grebe, heavily preening and scratching and moving to and fro. It then swam to the vent of the Inviting bird, gradually spread its ornamental feathers while paddling with its feet in preparation of the jump and grumbling. It finally mounted with a big jump. During copulation, the mounting grebe's body was slightly inclined from the upright, the neck was bent in S-form. The wings were slightly lifted. Its mate on the platform retracted its neck and lifted its head, the bill pointing upward. Still uttering quick soft calls, the mounting grebe dismounted, running upright over the head of the mate. It thus landed in the shallow water where it started slow Head Turning with the neck bent in S-form. The bird on the platform generally stood up quickly, pushed its breast out, bent its neck and also engaged in slow Head Turning. Occasionally, the platform bird did not get up, but simply extended its neck vertically for the Head Shaking. Both grebes could continue the Head Turning while extending their necks vertically or they interspersed it with Habit Preening. During the post-copula display, the mounting grebe kept its crest depressed and the ear tufts fanned out while its partner kept its ornamental feathers sleeked.

In Eared Grebes, basic platforms existing early received much attention, too, even if not suited for later nesting. A pair repeating the mounting regularly ended up with three or more pairs surrounding it. Some of these could show Inviting on the open water surface. Occasionally, one grebe tried to disturb the pair preparing for the copula. In these cases, short pursuits resulted; they were generally preceded by Head Scratching or Habit Preening (displacement activity). The troublemakers always retreated quickly. In areas with several platforms, a pair engaging in mounting stimulated others in its vicinity to do alike. In an area without emergent vegetation, an Eared Grebe was observed to rear on a protruding stone (Fig. 32); up to four other grebes surrounded the flat stone. Three of them immediately afterwards also reared there before all left together.

Copulation was introduced by one partner jumping onto the platform. It generally first reared before settling down. Still upright, it bent its neck forward and down. The crest was depressed, the ear tufts sleeked. With chin, neck and back feathers raised, it then performed wing quivering that could be repeated once or twice. Simultaneously, it could throw its head to one side and it flared out the ear tufts. It then settled down for Inviting with the neck more or less extended forward. At times, it slightly lifted its head and turned it to one or the other side so as to observe the behaviour of its partner. Depending on the circumstances, it could repeat the Rearing before resuming Inviting. The mate in the water preened heavily, approached its partner several times and moved again away before staying close to its back. Just prior to mounting, the neck of the platform bird was rather extended forward and low, with the chin often resting on the water surface, the bill slightly pointing upward. All ornamental feathers were sleeked. Its partner moved to and fro in its back. It finally advanced its neck several times over the mates vent to gain momentum, fully spread all ornamental feathers, uttered a call and mounted with a big jump. During copulation, it remained upright with the body inclined a bit forward and the wings slightly lifted. Its head was advanced, its crest was fully raised and the ear tufts flared out. It uttered grumbling calls. The platform bird now retracted its neck and slightly lifted the head. Its ornamental feathers remained shut. With fast tripping steps, protruding breast, neck retracted in S-form and ornamental feathers still raised, the mounting grebe dismounted over the head of its partner. It landed upright with its back turned in front of its mate that meanwhile had raised its neck, but could remain lying across the platform. More often, it quickly stood up. With the body in an oblique posture and the breast protruding, the neck folded in S-form, it performed slow Head Turning. The dismounting grebe did alike, the crest bulging forward and the ear tufts flared out. Continuing the Head Turning, it finally lowered its body into the horizontal plane. The Eared Grebe on the platform could now kink its neck forward and the post-copula display slowly ended. The partners could engage in another mating display immediately afterwards, they could start building or they simply swam away.

7 Comparison of displays in Black-necked and Eared Grebes

In the courtship of Black-necked and Eared Grebes as described in literature, problems in the terminology used and in the descriptions of the displays were identified. In addition, some rituals seemed to occur in one subspecies only. The present comparative study clarified most of the issues. It proposes changes to the terminology applied and provides enhanced descriptions for the displays observed in one or both subspecies. These clarifications were necessary for an accurate identification of rituals occurring perhaps in only one form and of persisting differences in the way a same ritual is performed by the European and North American populations.

7.1 Changes proposed to the terminology of displays

For a better understanding, most changes in terminology were already introduced in chapter 5 when presenting the findings of the study. They are only briefly summarized here.

With respect to Advertising, Fjeldså (1982) distinguished between Advertising and Display Calling. He used the first term in situations where a contact between mates was to be re-established and the second for solitary birds in search of a partner. In other grebe species, Advertising is generally used for unpaired birds. Simmons (1954) first used the term Advertising to describe the "sexual advertising" of unpaired Great Crested Grebes. Therefore, the term Advertising better serves the situation where a bachelor grebe tries to attract a partner and it should be maintained with its original meaning. It is proposed to use the term Contact Calling in the second context. A differentiation in the calls themselves is not excluded. A priori, Contact Calling birds could float higher on the water surface and have a generally more relaxed bearing. The definition of objective criteria for a differentiation between Advertising and Contact Calling needs further research.

The different forms of Head Shaking already applicable to the family of grebes were used in this study rather than the generic term. In ritualized preening, Habit Preening and Synchronous Preening were differentiated. With respect to Billing or the Hunched Display, it is proposed to skip Food Presentation as a synonym.

Four different posture adopted by the grebes during Pivoting were identified and led to the proposal to name these the Oblique Pivoting Posture, the Low Inviting Posture, the High Inviting Posture and the S-Pivoting Posture. In the latter, the head of the bird can be held more or less high. Occurrences of one grebe rotating in an Inviting posture on the open water surface while the partner remains preening in its back are considered to be part of the Inviting Display as originally described. Soliciting (McAllister 1958) may serve as a synonym for Inviting. Nest-Selection Display (Cullen et al. 1999) can however not generally replace the term Inviting as the display is also performed without apparent direct relation to nest selection. Nest Selection is retained as a ceremony consisting of Inviting on the open water surface followed by directed swimming into vegetated areas and Ceremonial Building.

With respect to Penguin Dancing, Fjeldså's (1982) recommendation is followed and a differentiation between a Tall and a Plump Penguin Dance is supported. If Penguin Dancing develops into a parallel progression, it is suggested to use the term Parallel Penguin Dancing and not Barging that is reserved for the occurrences without preceding Penguin Dancing. A new display called Discovery Dancing is described. It consists in Penguin Dancing that follows immediately Advertising and a diving approach without preceding emergence as a Ghost bird.

An additional new display was identified in the context of Advertising. In the Diving Display, the Advertising call is answered by the adoption of the Hunched posture facing away from the advertiser. Upon joining, both grebes dive rather simultaneously.

It is proposed to abandon the term Weed Trick (Fjeldså 1982) as synonymous to Weed Presentation as it suggests that the plant fetching is preceded by a highly ritualized diving or is followed by Weed Dancing.

A split between Racing and Barging and a clearer differentiation between both and Parallel Swimming based on defined criteria are introduced. The term Upright Rushing (Fjeldså 2004) is skipped as it may suggest a Rushing similar to that of *Aechmophorus* grebes. The Pattering Retreat is identified as a composing element of the more complex Retreat Ceremony that includes a repetition of the Discovery Ceremony (Simmons 1959 in Simmons 1975). The term Pattering retreat would apply to situations where the retreat is not followed by a Discovery Ceremony.

For Eared Grebes, Cullen et al. (1999) introduced Mate Guarding, also termed Unison Diving, as a separate display. The term Mate Guarding is misleading as it is already used for grebes in general to describe a behaviour by which a bird tries to avoid that its partner engages in pair bonding displays with rivals and, therefore, simply guards it. For the display meant, the occurrences of simultaneous dives by two grebes in the context of courtship, Unison Diving should sole be used. Whether we have to consider the guite long series of rather synchronous dives observed in Eared Grebes at Oak Hammock Marsh and that included intermittent Parallel Swimming as repeated Unison Diving, as an alteration of Barge Diving or as no display at all remains open.

7.2 Comparison of displays occurring in both subspecies

Prinzinger (1979) stipulated that courtship displays are marked by a wealth of rather rigid displays that show only little individual variation. Grebes in this study showed greater variability in the way a display was performed by individuals of the same subspecies than expected after Prinzinger's statement. This may partially explain why the comparison of rituals between both forms generally led to the conclusion that differences between the European nominate and *californicus* were inexistent.

This study revealed that ornamental and tail feathers of Black-necked and Eared Grebes could be more depressed, relaxed or even lifted during Advertising. Possible differences between both subspecies in the postures of Advertising were not confirmed and North American birds were neither more stationary nor less moving around than European individuals. In both subspecies, potential partners replied to Advertising in a similar way. Storer (1969) already suspected individual differences in Advertising calls of Eared Grebes and Nuechterlein and Buitron (1992) confirmed that the calls of paired and unpaired Eared Grebes differ. Males readily distinguish the sexes of unpaired callers as female calls are significantly higher in frequency than male calls. This research had no means to analyse calls according to sex, postures or pair bond status and possible differences in the calls or in the replies thus remained undetected. It is however suggested that postures in Advertising of unmated and in Contact Calling of mated birds differ.

The different forms of Head Shaking were recorded at a variety of intensities and degrees of completeness. They were a priori used similarly in Europe and in North America. Pumping in the context of Head Shaking was recorded for both subspecies, but it could not be clearly established whether it should be treated as a display or perhaps as displacement behaviour or a sign of hesitation. The occurrence of Head Scratching, not only as a displacement activity, but as a display was confirmed for Eared Grebes, too. Besides Head Scratching, two kinds of Habit Preening were identified for both forms: a shorter vigorous preening that could be interspersed to Head Shaking or Penguin Dancing and a prolonged rather synchronous preening newly termed Synchronous Preening. The ritualized latter form is often hard to tell apart from real preening.

The independent existence of Billing or the Hunched Display was identified for the Eared Grebes, however prey delivery was observed in neither subspecies. If we consider that in many observations the ritual was preceded by Advertising, it seems unlikely that food can be passed over as it would be lost with the opening of the bill for calling. Besides following Advertising, the Hunched Display was regularly observed to follow aggression in both subspecies. This supports Fjeldså's (1982) finding that the ritual corresponds to the Triumph Ceremony (term coined by Storer 1969) in other grebe species.

The Pivoting Display was observed and has now been described in detail for the nominate form, too. It might correspond to the Ceremonial Turning Away mentioned by Koop (2003), but not described in detail, or Fjeldså's (1982) pivoting after Billing. A close relation with Inviting on the open water surface was established. Both subspecies used Pivoting and Inviting in a similar manner except that Pivoting in an Inviting posture by both partners was only recorded in Europe. Both displays integrated frequently in both populations of *nigricollis*. The Pivoting of the grebes closely resembles the initiation phase of the Weed Dancing in Great Crested Grebes where, after Head-shaking, both rotate back to back on the water surface (Ceremonial Turningaway, Simmons 1968) before they drift apart in a stiff carriage (Ceremonial Sailing-away, Simmons 1968) and dive for weed. Similar to Great Crested Grebes, Eared and Black-necked Grebes also kind of froze their posture before they started the rotation. They could then change their bearing and the display could end with weed fetching. In other grebe species, Inviting frequently precedes weed fetching. Nigricollis grebes used both Pivoting and Inviting before diving for weeds. Both forms did not seem to really differentiate between both displays in this respect which could explain why both rituals alternated.

Prinzinger (1979) considered the appearance of Inviting as a clear sign that a firm pair bond had been established and that then platform initiation was imminent. In nigricollis grebes, Pivoting and Inviting where not necessarily followed by weed fetching. It seems that both displays have evolved from their original meaning closely related to platform initiation to independent displays without Weed Presentation that serve pair bond confirmation or strengthening. As Weed Presentation was associated to Pivoting or Inviting only later in courtship, it seems to correspond perhaps with an increased stimulation to engage in reproduction. Only with the addition of weed dives, the Inviting and Pivoting displays would be performed in their original sense related to platform initiation.

The analysis of the composing elements of a Discovery Ceremony was unable to detect any specific response to Advertising that would initiate the diving. It appeared that differences in the bearing of the head between both subspecies were rather attributable to the stages in the adoption of the Cat Posture than to diverging developments between the populations. In both forms, the process and the timing for the adoption and the release of the posture were very variable. The study provided no evidence for a very shallow dive producing wakes on the

water surface (Ripple-approach, Simmons 1975), neither in Europe, nor in North America. In both subspecies, the neck of the Ghost bird was always bent forward in the initial stages of its emergence. This confirms Fjeldså's (1982) description and contradicts Prinzinger (1979). In the displays following the ceremony, Eared Grebes could use less Habit Preening during Penguin Dancing and possibly they also rotated less in the Penguin Posture. Otherwise, both subspecies were subject to the same forms of Head Shaking, phases of breast contact alternated with those without, and dancing in a Tall and in a Plump Penguin posture was recorded. Fjeldså (1982) suggested that the Plump Penguin Dance may have a different origin and that it could represent a further development of the Head Shaking ceremony. The occurrences of Plump Penguin Dancing in Eared and Blacknecked Grebes following intense Head Turning seem to confirm Fjeldså's opinion. This Plump Penguin Dancing would then not occur in continuation of the ritualized attack in the Discovery Ceremony and a lowering of the carriage in the Tall Penguin Dance would still remain a Tall Penguin although resembling the plump dance. Independently of whether a Plump or a Tall Penguin Dancing was recorded, the statement of Bauer and Glutz (1987) that the dancing partners' breasts are not touching has to be rejected. In the dances of both subspecies, phases of breast touching did well occur.

Fieldwork confirmed the existence of Parallel Swimming, Racing and Barging as newly defined in both forms of *nigricollis* grebes. Both used all three displays in a similar manner, purely in courtship or in an aggressive context. Both subspecies also performed Unison Diving, especially in the terminal phases of other displays.

Although platform courtship was not the direct target of the present study, its findings in this respect showed that no differences between the two subspecies exist in this respect. Ceremonial Building was added to the list of displays performed by both forms. Early in the season, Black-necked and Eared Grebes are likewise expected to build copulation platforms at places not suited for nesting. These attract conspecifics and different pairs may use a same platform for Rearing, Inviting, Mounting and the Postcopulatory Display.

7.3 Displays not observed in one subspecies

The Barge-dive-display or Barge Diving as described in literature was neither observed in Black-necked nor in Eared Grebes. All Parallel Barging and Parallel Penguin Dancing could end with Unison Diving after which however the parallel movement was not resumed. Possibly the display is rarely performed in either subspecies.

It remained unclear whether a Pattering Retreat as performed in North America could exist in Europe; the observations were too partial to conclude. It is not known to what extent Fjeldså (2004) or Koop (2003) relied on descriptions for Eared Grebes to add the Pattering Retreat to the catalogue of displays performed by Black-necked Grebes.

Following Advertising, Discovery Dancing was only recorded in Eared Grebes, however the composing elements of the ritual are known in both subspecies. The ceremony could simply be a short version of the Discovery Ceremony occurring only later in the season in well-established pairs.

In the context of courtship, flight or pattering flight was observed in both subspecies. However, a Flight Display as described by Prinzinger (1979) was not recorded for the Eared Grebe. It remained unclear whether Black-necked Grebes could engage in this display that would in any case remain exceptional. In a number of observations in Europe and North America, the context of a flight or a pattering was not identified. This flying or pattering in the species, whether performed by singles or by a pairs, could be interpreted as an attempt to retreat from rival conspecifics in that ideally the selected partner joins. It could serve to continue courtship with the latter in isolation. An open question is to what extent the action is ritualized and represents a real display on its own. In two observations of Eared Grebes, the flight of a pair was oriented towards emerging vegetation. Each time, the partners alighted close to the vegetated areas and both disappeared inside. These cases may be homologous to Parallel Swimming directed towards potential platform locations. Other European authors (Bauer and Glutz 1987, Fjeldså 2004, Koop 2003) did not mention any flight display and all North

American authors remained silent in this respect. A final statement of whether both subspecies may exhibit differences in displays involving flight or pattering needs further research.

7.4 Arrangement of displays

The sequencing of displays in pairs of Blacknecked and Eared Grebes showed great variability in general. It appeared that their arrangement could be more stereotyped after a Discovery Ceremony in both subspecies. A Hunched Display initiated by Advertising was generally followed by less courtship in Black-necked than in Eared Grebes and a predominant sequence for other rituals thereafter could only be found in the North American subspecies. It has however to be admitted that much courtship of Black-necked and Eared Grebe pairs was interrupted by disturbing conspecifics and this may have prevented the appearance of a clearer pattern in the succession of displays.

Divergences in the arrangement of displays are known from most species of grebes. Especially later in the season when the partners are well acquainted to one another, they are likely to drop almost any ritual in the performance of a ceremony. For instance, Fjeldså (1982) stated that complete Discovery Ceremonies are rare and possibly occur only very early in pair bonding. Later, any element may be omitted. This is also the case in solitary breeders that remain undisturbed. The degree to which simplification occurs appears to vary directly with the strength of the pair bond and inversely with the strength of the stimulus for performing the ceremony (Nuechterlein & Storer 1982). In colonial species, interruptions of courtship may be regular as rivals will always be near and the latter may influence the sequencing by their mere presence or their behaviour. At the end, the arrangement of displays may be of minor importance.

8 Concluding remarks

Different populations of a same species are supposed to display in a same way and, therefore, their members are likely to form mixed pair bonds at random. Courtship in isolated populations
of the same species may evolve differences in time that initially are minor and do not warrant separate species status. If the allopatric distribution lasts for long enough, it may result in the formation of different species with incompatible elements in their displays. Differences in the rituals of closely related species may be similarly minor in appearance as those possibly occurring initially between isolated subspecies. As a consequence, it is largely a matter of human evaluation or of taste of whether a small deviation in courtship displays observed in allopatric populations leads to a classification into separate species or into separate subspecies.

In this study, it appeared that the displays of Black-necked and Eared Grebes showed differing degrees of intensity and differences in the way they were performed by different pairs and probably also in time. Variations in the form, frequency and duration of displays occur and many of these variations appear to have functional significance (Beer 1975 in Nuechterlein & Storer 1982). In grebes, the initial stages of pair formation are characterized by fearsome isolation of birds that must follow a cautious and highly ritualized approach to test a prospective mate (Fjeldså 2004). Similarly, the progress of pair formation varies (Fjeldså 1982). The same rituals performed later in well-established mates may unwind in a different manner; this may express in less hesitation, less intensity, greater proximity during performances, dropping of elements or differing positioning of especially ornamental feathers. A great deal of variability in the displays may be explained not by evolutionary drift, but by the circumstances of their occurrences.

Taking all these possible explanations into account, the differences in the displays performed by both subspecies and observed by this study were judged minor and about all possible deviations revealed by the existing literature proved inexistent. For displays that were seldom observed, a final assessment needs however further fieldwork.

Perhaps a bit untypical for colonial species of grebes, neither Black-necked nor Eared Grebes were observed to engage much in group courtship as is the case for instance in the Rushing of *Aechmophorus* grebes or the Barge Diving of Silvery Grebes. A group ritual was performed by a maximum of four *P. nigricollis* grebes and it generally developed out of an aggressive context

when one or two conspecifics joined into a parallel display of a pair. The performance of a ritual by one pair of Eared or Black-necked Grebes had however about always a contagious effect on other pairs in their vicinity. The stimulating effect of water courtship and later of platform courtship was obvious.

In conclusion, this study provided additional knowledge about the courtship of Eared and Black-necked Grebes and eliminated uncertainties about the displays performed by each subspecies. The findings translated into a modified and clearer terminology for the different rituals and into enhanced descriptions. In parallel, they insinuated that differences in the displays and ceremonies of both forms may a priori be minor and that their present subspecies status is well founded. The methodology applied did however not foresee any statistical analyses which could have revealed an imbalance in the usage of different displays between the subspecies. Such an imbalance could point to a possible disappearance in a near future (in evolutionary terms) of a ritual in one subspecies that could still be extensively used by the other. Similarly, the great variability in the way a specific display was performed by Black-necked and Eared Grebes was not analysed statistically and emerging alterations in the rituals themselves that would only concern one form can therefore not be completely excluded.

A single small difference may sometimes be crucial for a split as was the case in *Aechmophorus* grebes: a slight deviation in the Advertising calls of Western *A. occidentalis* and Clark's Grebes *A. clarkii* proved to be sufficient to prevent random mating in their areas of sympatry (Nuechterlein 1981). Both species evolved out of a common stem that divided into two geographically isolated subpopulations. More recently, both became again largely sympatric, but showed strong assortative mating (Storer & Nuechterlein 1992). Their percentages of mixed pairing could however increase in time (Konter 2011) and thereby prove that a single, even initially strong barrier to hybridization may weaken if constantly challenged.

Future comparative studies of the courtship in Black-necked and Eared Grebes should include a statistical analysis of the frequency of the different displays and an analysis of their calls with the help of sonograms and spectrograms.

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The Falkland Islands' White-tufted Grebe Rollandia rolland rolland (Quoy & Gaimard 1824)

Life history and comparison of its ethology to mainland White-tufted Grebes *R*. *r*. *chilensis*

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<u>Keywords:</u> White-tufted Grebe, Falkland Islands, mainland forms, water courtship, advertising call, placement of nest, copulation on land, geographical isolation, geographical differentiation, species, subspecies.

Abstract

The life history and behaviour of the Falkland Whitetufted Grebe *Rollandia rolland rolland* were studied at different places in the Falkland Islands in 2008 and 2010. The observations were complemented by indications in field guides and in the breeding atlas of Falkland birds and compared to descriptions in literature for the two mainland races, *R. r. morrisoni* restricted to Laguna Chinchaycocha de Junín in Peru, and *R. r. chilensis* distributed over continental low and high altitude southern South America.

The nominate form *rolland* exists in allopatry to the mainland forms that are both noticeably smaller. Birds from the Falkland Islands are twice as heavy and have heavier bills than their conspecifics from the continent. Differences in plumage are minor. *Rolland* pulli are in general similar to those of the subspecies *chilensis* except that a narrow dark line connects the middle dorsal stripe at the height of the crown with the two supraorbital stripes. In breeding plumage, differences seem to be absent.

The present investigation focussed on the ethology of Falkland White-tufted Grebes, mainly on the grebes' behaviour during pair bonding and mating. Water and platform courtship are described in detail. Besides similarities, the behavioural comparisons many between the nominate form and the continental forms a priori revealed quite a number of differences. In water courtship, the Advertising call of chilensis is "chorrh" and appears to be quite different from the duck like quacking of rolland. Plumb Penguin Dancing could only occur in the Falkland Islands and diving appears to be less common in the displays of the continental subspecies. In addition, Parallel Swimming is not mentioned for mainland White-tufted Grebes, Habit Preening is said to be absent and Inviting on the open water surface is not reported. The behaviour in platform courtship could differ in two additional aspects. Mounting in the islands' subspecies occurs regularly on land whereas mainland grebes always seem to use a floating platform and a mating display during which the partners press their vents together is not described for *chilensis*. With respect to aggression, Chasing in the Swan posture of rivals or neighbours is not listed for continental Whitetufted Grebes, and, similarly, a placement of nests on firm ground seems only to occur in the Falkland Islands where floating platforms could be much less common.

It is discussed to what extent the differences found are relevant with respect to the species status of the subspecies. Due to the allopatric occurrence of island and mainland forms, the biological species concept cannot be applied directly in the present case. It has to be assessed in how far diverging characters are fully diagnostic and have an adaptive value in insuring that a Falkland White-tufted Grebe will not mate with an individual from the continent. Besides size dimorphism, three additional differences could fulfil the condition: the divergences in Advertising calls, the regular occurrence of platform courtship on land and the building of non-floating nests in the Falkland Islands' form.

More generally, the behavioural differences found by the present investigation contribute further supporting arguments for two separate *Rollandia* species. They should however be cross-checked by additional studies in mainland White-tufted Grebes. It is also suggested to investigate the phylogenetic relationships among the present forms of *Rollandia rolland* through genetic analyses before finally discussing a possible split into Rolland's Grebe *Rollandia rolland* for the Falkland Islands population and White-tufted Grebe *Rollandia chilensis* for the continental forms. <u>Schlüsselwörter:</u> Rollandtaucher, Falkland Inseln, kontinentale Unterarten, Wasserbalz, Balzruf, Nestlage, Kopula an Land, geographische Isolation, geographische Differenzierung, Unterart, Art.

Zusammenfassung

Die Lebensweise und das Verhalten der Population des Rollandtauchers *Rollandia rolland rolland* wurde in den Jahren 2008 und 2010 an verschiedenen Gewässern auf den Falkland Inseln studiert. Die Beobachtungen wurden durch zusätzliche Angaben in Feldführern und dem Brutatlas der Falklandvögel ergänzt und mit Beschreibungen der kontinentalen Unterarten in der Fachliteratur verglichen. Auf dem Festland kommt die Art in zwei Unterarten vor, *R. r. morrisoni*, dessen Verbreitung sich auf den peruanischen Hochandensee Laguna Chinchaycocha de Junín beschränkt, und *R. r. chilensis*, der im ganzen Tief- und Hochland des südlichen Südamerika zu finden ist.

Die Nominatform *rolland* der Falkland Inseln kommt geographisch getrennt von den kontinentalen Unterarten vor, die beide viel kleiner sind. So sind Individuen der Falkland Inseln doppelt so schwer und haben auch massivere Schnäbel als ihre südamerikanischen Verwandten. Unterschiede im Federkleid kommen dagegen kaum vor. *Rolland*-Küken gleichen denen der Rasse *chilensis* außer dass eine schmale dunkle Linie den Mittelstreifen des Dunengefieders am Kopf auf Höhe des Scheitels mit den beiden seitlich davon verlaufenden Streifen verbindet. Im Brutkleid scheint es keine Unterschiede zu geben.

Die vorliegende Studie beschäftigte sich vorwiegend mit der Ethologie des Falkland-Rollandtauchers, vor allem mit seinem Verhalten während der Paarbildung und auf dem Nest. Die Wasser- und die Plattformbalz werden detailliert beschrieben. Neben vielen Ähnlichkeiten zeigten die Verhaltensvergleiche zwischen der Nominatform und den kontinentalen Unterarten a priori auch einige Unterschiede auf. So besteht der Balzruf der Unterart chilensis, aus dem Laut "chorrh", und erscheint damit ganz verschieden von dem entenähnlichen Quaken der Unterart rolland. In der Wasserbalz könnten zusätzliche Unterschiede darin bestehen, dass ein Plumper Pinguintanz (Plumb Penguin Dancing) nur auf den Falkland Inseln vorkommt, und dass das Einbinden von Tauchelementen in die Balzvorgänge dort ausgeprägter ist. Auch wird Paralleles Schwimmen nicht für die kontinentalen Unterarten erwähnt, und Scheinputzen kommt dort anscheinend ebenfalls nicht vor. Genauso wenig wird eine Einladungshaltung auf der offenen Wasserfläche beschrieben. Die Plattformbalz der drei Formen könnte in zwei weiteren Aspekten voneinander abweichen. Auf den Inseln finden Kopulas regelmäßig an Land statt, während kontinentale Rollandtaucher immer eine Schwimmplattform zu benutzen scheinen. Eine Nestbalz, bei der beide Partner ihre Hintern gegen einander pressen ist ebenfalls nicht bekannt für *chilensis*. Beim aggressiven Verhalten wird für die kontinentalen Rollandtaucher keine Verfolgung von Rivalen oder Nachbarn in der Schwanenstellung beschrieben. Den Bau von Nestern auf festem Untergrund scheint es nur auf den Falkland Inseln zu geben, wo Schwimmnester weniger verbreitet sind.

Inwiefern sind nun die festgestellten Unterschiede von Belang, wenn der Artstatus der Populationen diskutiert wird? Durch das geographisch getrennte Vorkommen der Inselunterart und der kontinentalen Formen kann in diesem Fall das biologische Artenkonzept nicht direkt angewandt werden. So muss bewertet werden, ob die abweichenden Charakteristika sicherstellen, dass die Rollandtaucher der Falkland Inseln sich nicht mit den kontinentalen Populationen verpaaren. Neben den Größenunterschieden könnten vor allem drei andere Abweichungen diese Kondition erfüllen: die unterschiedlichen Balzrufe, die regelmäßig vorkommende Plattformbalz an Land und der Bau von Nestern auf festem Untergrund im Gegensatz zu den üblichen Schwimmnestern der Lappentaucher.

Die in dieser Untersuchung festgestellten Verhaltensunterschiede sind zusätzliche Argumente für eine Spaltung der heutigen Rollandtaucher in zwei verschiedene *Rollandia* Arten. Dies sollte jedoch erst geschehen, nachdem sie durch zusätzliche Studien auf dem südamerikanischen Kontinent gegen geprüft wurden. Die phylogenetischen Verbindungen zwischen den existierenden Unterarten von *Rollandia rolland* sollten gleichzeitig durch genetische Untersuchungen gestützt werden, bevor eine Aufteilung der Populationen in Rollandtaucher *Rollandia rolland* für die Falkland Inseln und Weissbüscheltaucher *Rollandia chilensis* für die kontinentalen Formen abschließend diskutiert werden kann. <u>Mots-Clés:</u> Grèbe de Rolland, Iles Malouines, sous-espèces continentales, parades nuptiales, cri de parade, placement du nid, copulation à terre, isolement géographique, différentiation géographique, sous-espèce, espèce.

Résumé

La biographie du Grèbe de Rolland des Iles Malouines *Rollandia rolland rolland* et son comportement étaient étudiés à différents endroits sur les îles en 2008 et en 2010. Les observations étaient complémentées par des indications dans des guides d'oiseaux et dans l'Atlas des oiseaux nidificateurs des Iles Malouines. Elles sont ensuite comparées aux descriptions de la littérature pour les deux sous-espèces continentales. La forme *R. r. morrisoni* habite exclusivement Laguna Chinchaycocha de Junín au Pérou alors que *R. r. chilensis* est distribué à travers les plans d'eau des plaines et de haute altitude de la partie sud du continent sud-américain.

La forme nominale *rolland* est géographiquement séparée des formes continentales qui sont toutes les deux visiblement plus petites. En effet, les oiseux des Iles Malouines font le double du poids et ont des becs plus robustes que leurs congénères du continent. Les différences de plumage sont mineures. Les poussins de la sous-espèce *rolland* sont en général similaires à ceux de la forme *chilensis* à l'exception d'une fine ligne brun-noire qui relie la zébrure centrale de la nuque à la hauteur du sommet de la tête aux deux rayures supra orbitales qui la longent. Il n'y a pas de différences apparentes dans le plumage nuptial.

La présente étude s'intéressait avant tout à l'éthologie du Grèbe de Rolland des Iles Malouines, et plus particulièrement à son comportement pendant les périodes de formation des couples et de l'accouplement. Les parades nuptiales et les cérémonies de plateforme sont décrites en détail. A côté de beaucoup de ressemblances, les comparaisons comportementales entre la forme nominale et celles du continent révélaient à priori toute une série de différences. Lors de la formation des couples, le cri de parade émis par la forme chilensis pour attirer un partenaire est décrit par "chorrh" ce qui diffère sensiblement du cri coin-coin de la forme rolland et qui ressemble à celui d'un canard. Les danses de pingouin (Plumb Penguin Dancing) pourraient être réservées à la population des Iles Malouines et des plongés semblent être moins régulièrement intégrées dans les parades des Grèbes de Rolland du continent. En outre, nager en parallèle n'est pas mentionné dans les descriptions des cérémonies continentales, le rituel de lisser le plumage

est prétendu être absent et la pose de l'invitation n'est pas rapportée à être adoptée sur la surface de l'eau. Les parades de plateforme pourraient différer en deux aspects supplémentaires. La sous-espèce rolland monte régulièrement sur la terre ferme pour y copuler alors que les deux autres formes utilisent toujours une plateforme flottante. Les sous-espèces continentales ne pourraient également pas connaître une parade au cours de la laquelle les deux partenaires allongés en ligne pressent les derrières l'un contre l'autre. En matière de comportement agressif, une poursuite de rivaux ou de voisins dans une pose de cygne n'est pas mentionnée pour les formes continentales. De même, une construction du nid sur terre ferme semble être plutôt la norme aux Iles Malouines alors que les autres populations sud-américaines semblent toujours édifier des nids flottants.

Dans quelle mesure les différences constatées sont pertinentes par rapport au statut des trois formes? Due à la séparation géographique de la forme nominale et des deux sous-espèces du continent, le concept d'espèce biologique ne saura être testé directement. Il faudra plutôt évaluer jusqu'à quel point les caractères divergents des sous-espèces sont entièrement diagnostics et ont une valeur adaptative pour assurer qu'un Grèbe de Rolland des lles Malouines ne choisira pas un partenaire continental. A côté des différences de taille, trois distinctions additionnelles pourraient remplir cette condition: ce sont les cris de parade divergents ainsi que l'accouplement régulier sur terre ferme et la construction de nids non-flottants par la sous-espèce *rolland*.

En conclusion, les différences comportementales constatées par la présente étude sont des arguments supplémentaires en faveur de deux espèces de *Rollandia*. Elles doivent cependant être confirmées par des recherches ciblées sur le continent. Il est également proposé d'établir les relations phylogénétiques entre les trois sous-espèces actuelles de *Rollandia rolland* par des analyses génétiques avant de lancer la discussion finale pour une séparation éventuelle en Grèbe de Rolland *Rollandia rolland* pour la population des Iles Malouines et en Grèbe aux touffes blanches *Rollandia chilensis* pour les deux formes du continent.

1 Introduction

The White-tufted Grebe Rollandia rolland was first described by Ouoy and Gaimard (in Frevcinet 1824) from specimens collected in the Falkland Islands in 1820 by M. Rolland, a master gunner of the Uranie (Woods & Woods 1997) and was classified as Podiceps rolland (Fjeldså 2004). In 1891, the French Mission Scientifique to Cape Horn felt that mainland birds resembled the Falkland species very closely in colouration and named them *Podiceps* rollandi(i). However, Wetmore (1926 in Woods & Woods 1997) thought that the Falklands population was sufficiently distinct from the continental forms to be recognized as a separate species. His proposal was originally followed and the continental South American forms were listed separately (Peters 1931, Pinto 1938, both in Remsen et al. 2008). Following Storer's (1963) suggestions based on his morphological and behavioural studies, the mainland and Falkland forms were lumped under the name White-tufted Grebe that was placed in one genus together with the flightless Short-winged Grebe Rollandia microptera of Lake Titicaca. For Rollandia rolland, the subspecies rolland, confined to the Falkland Islands, morrisoni (Simmons 1962), endemic to the high altitude Lake Junín or Laguna Chinchaycocha de Junín in Peru, and chilensis (Lesson 1828), comprising all non-Junín continental populations, were recognized. Birds from Chinchaycocha are slightly bigger and have stronger bills and proportionally smaller wings than other mainland Whitetufted Grebes (Fjeldså 1981a).

Based mainly on the size dimorphism between the three forms, several authors have speculated that the Falkland form might be a species of its own (Fjeldså 1981a, Woods & Woods 2006) or they did at least not exclude this possibility. Thus, Fjeldså and Krabbe (1990) classified the form of the Falkland Islands as a mega-subspecies and they suggested to name the island form Rolland's Grebe *Rollandia rolland* and the continental forms White-tufted Grebe *Rollandia chilensis* in case of a split.

So far little research had been undertaken to investigate the species status more thoroughly. Except for a limited number of skin and skeleton measurements that all confirmed the larger size of the Falkland's White-tufted Grebe, I could not find any comparative study of behaviour or any genetic analyses. Especially ethologic differences appear to be of prime importance in closely related allopatric populations when deciding on their species status and this status could be crucial for conservation in *Rollandia* as the Falkland Islands' population is small.

With this aim in mind, I focused on behavioural aspects of Falkland Islands' White-tufted Grebes during two field studies organized in 2008 and 2010. In this paper, the findings are compared to published information about the mainland forms, particularly the widespread subspecies *chilensis* (Fig. 1). As so far no thorough general account for *R. r. rolland* has been published, the ethological part of the report is preceded by a more detailed introduction to the nominate form of the White-tufted Grebe.

2 Study area and methods

2.1 The Falkland Islands

The Falkland Islands were initially part of Gondwanaland and located at the south-east side of Africa. After separation, their small block was pushed up against the margin of the new South American continent some 150 million years ago (Summers 2001). During the last glaciations, with lower sea levels, a land bridge possibly connected the islands to the mainland. Falkland bird populations were probably established out of South American stocks as glaciations decreased during the Holocene period of the last 10,000 years (Falklands Conservation 2006). The islands are today situated on an extension of the Patagonian continental shelf in the South Atlantic, between latitudes 51° S and 53° S and longitudes 57°30 W and 61°30 W. They are centred about 500 km from the nearest point of South America on Tierra del Fuego to the south-west. They cover about 12,000 km² with two main islands, East and West Falkland, and about 750 offshore islands, more than half of them around the coast of West Falkland. The main islands have deeply indented coastlines with many sheltered harbours (Procter & Fleming 1999). Westerly winds dominate, with wind speeds averaging 27 km/h; stronger winds are frequent (Woods & Woods 2006).



Figure 1: Mainland White-tufted Grebe *Rollandia rolland chilensis* at Parque 3 de Febrero, Buenos Aires, Argentina (2007)

2.2 Timing and areas visited

The main part of the behavioural study was organized during a 14-days stay from 6 to 20 November 2010 on three islands in the north of the archipelago and on one main island. The first seven days were entirely devoted to research on wetlands on Pebble Island, just off the north coast of West Falkland from which it is separated by the Tamar Pass. In continuation, Saunders Island just north of Hill Cove on West Falkland and Carcass Island in the north-west of the Falkland Island archipelago and west of Saunders Island were visited for two days each. The last three days were spent on East Falkland with research on wetlands located between Goose Green and Mount Pleasant south of the Wickham Heights and north of the Choiseul Sound. The 2010 stay was entirely devoted to work on White-tufted Grebes and consisted of an average of nine hours of fieldwork per day.

The 2008 stay from 16 to 26 January served more to prepare the study of 2010, to collect some preliminary data during surveys and to make first behavioural observations at a late stage of the species' reproduction season. The first two islands visited are located in the southern part of the archipelago: Sea Lion Island, 14 km south of Lafonia on East Falkland, and Bleaker Island, close to the southeast coast of Lafonia on East Falkland. Thereafter, the wetlands of Pebble Island and of East Falkland were travelled.

2.3 Methods

All ponds visited were completely searched for White-tufted Grebes. They were surrounded in walking and they were screened using Zeiss 10x25 binoculars and a Sigma 800 mm AF lens attached to a Minolta Konica camera. During observations of displaying grebes, photos and video films with a Sony Handycam were taken and, wind conditions permitting, remarks were spoken into a voice recorder. Additional field notes were recorded in writing. Each evening, all photos, films and notes were analysed and the timely unfolding of displays was noted down in detail. With these notes at hand, a complete examination of all photo and film material was performed once back in Luxembourg.

3 General presentation of the White-tufted Grebe from the Falkland Islands

A first paragraph of each chapter is always devoted to descriptions existing in literature, additional indications relate to findings from my fieldwork.

3.1 Identification of Rollandia rolland rolland

The White-tufted Grebe of the Falkland Islands has a size of 33-36 cm from bill to tail (Woods 1988, Fjeldså 2004) or of 32 cm with a height in swimming position of about 15 cm (Strange 1992). The form chilensis measures only 24-30 cm (Fjeldså & Krabbe 1990). The bill is pointed and black (Woods 1988), fairly short and narrow (Strange 1992). The Falkland subspecies is much larger than the form occurring in South America (Woods & Woods 2006). Males are slightly larger on average and have stronger bills. The wing measures 13.5-13.9 cm, the culmen 2.2-3.07 cm, the tarsus 4.4-4.7 cm. The nominate sub-species is twice as heavy as mainland birds (n=18, Fjeldså 2004). Blake (1977) indicated measures of males and females separately. Males average 13.8 cm (range 13.2-14.5, n=17) for the arc of the wing, 4.85 cm (4.55-5.10, n=19) for the tarsus, 2.89 cm (2.48-3.59, n=14) for the exposed culmen, 1.83 cm (1.68-1.98, n=18) for the bill from nostril and 0.98 cm (0.88-1.12, n=16) for bill depth. The females measured on average 13.5 cm (range 12.9-14.2, n=18) for the arc of the wing, 4.78 cm (4.64-5.17, n=17) for the tarsus, 2.41 cm (2.25-2.56, n=16) for the exposed culmen, 1.51 cm (1.42-1.62, n=17) for the bill from nostril and 0.94 (0.82-1.02, n=12) for bill depth.

3.1.1 Breeding plumage

Adult breeding birds have shiny black (Woods 1988) or blackish brown (Strange 1992) upper parts, a black upper neck and chestnut under parts with black-streaked flanks that are seldom seen in the field (Woods 1988). The rump is red-brown and the under tail white (Strange 1992). The iris is glowing crimson (Woods 1988). The head is black with a distinctive white, fan-shaped patch marked

with a few black feathers fanning out from the bright vermillion eye (Strange 1992). In flight, this grebe shows a broad white bar along the trailing edge of the secondaries. It has white under-wing coverts (Woods 1988). The feet are olive green (Strange 1992), the tarsi blackish grey, the lobes grey (Brooks 1917). When not at rest, it usually displays the crest (Strange 1992).

The adult breeding bird (Fig. 4) has a grey blackish loral stripe of bare skin leading from the onset of the black beak to the bare eyelid margin at the lower eye. In some birds, especially the lower part of the eyelid ring is rather white. In them, the loral stripe often appears light grey. Directly below the lower eyelid margin, a thin white line that may be more or less marked underlines the eye. The eye lens is dark red so as to appear black in the field. It is surrounded by a crimson iris. In some grebes an outer more golden ring is visible. These are perhaps younger adults that, similar to Red-necked Grebes Podiceps grisegena, differ from elder grebes by having an outer ring of different colour to the iris. Directly behind the eye extends a small black triangular patch separating the eye from the ear tufts that fan out from there. In their upper part, the mostly white ear tufts reach forward to about completely over the eye. Below, they start at the lower back eye. The extent of blackish feathers providing an irregular thin lining to the tufts seems variable, but in all birds, two or three more prominent black lines prolong the triangular patch behind the eye. The ornamental feathers of the crest lengthen from forehead to crown. They become again of ordinary length further back. Otherwise head and upper neck appear mostly black. In the lower parts, the neck seems less deep black, more greenish or brownish black, similar to the back. In the upper breast or lower fore neck, the dark feathers are partially mingled with tiny light rufous to golden sandy brown spots and the area fades into a mottled rufous and black lower breast. The under parts are more light red brown speckled with white and dark grey spots. The short tail feathers are blackish, the under tail coverts are white and surrounded by rufous feathers below. The rufous feathers of the flanks are mostly covered by blackish feathers close to the neck, but they become increasingly visible closer to the tail. The rufous of flanks and tail region appears darker in males.

With folded wings, the visible coverts are blackish. If unfolded, the primaries are mostly grey and not as dark as the coverts. The secondaries are light grevish brown with white outer edges and they display a rather white bar more representative of the outer web of the secondaries in flight. The extent of white in the secondaries depends perhaps on the age of the birds as is the case in other grebe species, for instance the Great Crested Grebe Podiceps cristatus (Kop 1971). The under wing coverts are mostly white, except for at least in some birds a small light rufous patch at the height of the carpal joint. Tibiotarsus and tarsometatarsus are greenish black, their serrated posterior part is more olive grey. The toes are mostly in olive grey, the lobes can be more vellowish white laterally above.

3.1.2 Winter plumage

In winter, the throat of adults turns white, the under parts off-white, the upper parts brown and fore neck and crown are dull reddy-brown (Strange 1992).

No winter birds were seen during this study. It was however noticed that the feathers of the mantle get an increasing fawn brown tinge late in the breeding season.

3.1.3 Juvenile plumage

Immature birds resemble non-breeding adults, but they have two irregular black lines across the cheek (Woods 1988).

In juvenile White-tufted Grebes (Fig. 2), the beak turns first to more ivory greyish before becoming olive brown with a more fawn brown culmen. The bare loral line is dark grey and hardly distinguishable from the surrounding plumage that is mostly dark brown. The centre of the eye is dark brown appearing black surrounded by a fawn to red brown iris. The eye is underlined immediately below by a thin white line. The forehead, the still rather short crest, the nape and the hind neck are covered with dark brown feathers mottled with rufous. The field covered by the short white ear tufts is elongate. The tufts are separated from the posterior eye by a small dark triangle and they have a tinge of rufous here and there. Two irregular dark stripes run through the otherwise mostly white triangular form of the tufts. Chin and

throat are similarly white with a tinge of rufous. A washed dark grey line separates this area from the ear tufts. Below, a similar thinner and shorter line extends from the bill. Generally, the original striping of the pullus remains guessable in the head pattern of the young immature bird, but it fades in time. The light throat is ending rather sharp and the upper fore neck starts with a sandy to more light orange or beige brown colouring. This colour runs down to the breast and grades laterally into the dark or grey brown sides of the neck and upper parts that are mottled with orange rufous. The under tail coverts are white, the region of the vent washed white to light grey. The flanks are rather light rufous mottled with black and white. The extent of darker feathers remains more limited than in breeding adults. The ventral area is still rather white, especially in its centre. It is partially changing for a dirty whitish grey and has a tinge of rufous.

3.1.4 Downy plumage

Downy young are sooty brown above with some of the feathers light buff terminally. The sides are indistinctly barred with grey and rufous buff. Breast and upper abdomen are white, the lower abdomen and crissum are grey. The stripes on the crown are light rufous and black, the lores are grey with a tinge of buff. The sub-ocular stripe is white immediately beneath the eye, light rufous fading to dirty white posterior to it. A small malar spot of black exists on each side of the head. The neck is striped in sooty brown and dirty white with a slight buff cast. Chin and upper throat are white, the upper breast feathers light rufous with grey terminations. The eyes are dull grey-brown, the legs and the toes of slate colour (Brooks 1917). The pulli are in general similar to those of the subspecies chilensis except that a dark bar joins the middle dorsal crown stripe with the two lateral ones. In all forms, downy White-tufted Grebes appear to be unique among grebes in having neither a bare area nor a well-marked spot of rufous down on the crown (Storer 1967a).

The bill of the young pullus (Fig. 3) is divided vertically into five colour fields. It ends in a cream white tip separated from a bluish or window grey central area by an irregular vertical band in blackish brown that is repeated immediately behind. Both mandibles are again bluish or window grey at the onset and may display a tinge



Figure 2: Two immature White-tufted Grebes at Adventure Sound, Lafonia (2008).



Figure 3: Chick, hardly two weeks old, with light crown feathers, Long Pond, Pebble Island (2010).

of fleshy pale red. The beak is connected to the eve by a bare line in sandy brown. Immediately above this line, a fleshy bare field is displayed. It turns into red if the bird is upset. Between it and the supercilliary dark stripe, a bare light blue grey field appears at birth. It is relatively fast overgrown by sandy to orange brown down. The centre of the eye is black. It is surrounded by a dark fawn brown iris and a beige red eye lid ring of bare skin. The crown is marked by an oblong blackish brown spot reaching pointed into the forehead, widening in its central part and narrowing in the nape from where it continues as the mid-dorsal stripe down the hind neck to the back. The crown patch lacks a bare area and displays a few central feathers in either orange brown or in some birds also in bluish window grey. With increasing age, the area darkens. Two additional blackish brown stripes run parallel to the mid-dorsal stripe on each side and pass at the height of the supraorbital arch. They originate at the upper onset of the beak from where they fan out and continue into the hind neck. At the height of the crown, they are connected to the central patch by two narrow dark bars. A second narrower pair of stripes also fans out from the onset of the upper beak and

extends at the height of the supercilium. On both sides, these stripes touch the posterior upper eye, but leave a small sandy brown field above the eve. They turn more downward at the height of the ear coverts and continue in a broken line at the side of the neck. A shorter stripe starts in a narrow winding line at the gape and continues as a broader irregular moustachial patch over the cheeks It ends before reaching the supercilliary stripe on its way down. Below, an irregular small dark spot is visible. Chin and throat are delimited by two thin blackish brown lines or malar stripes that end at the upper front neck. A similar line extends at the centre of chin and throat. Generally, there is much individual variation in the form of the dark stripes and lines. The areas in between them are of orange brown to sandy brown colour. They are darkest above the eye and in the forehead and fade more downward. Below the moustachial stripe, they turn more and more white and chin and throat retain nothing but a glimpse of sandy brown.

The striping of the neck and the back is in dark brown or black and sandy brown, the sandy colour appearing darker, a bit orange brown at the



Figure 4: Pair with chick on the back, Big Pond, Pebble Island (2010).

Table 1: Ponds visited and White-tufted Grebes recorded in 2010 and 2008

¹ reduced to about 50% of normal size during survey, ² reduced to about 10% of normal size during survey

		Coordinates		~Size	Grebes	Pop. in	
	Pond	S	W	in ha	observed	BP	Remarks
Pebble	Big Pond	51°18'842	59°34'199	40	5x2 + 2x1	6-7 BP	2 pairs with 1 chick
	Long Pond	51°18'906	59°33'545	20	7x2 + 2x1	8-9 BP	1 pair with 1 chick
	Quark Ponds	$51^\circ 17' 580$	59°32'026	15	0		
	Betts Pond	51°17'677	59°31'676	20	1x2	1 BP	
	Green Pond ¹	51°18'228	59°30'755	40	0		Shallow, partially dry when visited
	Swan Pond	51°17'350	59°30'284	50	0		
	"Little" Pond	51°18'939	59°35'149	2	0		
Saunders	Rookery Flat Pond 1	51°18'942	60°05'473	1.2	0		possibly too small, dries
	Rookery Flat Pond 2	51°19'094	60°05'442	3	1x2	1 BP	nest with 2 stained eggs
	Big Pond	51°22'286	60°06'189	20	4x1	2-4 BP	
	"Gentoo" pond	51°18'512	60°31'432	0.5	0		too small for grebes
ass	"Airfield" pond 1	51°15'344	60°35'553	2	0		
Carce	"Airfield" pond 2	51°15'612	60°35'826	5	0		11 ex. seen in 08. 2010
	"Airfield" pond 3	51°16'226	60°35'792	0.5	0		
	Goose Green pond 1	51°49'687	58°58'759	0.3	1x1	1 BP	small
	Goose Green pond 2	51°49'722	58°58'530	0.3	0		small
	East of Isla Pond	51°49'379	58°45'089	15	2x2 + 3x1	4-5 BP	1 pair on nest
	Laguna Ronde	51°49'126	58°44'078	50	2x2 + 1x1	3 BP	1 pair with 1 chick, 1 adult with 1 chick
	Pond W of Ronde	51°49'872	58°42'794	10	0		shallow
q	Shingly Pond ²	51°49'810	58°41'100	130	0		mostly dry (seen from plane)
lan	Ewe Pond	51°50'110	58°44'078	10	1x2 + 1x1	2 BP	
alk	Laguna Isla	51°49'606	58°46'160	130	3x2 + 1x1	4 BP	1 pair with nest
St F	Laguna Verde ¹	51°47'867	58°53'254		0		
Ea	Swan Inlet Pond 1	51°49'763	58°38'999	100	1x2	1 BP	with nest
	Swan Inlet Pond 2	51°50'778	58°38'659	90	2x2	2 BP	
	Swan Inlet Pond 3	51°50'777	58°37'353	30	2x2 + 1x1	3 BP	
	Swan Inlet Pond 4	51°50'663	58°36'625	50	4x2 + 6x1	7-9 BP	1 pair with 1 chick, 1 adult with 1 chick
	Swan Inlet Pond 5	51°50'337	58°36'865	5	0		small
	E of Mt. Misery pond	51°51'363	58°38'218	75	2x1	1-2 BP	
	Extension Bodie Creek	51°13	59°02		1x2	1 BP	Ken Greenland, 13.11.10
Total 2010 47-55 BP							

	D 1	Coordinates		~Size	Grebes	Pop. in	D 1
	Pond	S	W	in ha	observed	BP	Kemarks
	Big Pond	52°12	58°51	14	$2x^2 + 1x^1$	3BP	
leaker	North of Big Pond1	52°12	58°51	0.5	0		
B	North of Big Pond2	52°12	58°51	0.5	0		
2	Long Pond	52°26	59°05	5	0		
Lio	Beaver Pond	52°26	59°05	20	0		
Sea	Next to Beaver	52°26	59°05	6	0		
	Tussac Pond	52°26	59°05	5	0		
	Total					50-58 BP	

mantle and lighter at the flanks. The lining is quite irregular. Due to the extent of dark feathers, the general appearance of back and flanks is comparatively dark. The under tail coverts are white as are the under parts. The legs are light to dusty grey with perhaps an olive green tinge.

3.2 Distribution and numbers

3.2.1 Winter distribution

In winter, like other grebes, White-tufted Grebes are found on salt water generally near to the shore (Brooks 1917). They are often seen feeding in coastal waters amongst kelp beds and in tidal creeks (Strange 1992) or in sheltered coastal bays where they occur more frequently at this time of the year (Woods & Woods 1997, 2006).

During migration, they may appear on ponds located on islands that they do not necessarily use for breeding. Thus, 11 individuals were observed in August 2010 on one of the airfield ponds at Carcass Island, but none were seen during the breeding season.

3.2.2 Breeding distribution

Garnot (1826 *in* Woods & Woods 1997) said that the species could be found on the sea and the edges of rivers. Darwin collected specimens in March 1833 or 1834 and stated that "it was common at the head of the tortuous bays which intersect these islands" (Gould & Darwin 1838-41 *in* Woods & Woods 1997). Abbott (1861 *in* Woods & Woods 1997) felt

that White-tufted Grebes were rather common on fresh and salt water though more frequent on the freshwater streams. Vallentin (in Boyson 1924) stated that it was generally distributed over northern East Falkland and that it was found in all of the larger ponds and pools on West Falkland.

The species was reported by Cobb to nest on Cockhouse Pond, North Arm, and on Grebe Pond, Cattle Point, in 1907, on First Pond, Hog Ground, in 1919, 1922 and 1927 (Woods 1996). From a pond close to the sea at San Carlos, East Falkland, a pair with two downy chicks and seven additional adults were reported (Brooks 1917). Cawkell and Hamilton (1961) stated that these grebes were commonest in Lafonia.

Woods (1988) considered the species as widespread throughout the Falklands and fairly common. Data collected during the breeding birds survey of 1983-1992, the only island-wide survey of Falkland breeding birds, indicated that White-tufted Grebes were recorded in 90 out of 234 Universal Transverse Mercator (UTM) 10x10-km squares (38%), but counts or estimates of population were given for only 51 squares (57%). In 36 squares, no evidence of breeding was registered. Breeding was confirmed in 39 squares and probable in another 15. The species occurred significantly less commonly in squares located over 500 feet above sea level. White-tufted Grebes were mainly found in the low lying parts of the Falklands, particularly in Lafonia, for example at Fanny Cove, North Arm, and S of the Wickham Heights along the N side of Choiseul Sound. They also bred at ponds in the N part of East Falkland and central West Falkland N of Fox Bay and they occupied wetlands at some offshore islands such as Pebble, Bleaker, Saunders, Speedwell and Lively (Woods & Woods 1997).

Ponds and lagoons where White-tufted Grebes were observed during the 2008 and 2010 fieldwork of this study are listed in Table 1. Except for the extension of Bodie Creek and the ponds at Goose Green, all wetlands listed for East Falkland are located south of the Wickham Heights. In addition in 2008, the pond in North Arm, Lafonia, held no White-tufted Grebes. In the region of Volunteer Point where six ponds close to Volunteer Point and two ponds close to Mount Brisbane were visited, only one pond close to Mount Brisbane held one adult. The species was not recorded on Sea Lion Island in 2008 and Carcass Island in 2010.

3.2.3 Breeding population

For the period prior to 1980, no population estimates or counts exist. According to the atlas of breeding birds (1983-93), the total population of the Falkland Islands' White-tufted Grebes consisted of a minimum of 195 BP, a maximum of 1,950 BP, an average of 1,073 BP and an estimate of 750-1,400 BP (30% variation from the average). Per square with a positive record, the estimate was thus of 8.3-15.5 BP (Woods & Woods 1997). Other statements about the population size in literature are more speculative. O'Donnell and Fjeldså (1997) estimated that the total population probably numbers less than 10,000 and that the subspecies could be vulnerable because of its small area of occupancy. Fjeldså (2004) indicated that there might be "probably several thousand".

In 2010, the present study recorded a total breeding population of 47-55 pairs. Long Pond (8-9 BP), Big Pond (6-7 BP), both on Pebble Island, and Swan Inlet Pond nº 4 (7-9 BP) on East Falkland held the most important populations. In 2008, the species was in addition recorded on Bleaker Island (Table 1). If applying the 10x10 km square subdivision of the UTM grid system used for the breeding atlas, the White-tufted Grebes found were spread over seven squares. Five of the squares were completely surveyed and the remaining two for over 80%. On average, the squares surveyed held 7.1-8.3 BP. Mathematically, a correction of one additional pair per square could be applied to cater for the parts not surveyed in two squares. The increase is based on the assumption that in

both squares the population relative to the water surface in the parts surveyed and not surveyed were identical. Assuming that the seven squares are representative and that the species was still present in 90 squares, the figures lead to an estimated total population of 700-850 BP (Konter 2011). This is at the lower end of the estimate by Woods and Woods (1997). It is however wrong to conclude that the population has declined over the last 20 years. This survey provided just another estimate based on a different method. The figures might be more precise for the wetlands visited, but the overall coverage was low and the total number of squares with breeding Whitetufted Grebes could have been quite different in 2010 from that of the period around 1990.

Due to the lack of data before 1983, population trends cannot be assessed. However, the species could possibly be less numerous than in the mid-19th century because native grasslands have been seriously overgrazed and because many bird species were seen as pests, as potential food or as objects to be hunted for sport. The Whitetufted Grebes were still shot as waterfowl in the early 1960s (R. Woods unpublished). According to Procter and Fleming (1999), the White-tufted Grebe is rare and numbers may have declined.

3.3 Breeding ecology

3.3.1 Breeding habitat

Breeding activity of White-tufted Grebes occurs in shallow freshwater ponds supporting aquatic or emergent vegetation or on slow moving rivers and streams (Cobb 1933, Strange 1992, Woods 1988, Woods & Woods 1997). The ponds not far from the sea are of varying size (Brooks 1917). In his field notes assembled by Woods (1996), Cobb described two nest sites. One platform was built in 1919 on a soft peaty side of a pond quite sheltered from western and southern to northern winds being in a slight recess of a bank. The second found in 1927 was a heap near a bank on the east side of a pond. Cobb (1933) reported nests to be built in shallows of ponds or under grass overhanging the water at the edge of ponds or streams or under the bank of a pond. A resident told Brooks (1917) that these grebes nest on the shore very near to the water. Woods (1988) and Woods and Woods (2006)

indicated that the solitary nest is a floating mass of waterweeds and grass usually placed under the overhanging bank of a large pond or stream or in rushes *Scirpus* and *Juncus sp.*. According to Strange (1992), the often floating nests are placed under the cover of banks and amongst Brown Swamp Rush *Rostkovia magellanica* in shallows of ponds.

Three platforms were recorded in 2008, one located in a notch of the bank under overhanging grasses and two were floating inside Water Milfoil or Pondweed Myriophyllum quitense. One of the latter was surrounded by three platforms of Silvery Grebes P. occipitalis containing eggs. In 2010, a total of 13 nests and platforms were found. Seven of them existed under the overhanging bank of a pond, 3 were built on Tussock Grass Poa flabellata islands, one inside rushes Juncaceae in the shallow of a pond and two in a small ditch about 1 m wide and with less than 50 cm water depth connected to a larger pond. Inside the ditches, the nests were also placed under the overhanging bank (one of them located about 50 m away from the pond itself). Not a single of these 13 platforms was really floating. Nine were resting on a muddy projection of the elevated bank (Fig. 5) and three were squeezed between stands of Tussock Grass forming an island (Fig. 6), all above water level. The last was built inside rushes in water about 10-15 cm deep with its base completely sunk to the ground. Two of the nine nests found under the bank were inside a kind of tunnel. There, in time the action of the waves had excavated a rather deep cave into the bank. The overhanging "roof" became too heavy and collapsed in a way to form the tunnels. The inside was now completely protected against direct wave damage (Konter 2011). All White-tufted Grebe pairs recorded were strictly territorial.

K. Greenland (pers. communication) reported a pair of White-tufted Grebes using the wreck at the bay of Goose Green for nesting. After displaying, a pair inspected the inside of a floating barrel connected to the disintegrating jetty of Big Pond on Pebble Island in 2008, possibly in search of a nesting place (pers. observation).

White-tufted Grebes incubating under the excavated overhang of the bank are somewhat comparable to cave-nesting species. Often, they have their view about completely obstructed.



Figure 5: Nest under the overhanging bank of Big Pond, Pebble Island (2008).





Figure 6: Nest inside an island of Tussock stands, pond east of Laguna Isla, East Falkland (2010).

They are well hidden from possible predators to themselves and their eggs, but can only look and escape to the front. According to the 2010 observations and in contrast to the general behaviour of the members in the family Podicipedidae, floating nests could be more exceptional. They seem to appear later in the season when the development of floating vegetation has progressed, even though at this moment in time, the risk that the shallower ponds dry out is increasing. In general, a Falkland Islands White-tufted Grebe could more regularly build on solid underground where the platform is possibly better protected from high waves, especially if the bird is sitting and, thereby, holds the nesting material. With respect to the water levels, some of the nests in a notch of the bank were rather elevated and they were only accessible with a big jump.

3.3.2 Timing of breeding, multiple breeding

The breeding season starts in late September with courtship and nest-building (Strange 1992). According to Cobb (1933), nests with eggs have been found from mid-October to January. Woods (1988) confirmed breeding from mid-October to January and Strange (1992) indicated laying in October, but sometimes late in December. Breeding is generally solitary (Woods & Woods 2006).

Possibly a consequence of the mild winter, an earlier clutch initiation than so far reported was noted in 2010. Assuming an incubation time of three weeks and considering the age of chicks encountered, first eggs must have been laid at the end of September and very early in October (Konter 2011).

The literature is silent about multiple breeding. The subspecies could be partially double-brooded, at least in favourable years or in part of its range. Thus, A. Henry recorded a first successful clutch of a pair at a pond near Stanley airport producing one chick in November 2007. The female was again incubating in January 2008 (pers. communication). The pair nesting at Big Pond, Pebble Island, in January 2008 was very likely breeding for the second time in that season, too. A juvenile kept trying to stay close to the off-duty member of the pair. It was continuously chased. It is reasonable to assume that the juvenile was from an earlier brood in that season by the same pair.

3.3.3 Clutch size, time of incubation and time to fledging

Nests found by Cobb between 1907 and 1927 held 3, 2, 2 and 2 eggs (Woods 1996) and he reported nests to hold generally 1-3 eggs. As in other grebes, eggs are covered if the incubating bird leaves (Cobb 1933). Cawkell and Hamilton (1961) indicated that the clutch consists of two eggs. Woods (1988) confirmed the clutch range of 1-3 eggs and added that the initially white eggs become rapidly stained. The clutch size is comparable to that of mainland forms for which Burger (1974) reported an average of 2.0 eggs, range 1-3, and Petracci and Basanta (2002) indicated 2.6 eggs (n=12).

During this study, the full clutch size was recorded for two nests, one on Pebble Island in 2008 and one on Saunders Island in 2010. It consisted each time of two stained eggs.

I found no indications of egg dimensions for Falkland Islands, but they should exceed those of the continental subspecies for which $40.1\pm2.1 \times 28.0\pm1.6 \text{ mm}$, range $36.7-49.1 \times 25.0-37.9 \text{ mm}$ have been measured (Burger 1974).

According to Fjeldså (2004) incubation time and time to fledging are not known for the species as a whole.

3.3.4 Hatching and fledging success

The literature is rather silent with respect to hatching or fledging success of all three forms of White-tufted Grebes. Only Petracci and Basanta (2002) indicated that in their study chicks hatched in 9 out of 12 *chilensis* nests.

Assuming that the numbers of grebes recorded during this study in January 2008 were representative, 16-19 pairs of White-tufted Grebes had produced only five fledglings. The fledging success of the population would be of 0.26-0.31 young per pair. In 2008 and in 2010, 11 pairs tending young were found. 10 of them cared for one chick and only one had 2 chicks. The breeding success of successful pairs appears to be of one chick as a rule and two chicks could be less common (Konter 2011).

3.4 Food and feeding

The food consists of fish up to 15 cm in length, crustaceans and aquatic plants (Woods 1988). Strange (1992) added that the small fish belong predominantly to *Galaxias* species and that the grebe takes insects, too. In winter, the birds are often seen feeding in coastal waters amongst kelp beds and in tidal creeks. All food is obtained by diving. On average, a dive lasts for 15 seconds with a maximum of about 20 seconds (Woods 1988).

The diving time indications were confirmed by own timing of dives in three different grebes in January 2008. The average dive times were of 14.2 ± 1.92 seconds (n=5), 13.6 ± 5.88 seconds (n=7) and 15.6 ± 4.72 seconds (n=14) in three series of successive dives or of 14.77 ± 4.62 seconds (n=26) for all three grebes together. Maximum diving times were of 16, 20 and 24 seconds respectively. Average up-times between dives were of 10.4 ± 6.93 seconds (n=19) with a maximum of 29 seconds. The up-times appeared to be unrelated to the duration of the preceding dive or the catching success. All prey brought up was handled quickly and swallowed immediately. All items recorded were small, probably aquatic invertebrates.

In 2008, White-tufted Grebes were occasionally observed collecting tiny prey from the water surface in dense floating vegetation or spearing below water and catching food by a short stabbing movement of their neck and head. In 2010, several individuals were seen to collect insects from the water surface. These were probably land insects (*Chironomid* midges were seen ashore) blown to the ponds by the wind. The grebes appeared to wait at the entrance of bays for the waves to transport the food towards them. Diving grebes often surfaced with fish of differing size or with a kind of yellowish worm.

During preening, several individuals swallowed their own feathers. One grebe was observed to regurgitate food debris (pellet casting). Thereafter, it drank water.

3.5 Possible threats

A priori, predation risk to adults seems very limited if not inexistent in the Falkland Island. Naturally occurring birds of prey such as Southern *Caracara* A. Konter

plancus and Striated Caracara Phalcoboenus *australis* are not numerous. On the mainland, the Southern Caracara was reported to feed on Whitetufted Grebe eggs and on adults that it caught on the nest (Burger 1974). The Variable Hawk Buteo polysoma is more numerous, but no acts of predation by birds of prey have been reported. Hazards could concentrate on eggs and chicks. Loss of wetlands or increasing numbers of days with high wind speeds or storms as a consequence of climate change may reduce breeding success as nests are highly vulnerable to wave action or may be abandoned if they fall dry or get out of reach for the grebes. On two ponds on Bleaker and Pebble islands, I observed cattle walking into the shallow water and feeding on Water Milfoil not far from existing grebe platforms. This may occasionally either directly destroy or destabilize nests. Clutches in nests built in floating vegetation may be more easily subject to predation by Kelp Larus dominicanus, Brown-hooded L. maculipensis or Dolphin Gulls Leucophaeus scoresbii, respectively by Falkland Skuas Catharacta antarctica. Nests under the bank may be accessible for predation to rats Rattus sp. that are found on the main islands and on some offshore islands (Woods & Woods 2006). Local people reported of Falkland Skuas harassing adult grebes carrying chicks to make these dive and lose their young that the skuas then collected when surfacing. Southern Giant Petrels Macronectes giganteus may at rare occasions try to grasp young chicks if the grebes are inattentive, especially during feeding. Generally, evidence for perceptible damage by any possible predator is lacking and the small population size coupled with the limitations in wetlands available for breeding may contribute most to the subspecies' vulnerability.

4 Aggressive and courtship behaviour

The antagonistic behaviour, water courtship and platform courtship as described in literature for the mainland forms are summarized first and serve as a basis for the observations in *Rollandia rolland rolland* that follow.

4.1 Antagonistic behaviour and displays of the mainland forms in literature

4.1.1 Antagonistic behaviour

Forward Threat: The bird is deep in the water, with head feathers sleeked. The neck is extended forward during advance and bent at the middle and somewhat withdrawn when stationary; it may then be partially submerged. The bearing corresponds to a pre-attack situation. During sustained stationary threat, the opponents utter a deep growling "hrrrr" (Fjeldså 1985). In the Forward threat posture, the aggressor may swim rapidly at a conspecific. If two grebes face in this posture, one may back away or turn around and swim away from the other, only to pivot back quickly. This then makes the opponent turn around, too, and swim in the opposite direction. Occasionally, the opponents raise their wings and show the white rear edge of the secondaries (Storer 1967b).

Hunched Threat: During lasting disputes or if threatening near a territory border, the birds often hold their necks higher and expand the plumages, even holding their wings somewhat lifted (Hunched posture). Maintaining the Hunched posture, the birds turn head and neck from side to side and then pivot and display the pale rear towards one another. Opponents often back and pivot by turns. Triumph Ceremonies in couples may occur in this context (Fjeldså 1985). According to Storer (1967b) who used the term "Wing raising" in the antagonistic and in the display situation, the opponents may raise the wings several times in the course of an extended aggressive encounter.

Token Diving: Threatening may be interrupted by token dives that are often repeated. The threatened bird then regularly peers under water. Sometimes two opponents take turns in making token dives and peering (Fjeldså 1985). The token dives consist in rather shallow dives that feign an attack, the diving grebes re-appearing at rather the same place from where they submerged.

Pattering: Pattering generally follows Forward Threatening at a few metres range. One bird may perform a sudden forward dash or, raising its body out of the water and pattering forward with kinked neck so that the bill is horizontal. The wings remain folded away. After a few meters, the grebe breaks and resumes the threatening (Fjeldså 1985).

Attack-across-land: A pattering attack may be launched running across the bank (Fjeldså 1985).

Fighting: Open fights occur during territory establishment. They are preceded by attack-dives or pattering. Birds then bounce up with necks bent back, colliding breast to breast, apparently attempting to overthrow one another. Fighting may be followed by chasing (Fjeldså 1985).

Chasing: Chasing may occur above and below water. On the water surface, the attacking grebe rushes with the raised body rather horizontal and the neck kept forward. The chased bird raises its neck higher, up to 80°. After an initial phase, the chasing bird adopts the same behaviour as its victim, but the chased bird holds its neck on one line with the body, not forward, and it may dive from this posture. Chasing sometimes involves several birds that may spread out in a fan (Fjeldså 1985). If the grebe that is pursued dives, the other may do so, too, and the chase continues under water (Storer 1967b).

Escape: White-tufted Grebes sometimes splatter across the water when in danger, but Fjeldså (1985) has never seen birds of any Andean population fly.

Appeasement: If threatened and in order to appease an opponent, White-tufted Grebes extend the neck and sleek the plumage with the rear of the body deep in the water (Fjeldså 1985).

Aggressive encounters may end with Parallel Racing involving several birds (Fjeldså 2004).

4.1.2 Water courtship

Displays of the White-tufted Grebe are simple and usually slightly differentiated from non-ritualized activities. They may involve more than two birds (Fjeldså 1985).

Advertising: Unpaired grebes in search of a partner or mated birds separated from it (Storer 1967b) Advertise with the neck fully extended, erect or leaned slightly forward, and thin. The crown feathers are erect, the head looks laterally compressed and the body is sloping backward. The call "chorrh" can be heard at close range. The behaviour is rarely noted in this species (Fjeldså 1985).

Approach: Following a positive response to a grebe's Advertising, and still well apart, one grebe initiates a series of dives towards the other. At a distance of 10-15 m, the other dives, too. Under water, the two apparently turn and emerge swimming side by side (Fjeldså 1985). The dives may be shallow (Ripple Diving, Fjeldså 2004). A second grebe may also simply swim with its head somewhat raised toward the Advertising grebe that raises its head and fully spreads its ornamental feathers. The second grebe dives and surfaces again beside the other in a Wing Raising Display (Storer 1967b).

Circling: Following the approach and upon surfacing, the birds swim side by side and start circling around one another with necks straight, occiput feathers raised and ear-coverts flared out (Fjeldså 1985).

Wing Raising: The displaying bird keeps its head low, fluffs out its head and body feathers, raises its wings over its back and spreads its secondaries slightly so that the white tips are conspicuous. Partners may approach thus, turn away, swim together again and then perform a complete turn. Also, members of a pair facing in opposite directions may swim in a tight circle, one or both showing Wing Raising. Following the approach after Advertising, one mate may surface in a Wing Raising Display and, facing, they perform several rapid Head Shakes (Storer 1967b).

Bumping Ceremony: This ceremony may follow Advertising, Approach and Circling. It involves several elements. In its central part, the partners dive by turns below each other and, surfacing again, bump one another with the breast. There is no precise sequencing of elements in the ceremony (Fjeldså 1985). It starts with a pair of grebes facing each other on the water, the bodies horizontal, the necks stretched upward and the crests raised (Storer 1967b). The different composing parts are described as follows:

- Head Turning: Facing with fully extended necks, bills horizontal or sloping, bodies sloping slightly backwards, most of the time both grebes quite deep in the water, occasionally with back feathers raised, a few initial Head Shakes are performed. Later, in between bumping, one or both birds may show head-jerks or bill-flicks or rather slow Head Turning (Fjeldså 1985).

- **Stabbing:** Close together, one partner bows its head so as to dip the bill, then abruptly extends the neck and makes a thwarted thrust with the bill that may be repeated by the partner (Fjeldså 1985).
- **Diving:** One bird makes a rather clumsy dive directly from the upright, head first. The partner arches its upper neck as if to watch the submerged bird and turns so as to face it when it emerges (Fjeldså 1985).
- **Bouncing:** The diving bird sometimes emerges a bit ahead or to the side of the surface bird. It just puts its head up or pops up with the neck thrown back like a Z and dives again immediately (Fjeldså 1985).
- **Bumping:** The underwater bird rises below the surface bird and hits it with its protruding breast. Halfway out of the water, neck and body may lean back, but at full height, both birds are vertical and tread water for a moment (Fjeldså 1985). The diving and Bumping is then repeated either by the same bird or by its companion and in total, six to more than eight Bumping may occur (Storer 1967b).
- **Barging:** Once the partners turned and swam about 1 m with their necks extended and slightly bent forward and their ornamental feathers spread before one submerged (Fjeldså 1985).
- **Bumping without diving:** One bird, raising its body partly, collides with the other and thereby gently pushes the other back with its projecting breast (Fjeldså 1985).
- The ceremony may end in several ways (Storer 1967b):
- Swimming away: The birds finally adopt a furtive upright postures, turn away from one another and depart (Fjeldså 1985) in opposite directions or one bird merely swims away from the other (Storer 1967b).
- Weed Fetching: In some ceremonies, Bumping is immediately followed by weed fetching and swimming with weeds (Fjeldså 1985, Storer 1967b).
- Head Shaking: Storer (1967b) observed one ceremony that ended with Head Shaking.

Triumph Ceremony: Established mates often meet and mill around one another in Hunched postures, duetting. In low intensity, the partners just meet and turn parallel. In intense cases, the neck is retracted, sometimes partially raised, plumage flared out, wings more or less elevated and tilted, sometimes partially spread. As the grebes move parallel, one bird sometimes moves a little ahead with its neck held forward. It then makes a short Pattering (Fjeldså 1985). Storer (1967b) reports of two pairs that separated after an aggressive encounter; each then performed a series of displays involving Wing Raising and turning.

Head Shaking: According to Fjeldså (1985), this display is poorly ritualized. Storer (1967b) observed it in the context of the Bumping Display that is preceded by two or three very rapid Head Shakes and during Wing Raising. In addition, it may be used by members of a pair after separation, with or without further displaying.

Habit Preening: This display is apparently absent in mainland White-tufted Grebes (Fjeldså 1985).

Skittering: Under "general behaviour", Storer (1967b) reported mainland White-tufted Grebes to skitter not infrequently across the water, flapping their wings and paddling with the feet at the same time. A group was observed to skitter up-wind from the lee side of a canal.

4.1.3 Platform courtship

Rearing: One partner jumps upon the platform and, remaining high on its feet, sways a little from side to side. The bird flares its mantle feathers and loosens its wings to shake-off water in its plumage. The neck is sloping, the bill usually pointing down, but sometimes it is moved as in intention to remove plant debris. In Rearing, the bird "freezes" in an upright posture with its neck arched downwards and intermittently shows Wing Quivering (Fjeldså 1985) with its tail cocked. The behaviour differs very little from that of a bird settling down to incubate (Fjeldså 2004).

Inviting: After Rearing, the grebe settles down as for incubation. Fjeldså (1985) distinguished a Prone posture where the neck is retracted, but the head is still held up, and the Inviting posture itself, assumed when the water bird comes close to and behind the platform bird. In the latter, the

head is extended forward and lowered till it rests on the nest.

Mounting/Copulation: The second grebe jumps onto the back of the Inviting bird that first keeps its head low, but then usually retracts it and turns it from side to side. The copula is accompanied by a humming "jrrmmmmm". At first, the Inviting grebe keeps its head low, but then usually retracts it and turns it from side to side (Fjeldså 1985). It may then bounce up so that the partner is thrown off (Fjeldså 2004).

Post-copulatory Display: Usually, the second grebe dismounts over the head of its partner and lands in the water in an upright posture, splashing strongly with its feet. The initially inviting bird throws its neck back and then looks away. At the same time, it rises up remarkably fast, freezing in an ecstatic posture with the breast pushed out, the neck folded to the back and the beak resting on the upper breast. The dismounting grebe quickly adopts a furtive upright posture with moderately raised feathers on forehead and occiput. It usually performs a few irregular head-jerks and sometimes a bill-flick or body-shake. It may turn to face its mate, but usually swims right away. The other grebe remains in the ecstatic posture for some 10-15 seconds, then it lies down and pulls nest material, sometimes rises up, waddles around or preens before settling again (Fjeldså 1985).

4.2 Observations of aggression and courtship in the nominate form

To avoid much repetition in the description of the behaviours as observed in the Falkland Islands' White-tufted Grebes, it is useful to name and clearly define some postures and positioning of feathers. The naming of the different degrees in erection of the ear tufts relies to a large extent on Julian Huxley's (1914) descriptions for the Great Crested Grebe *P. cristatus*.

4.2.1 A few postures of Rollandia rolland rolland

Ear tufts: the ear tufts function like a fan and may be subject to lateral and vertical positioning. Vertically, they may be **fanned out** completely, **shut tight** or **relaxed**. In the first case, they are most conspicuous as the area covered by the white tufts is maximal. In the second case, this field is minimal, the tufts appear more oblong (closed fan). In the third case, the area is intermediate and the fan shape is less apparent. Laterally, the tufts may be completely pressed against the head or they may be flared out. I have neither observed a complete lateral erection of the tufts as can be seen in the Great Crested Grebe during its Cat display nor vertically relaxed and laterally depressed tufts. This means that in total five positions remain possible for the positioning of these ornamental feathers. In the vertical fanning with lateral depression, the tufts curve towards the nape in their endings although they often appear vaulted in their lower part. This vaulting is possibly due to the erection of cheek feathers underneath. From facing, the head form recalls a pear and, this positioning of the tufts is therefore called pearshaped fanning (Fig.14, 15). If vertically fanned out and laterally not depressed, the tufts are flared out. If vertically shut tight and laterally pressed against the head, the tufts are sloping in the rear part and they are sleeked. If vertically shut tight and laterally more flared out, from facing they leave the impression of a slight and gradual lateral widening, a bit like it is the case in a funnel. Therefore, the tufts are called funnel-shaped (Fig.13). If the tufts are vertically and laterally relaxed, they are simply called relaxed.

Head: the form of the head largely depends on the degree of erection of particularly ornamental feathers. With the crest raised and the ear tufts in pear-shaped fanning, the head takes the form of a pear and is therefore said to be **pear-shaped** (Fig.14, 15). With the crest depressed and the ear tufts in funnel-shape, the entire head of the bird appears to be widening, funnel-shaped, from the bill to the nape. The head is advanced with respect to the neck; this results from the kinking of one or two upper cervical vertebrae that prolong the head. This bearing is called the **Funnel look** (Fig.13). In it, a few upper feathers of the ear tufts form a kind of broken edge to the vertical field formed by the tufts below.

Neck: the neck may be held vertically rather straight or it may be curved to a greater or lesser extent. If not straight, the neck may take three basic forms. First, there is the **high S-form** (Fig.9) in which the upper neck and the head are slightly kinked forward and the lower neck is slightly vaulted forward. Second, in the low s-form, both curvatures are more marked and the entire form described by the neck is more compressed. Third, the neck may be kind of retracted or folded with more angular curves: in this case, it is said to be in z-form. A neck that is held in one line may be more or less extended. If not particularly extended, it is simply straight. It may be extended to maximum length or fully stretched. In the intermediary case, it is simply said to be extended. In all three conditions, the neck may be held **vertical**, it may be slightly advanced from the vertical plane or obliquely advanced, and it may slope slightly backward or be hold back. In addition to the bearing of the neck itself, the positioning of its feathers is of importance. These may be depressed, relaxed or erected. It is noteworthy that quite often not all neck feathers are in the same condition. Thus, especially those of the upper neck may be fully erect while those of the lower neck look more depressed (Fig. 11).

Back: the long feathers of the mantle may be depressed giving to the body a slim appearance or they may be partially erected giving to the back a vaulted look. In some behaviour, the feathers of the mantle are erected fully, but the wings remain folded away. In others, in addition the wings are lifted to some degree, however without lateral extension. This bearing remembers the **Swan posture** of the Red-necked Grebe (Wobus 1964) and this naming is also retained for the White-tufted Grebe.

Body: the grebe's body may be **horizontal** on the water surface. If the breast is elevated and the vent lowered, the body is **sloping**. Whether horizontal or sloping, the body may be high or deep on the water surface. If the breast is completely protruding and the rear of the rump submerged so that the body is in a rather vertical plane, but with limited elevation, the grebe is in a **Plumb Penguin posture** (Fjeldså 1982).

4.2.2 Aggression in the Falkland Islands

The antagonistic behaviours observed in the Falkland Islands included all threat postures and behaviours described for the mainland forms. In **Forward threatening** however, no case of Wing raising was seen, except if feigning a Patter attack. Instead, a vaulting of the mantle feathers could occur (Fig. 7). If threatening lasted for longer, the vaulting alternated with a depressing of the back feathers. The Hunched posture (Fig. 8) was especially common in lasting disputes, after retreating from a Patter attack or after Token diving. Similarly to mainland White-tufted Grebes, birds in the Falklands could expand their mantle feathers or even lift their wings partially. While threatening in the Hunched posture, a deep grunting sound was audible at close range. In Pattering or Patter attacks, birds from the continent keep their wings folded, and in literature, it is not mentioned whether they could unfold them during Chasing. White-tufted Grebes in the Falkland Islands could open their wings briefly during Pattering or even flap them during Chasing. They could unfold their wings while escaping. The crest of the attacking grebe was depressed and the tufts were shut tight or sleeked. The head continued the line formed by the neck that was extended in a horizontal plane. In contrast, the escaping grebe pattered with its neck extended vertically. It often dived after a short distance. In one observation of an underwater pursuit with several dives in a row, the persecutor seemed to by-pass the escaping grebe below water (that then escaped with Pattering) before returning to its mate. Many duels ended with the aggressors returning to their mates for a bout of Circling that possibly served as a Triumph Ceremony.

On a few occasions, two or three pairs were seen to engage in mutual courtship during which aggression occurred. This included short Patter attacks, stabbing with the open beak at others or quickly swimming at them. Also, if more than two grebes were simply close together for feeding or resting, one grebe could be chased by a sudden peck in its direction.

A few aggressive behaviours so far not described were observed: White-tufted Grebes in the Falkland Islands could chase others in a swan-like posture, in a Plumb Penguin posture or by swimming fast at them, and they used High threatening.

Especially if chasing was prolonged and the opponent(s) expelled without much resistance, a grebe could drive others away remaining high on the water surface with its body slightly sloping, the neck in high S-form, the neck feathers raised, ornamental feathers rather relaxed and the bill pointing downward. It uttered a deep grunting



Figure 7: White-tufted Grebe in Forward Threat with vaulted back and swaying its head, Long Pond, Pebble Island (2010).



Figure 8: Threatening in Hunched posture with the back turned at the opponent, Long Pond, Pebble Island (2010).

sound. The mantle feathers were erected. In many observations, the wings were at least slightly lifted and the posture resembled an aggressive swan or the swan-posture of the Red-necked Grebe. Therefore, I have chosen the name Chasing in Swan posture (Fig. 9) for this antagonistic behaviour.

Partners often reacted towards rivals showing up by engaging in short displays, particularly Circling with or without Wing Raising. One mate could then adopt a **Plumb Penguin posture** with vertically extended neck, turn toward the troublemaker(s) and swim at it (them).

A pair could also swim fast at a rival, mostly lying deep in the water with sloping bodies, necks extended vertically. The postures observed were quite variable as were the degrees of erection of neck and head feathers. The targeted grebe often dived and the pair could pursue it under water or it simply stopped its progression with or without further displaying.

In High threatening (Fig. 10), the grebe held its fully stretched neck obliquely advanced. The ornamental feathers were sleeked and the mantle

feathers raised. Probably this way of threatening is less intense than Forward threatening, but it might also replace the latter in higher waves when Forward threatening is difficult. High threatening sometimes preceded either Forward threatening or even a Pattering attack.

The following descriptions summarize a few aggressive encounters and serve as examples for the behaviour of the White-tufted Grebes in the Falkland Islands.

On Big Pond, Bleaker Island, two pairs and one single grebe were present in 2008. Resting White-tufted Grebes were not easily detected inside the extensive growth of Pondweed. One pair was resting together when the second pair arrived, swimming and diving into its direction. The resting pair dived, too, and separated under water. Both mates of the second pair now targeted one partner of the escaping pair and started to pursue it for over 30 minutes. The pursued bird again and again changed direction while diving and tried to hide in between the vegetation, remaining low on the water surface and spearing over the weeds to detect the opponents. These searched the milfoil, stretching their necks. Once



Figure 9: Chasing in the Swan posture, Big Pond, Pebble Island (2010).



Figure 10: Out of the Triumph Ceremony, the male (right) adopts a High threatening posture, Long Pond, Pebble Island (2010).

detected, they again dived in its direction. On two occasions, one persecutor surfaced in close vicinity to the isolated grebe that escaped with a low pattering flight. The pursuing pair did not fly behind. It rather continued diving until closer again. The escaping grebe twice reached its mate, but the surfacing of one or both opponents not far away separated both again. The aggression ended with the pursuers coming together and Circling in a kind of Triumph Ceremony.

In 2010, two neighbouring territory holders at Long Pond, Pebble Island, had platforms at some 50 m from one another. Possibly one pair was already incubating and one partner never showed up outside of the tussock islands. At times its conspicuous ear tufts could be seen at always the same place inside the vegetation. The platform of the other pair was visible, but often unoccupied. Especially during disputes, the female was always out, but it remained at some distance in the back of its mate. Both males engaged in intense border conflicts on three occasions. A typical course of events was as follows. One male moved out of the vegetation into the direction of the other posture, remaining deep in the water and swaying its head from one side to the other. The second male showed up quickly and threatened alike. In turns, both performed short Patter attacks. The opponent responded by a Pattering escape with the neck vertically extended. The grebes always covered only a few metres in Pattering and the attacker retreated, resuming threatening. The opponents thus moved to and fro, at times turning the back at the neighbour in a Hunched posture, swaying the head and threatening over the shoulder. Occasionally, the grebes used High threatening or they adopted the Chasing Swan posture with partially lifted wings. The single male was slowly pushed back. The rival returned to its waiting mate, adopting en route a few times a Hunched posture without however turning around. The opponent was quick to again occupy the deserted surface so that the pair had hardly time to engage in courtship and the male pivoted to return to the arena. After new bouts of Forward threatening and Pattering, both engaged in Token diving. In between, they moved to and fro on the water surface in threatening postures.

territory and quickly adopted a Forward threat

Occasional forward dashes made the opponent retreat momentarily. During the entire conflict, both grebes maintained a minimum distance of 2-3 m to each other and no grebe seemed really interested in a physical dispute. Finally, the single male retreated far enough into its own territory. The aggression ceased for some time only to revive shortly afterwards.

On Big Pond, Pebble Island, pair A cared for a single chick less than two weeks old in 2010. Its feeding territory included a ditch and another area with short rushes that attracted the interest of two additional pairs in search of a suitable place for platform courtship or nesting. Pairs B and C profited from a momentary absence of pair A that had moved inside the ditch to inspect the rushes one after the other. After a bout of common courtship ending with diving, pair C moved again farther out to feed. Some time later, pair A returned and swam directly at pair B that was still inspecting the vegetation. Male A led in the Chasing Swan posture and grumbled. It progressed quickly, leaving the female with the chick behind. Out of the Swan posture, the male launched short Patter attacks at the opponents, briefly lifting its body completely out of water and dashing forward for a handful of paddling steps on the water surface. During Pattering, the body was about horizontal, the neck extended forward and the head in the same plane. The grebe quickly fell back onto the water surface. It adopted Forward threatening before resuming Chasing in the Swan posture. The female in its back followed with the head in Funnel look, the neck in low s-form, the wings slightly raised and turning its head. After three or four Patter attacks, the male returned to its mate for a short Circling, both grebes with the neck in low s-form and the head in Funnel look. The display ended in a few preening movements before the male resumed chasing. Male A approached pair B in the Chasing Swan posture. Pair B hesitantly swam in front, the neck in high S-form and the head pear-shaped, pivoting on the water surface and observing male A. When the latter adopted a Forward threat posture, pair B dived quickly and so did male A. All three grebes now entered a neighbouring territory owned by another pair with a chick. Pair B was now captivated in a pincer movement and escaped by quickly diving. Male A directed its threats and Pattering attacks at the neighbour that was however less willing to retreat. After mutual

Token diving, male A resumed the persecution of the initial opponents. In the meantime, these had joined pair C on the open water surface. The four birds were milling around there, Circling briefly and watching male A. With Forward threatening, Pattering and diving, the latter launched a general chasing of all four grebes that separated during their escape. Male A targeted them one by one using under water attacks. Three times, it apparently surprised the opponent(s) that disappeared with a splashing fold-in-the-middle dive. Male A pushed the others ever farther out, using threatening, Token diving and Pattering. Especially during the final stages, when all grebes were already some 50 m away from the initial place, Chasing in the Swan posture was common and served to expel pairs B and C for an additional 50 m. The entire pursuit lasted for over 20 minutes whereafter male A returned to its female.

4.2.3 Water courtship in Rollandia rolland rolland

4.2.3.1 Pair bonding displays by two grebes

Water courtship was initiated by a grebe Advertising (Fig. 11) in search of a partner. The call resembled a repeated duck like quacking. Advertising White-tufted Grebes adopted guite differing postures. The neck was extended or fully stretched, vertical, slightly advanced or in S-form. It appeared very thin in spite of the erection of all neck feathers to some degree. At times, the grebes could adopt a more relaxed bearing high on the water surface with horizontal bodies and ornamental feathers flared out or in pear-shape. Very often, the body was however sloping during calling, and the crest and the ear tufts were rather relaxed. If the calling was repeated several times, the neck could be more obliquely advanced with all feathers raised, the body still sloping, the crest depressed and the tufts rather relaxed. The opening of the bill was obvious and the throat protruding. While waiting for an answer, the head could adopt a pear-shape and the neck was in the high-S form. Sometimes it was held slightly back. If a second grebe approached, the advertising bird could either adopt the Funnel look with the neck fully extended and the upper neck feathers raised, sometimes also with the neck simply straight and all neck feathers raised, or the neck was still in the high S-form with the head in pear-shape.



Figure 11: Advertising with extended neck in S-form and ear tufts in pear-shape, Long Pond, Pebble Island (2010).

In the Funnel look with fully extended neck, the neck had the form of a double cone with pointed ends touching in the middle or of an elliptic hyperboloid of one sheet. In a few observations, the Advertising grebe had its head in pear-shape, but intermittently adopted the Funnel look. The waiting bird mostly pivoted slightly on the water surface in between or after its Advertising, even if a conspecific had already started to move towards it. The tail of the Advertising grebe was often cocked, but could also be depressed or change its posture in the course of events, possibly depending on the assessment of the situation. Probably due to the mostly windy conditions during the observations, only in two cases a second grebe was heard to answer with a similar call.

The bearing adopted during and after Advertising could differ between unpaired grebes and mated grebes momentarily separated from their partner. It would then make sense to separate Advertising and Contact Calling. The present study was possibly too short to establish a clear separation that might anyway be difficult in a species with less ritualized courtship behaviour. The observations suggested the following provisional pattern. During the first pair bonding attempts, the alternation between a "friendly" pear-shaped head and the Funnel look derived from aggression would express contrasting internal motivations in the Advertising bird. The repeated approach by the same conspecific would result in an increased confidence and the disappearance of the Funnel look in a first step. It would only reappear in other displays once the pair bond was confirmed.

A visible reply to Advertising was the **Approach** of a (possible) mate. This could happen in several ways. Most often, the partner either dived or swam fast, deep in the water, the neck extended and rather vertical, the crest raised and the ear tufts pear-shaped. If diving, the grebe could either pop up directly in front of the waiting bird or it could surface a few metres away and swim for the remaining distance. White-tufted Grebes Advertising close to the shore remained mostly stationary during the approach phase and the responding partner had to cover the entire separating distance. In a few observations, the advertiser moved for 2 or 3 m in the direction of

a mate arriving above water. If calling at some distance from the shore, both grebes could dive to join, sometimes performing two or three dives in a row. In no case, the partners appeared to meet below water and to turn; they were never seen to emerge side by side. On the contrary, they were rather facing. On two occasions, the partners arrived covering some distance with a pattering flight over the water surface. They landed when still well apart and dived for the last metres.

The following example of Advertising and Approach possibly illustrates a very early pair bonding attempt in which the fear of the female still outweighed her wish to mate.

A female Advertised for some time at Swan Inlet Pond IV, East Falkland. It held its neck vertically extended, the ornamental feathers were relaxed, the body slightly sloping. In between Advertising, the neck of the grebe was held in the high S-form, the head adopted the pear-shape and the female pivoted much on water surface, raising and depressing ornamental feathers. The calls were finally answered by a male arriving from very far and covering most of the distance in fast swimming. The male progressed with its head in pear-shape and performed Head Turning on its way. Meanwhile, the female, continued the Advertising and the pivoting with cocked tail. Intermittently it changed the bearing of its head from pear-shaped to the Funnel look and erected the feathers of the mantle. With the male at only some 5 m distance, the female relaxed its posture. It seemed to prepare for a bout of Circling. It milled around briefly while the male had halted its progression. Suddenly, the female rotated completely, extended its neck and dived. This started mutual diving during which both grebes sometimes surfaced at some 20 m distance from one another, at other times they were only 2 to 5 m apart. If well separated, they sometimes swam at one another's encounter. They dived on their way and surfaced again at greater distance from one another. If surfacing at some 5 m from one another, both grebes remained sometimes on the water surface for a while, at times Advertising or pivoting on the water surface as if they were Circling at distance. At some point in time, the male abandoned and seemed to leave. The female Advertised again and the male returned for another mutual diving. Occasionally, the direction of their immersions insinuated that both could meet below water, but they never surfaced together. At the end both grebes separated again without having achieved any real meeting.

If Advertising and the Approach were followed by courtship, the bearing of the partner(s) gave already an indication about the display that could be expected to follow immediately. It always consisted in milling around one another or in a kind of Circling. However, Falkland White-tufted Grebes could adopt postures quite different from the one described for Circling by Fjeldså (1985). Also, if a lifting of the wings was associated with the Circling, the display could still differ from Storer's (1967b) Wing Raising. Therefore, it was necessary to re-think the naming and the descriptions of the displays. Four different displays were finally distinguished:

Circling (Fig. 12): grebes did not necessarily dive during the Approach, but otherwise the observations in the Falkland Islands closely match Fjeldså's (1985) description. The waiting grebe held the neck fully stretched, vertical or slightly in a high S-form. Its head was pearshaped and all neck feathers were slightly raised. The neck appeared nevertheless thin. The bird remained rather high on the water surface with its tail mostly cocked. Its mantle feathers could be lifted to some degree. The diving partner surfaced directly in front of the Advertising grebe and adopted the same posture; the swimming mate adopted the posture well before joining. Once together, both circled thus around one another and turned their heads while doing so. Occasionally, Head Jerking was observed. If the grebes remained breast to breast for longer, their bodies could be more sloping. In intense Circling, the feathers of the mantle were fully raised. In some observations, the Circling was very short and consisted simply in the grebes joining breast to breast and pivoting into opposite or the same directions. No other courtship followed. The shorter version is possibly used as a kind of greeting in well-established pairs.

Circling with Wing Raising: in a few cases, the Circling grebes raised their wings during Circling while their tufts retained the pearshaped fanning.



Figure 12: Circling, Big Pond, Pebble Island (2010).

Stiff or Funnel Circling (Fig. 13): after Advertising, the White-tufted Grebe could adopt a stiff posture associated with the Funnel look. Its neck was vertically extended or even fully stretched. The upper neck feathers were raised, the lower neck feathers depressed so that the neck was thinnest in the middle and appeared swollen at the height of the throat. The mantle feathers were erected and the wings lifted. The degree of lifting was quite variable and could change during Circling. As mentioned by Storer (1967b) for mainland birds in his Wing raising, the secondaries could be slightly spread and their white tips became conspicuous. However, head feathers were not "fluffed out" in the Falklands and, at least initially, the head was not held low. Both partners met in the same posture, holding their necks slightly back while breast to breast with elevated heads. They maintained the posture during Circling, pivoting on the water surface. During Stiff Circling, besides Head Shaking, Head Turning or Head Jerking, a rather short preening of either the mantle, the flank or the breast feathers going beyond the simple feather

lifting observed in Great Crested Grebes was recorded. In intense displays, at close range a grumbling sound was heard and even wing quivering occurred. In other displays, a protruding throat indicated that grumbling was probably always associated with Funnel Circling.

Low Funnel Circling: this kind of Circling was not observed to follow Advertising. It was rather started by two grebes that were already close together and occupied with comfort activities, for instance preening or resting. It often occurred in a competitive or aggressive context. The neck was vertically straight. As all feathers were raised, it appeared thick. The head was kinked forward and held lower, but still in a kind of Funnel look. This Circling seldom lasted for long, the mates only milling around shortly. It then either ended or graded into another kind of Circling, often Stiff Circling.

In displaying Falkland White-tufted Grebes, especially the three first kinds of Circling could grade into one another. It seemed that Circling



Figure 13: Funnel or Stiff Circling with only upper neck feathers raised, Long Pond, Pebble Island (2010).

was used more commonly early in the pair bond whereas Funnel Circling appeared later. The latter display was still present in well-established pairs. On one occasion, a mate returned from far with a fish in its beak. Its partner that cared for a chick adopted the Funnel look. Both started Funnel Circling, the returning mate brandling the fish in its beak before feeding the pullus on the back of the second grebe. In the end phase of Circling and Circling with Wing Raising, when the partners started already to drift apart, one grebe could suddenly freeze its posture (Fig. 14). Floating high on the water surface with the body horizontal to it, the neck was extended vertically and appeared swollen due to the full erection of all neck feathers. The head was not advanced with respect to the neck. The crest was raised and the ear tufts were flared out. The wings were slightly lifted and the tail was cocked. The bird remained motionless for a glimpse, then it relaxed the bearing and the courtship ended.

Quite often, it occurred that during Circling, Circling with Wing Raising or Funnel Circling the bodies of Falkland White-tufted Grebes became more sloping or even rose into a **Plumb Penguin posture** (Fig. 15) with the breast completely protruding and the vent entirely submerged. This could happen while the partners were breast to breast, side by side or even back to back. Especially if not breast to breast, only one grebe could elevate itself into the Plumb Penguin posture. The **Plumb Penguin Dancing** that followed could take different forms:

The partners could remain breast to breast with their heads either pear-shaped or in the Funnel look and perform Head Turning or Head Waggling while Penguin Dancing.

They could pivot to side by side and progress slowly in the Plumb Penguin posture in one direction (Parallel Penguin Dancing).

Both could dive while progressing side by side in the Plumb Penguin posture, surface again and start a new bout of Circling or even another Plumb Penguin Dancing.

During Circling, they could pivot to one behind the other. In most of these occurrences, only the leading bird rose into the Plumb Penguin posture and progressed slowly in one direction, showing Head Turning on its way. The partner followed, also turning its head.



Figure 14: End of Circling with the head of the left partner in pear-shape and the right partner in a frozen stiff posture with all neck feathers raised, Big Pond, Pebble Island (2010).



Figure 15: During Circling, the partner on the right rises into the Plumb Penguin posture with the head in pear-shape, Big Pond, Pebble Island (2010).

Both grebes could face in opposite directions when one of them adopted the Plumb Penguin posture and then rotated on the water surface.

More generally, while in the Plumb Penguin posture, the two birds could mill around just as in Circling.

Neither Fjeldså's (1985) nor Storer's (1967b) descriptions of the courtship in mainland Whitetufted Grebes mention Plumb Penguin Dancing and they remain silent about how the Circling Displays could end. In the Falkland Islands, if no additional display followed, White-tufted Grebes dived and separated or they simply slowly drifted apart. Quite often, circling came to an end with simultaneous preening by both grebes (Fig. 16). This preening was less ritualized than for instance in Great Crested Grebes, but it was comparable to Habit Preening in Black-necked Grebes P. nigricollis. This could develop into real preening before the pair came to rest in the pork-pie posture. For the subspecies chilensis, Fjeldså (1985) mentioned that Habit Preening does possibly not occur. In the Falkland Islands, it was present, also outside a context of circling.

Courtship did not necessarily end after Circling or Penguin Dancing. Additional displays could succeed.

The displaying grebes could dive rather simultaneously and surface again at little distance for another bout of Circling or they could simply pivot slightly on the water surface before relaxing. Occasionally, both birds surfaced a bit apart. One bird could then adopt a Plumb Penguin posture and progress thus in the direction of the mate that had only slightly elevated its breast. On a few occasions, during Stiff Circling one partner adopted a Plumb Penguin posture and then passed underneath its mate. After surfacing, the partners continued their displays either with Plumb Penguin Dancing or resuming Stiff Circling.

After Circling, the partners could swim side by side or one behind the other into one direction. It is difficult to judge whether in all cases these movements can be considered as a display, but in some occurrences their posturing was obvious: **Parallel Swimming** (Fig. 17) occurred. The bearings adopted by the grebes were quite variable. Their bodies could be low on the water surface and sloping, the extended necks thin and



Figure 16: Habit Preening after Stiff Circling, Long Pond, Pebble Island (2010).



Figure 17: One way of Parallel Swimming, Big Pond, Pebble Island (2010).

the heads in Funnel look. The grebes could be higher on the water surface with vaulting backs and extended necks in high S-form, their heads pear-shaped. They could turn their heads while progressing. Occasionally, they even waggled their heads. At times, the Parallel Swimming was directed at single grebes or pairs in the vicinity. It was often directed towards a particular vegetated area at the shore. After a short distance side by side, mostly one partner took the lead. Once arrived, the vegetation was inspected. In a few cases, simultaneous diving and surfacing preceded or accompanied the Parallel Swimming.

Once, a kind of **Parading** and **Splash Diving** occurred during Circling performed by two White-tufted Grebes. In other observations of Splash Diving, always more than two grebes displayed together. At Laguna Isla, East Falkland, after Circling, two grebes were kind of Parading with fully stretched necks obliquely advanced, bills horizontal and head feathers sleeked. Moving parallel to one another, and then rotating slightly to one side or the other, they performed ticking movements with their heads. All of a sudden, both Splash Dived with a fold-in-the-middle dive

and surfaced some 3 m apart. They faced for a moment in the Parading posture and remained motionless. Then both repeated the Splash Diving. They popped up still well apart, but this time both swam together to perform Stiff Circling with their wings lifted. They finally drifted apart and preened.

The Bumping Ceremony of Falkland White-tufted Grebes included all elements that were described for mainland birds. After displaying on the open water surface, two grebes swam to a possible mating or nesting place and inspected it, pecking at the rushes here and there. Finally, they moved to side by side or to facing with their necks fully stretched and vertical and their ear tufts sleeked. They performed Head Turning and a bout of Habit Preening; they lifted some weeds, brandished them in their beaks and deposited them in Ceremonial Building. Stabbing was observed once before one grebe dived out of a posture with the neck fully stretched. It now either simply exposed its head for a short moment or it surfaced in the Bouncy posture, the breast protruding and the neck bent backward. In both cases, it dived again quickly and the partner followed its disappearance, arching its neck, inclining its head and, if necessary, slightly pivoting its body. The diving bird now popped up with the breast protruding and the neck folded to the back, thus **Bumping** the breast of its mate. During breast contact, it already fully stretched its neck upward as did its partner. Plumb Penguin Dancing breast to breast (Fig. 18) followed. The elongated necks of the birds looked thin and both grebes showed Head Turning and Head Jerking. In between, they briefly arched their neck backwards to touch the mantle with the bill in Habit Preening (Fig. 19). Then, one partner dived again to repeat the Bouncing and the Bumping. A maximum of six Bumping in a row were observed. They were performed by both grebes, however not necessarily in alternation. Once, the grebes engaged in Ceremonial Building between two Bumping and one partner still held the weeds in its bill when both engaged in mutual Head Turning. The last Bumping was followed by Plumb Penguin Dancing during which the grebes started to rotate while still turning their heads. They could now mill around, show Habit Preening or Ceremonial Building, Parallel Swimming or both simply departed one after the other.

Another display performed by all Podiceps species possibly exists in Falkland White-tufted Grebes, too. In four observations, Inviting on the open water surface may indeed have occurred. In the first case, after Plumb Penguin Dancing and diving, both grebes surfaced a bit apart. One partner, high on the water surface, retracted its neck in z-form with the head lowered forward as in inviting on a platform. With sleeked head feathers, the partner swam to its vent where it extended the neck vertically. Both maintained their respective postures briefly. Then they turned parallel and relaxed. In the second case, a grebe swam away from its partner into a small area of floating Pondweed where it halted. The mate followed and placed itself in front of the partner. Then it adopted a posture as if inviting and swayed its head. In continuation, the grebe in the back moved to its side and adopted a similar posture, also swaying its head, before both adopted the pork pie posture. In two cases, twice the same male swam towards an existing platform hidden inside an island of Tussock Grasses. The female hesitantly followed. In front of the vegetation, the male halted and adopted an inviting posture before it continued its way and jumped onto the platform where it Reared.

The displays themselves left room for much variation in their execution. In addition, the sequencing of displays observed differed greatly from one pair to the next and between two performances by a same pair. On Big Pond, Pebble Island, a succession of displays observed in 2010 was as follows:

A White-tufted Grebe Advertised and, thereafter, waited with the neck in high S-form, the head pear-shaped, the back vaulted and the tail cocked. In reply, a second grebe dived and swam in its direction. The waiting bird was pivoting on the water surface until the partner was closer. Then it adopted the Funnel look with fully stretched neck and upper neck feathers lifted. The wings were partially raised. The partner dived and surfaced directly in front of it. Both immediately started Stiff Circling with Wing Raising, moving from breast to breast to side by side. During the display, they performed Head Turning. One grebe rotated its back to the partner and rose into a Plumb Penguin posture with extended neck and retaining the Funnel look. Thus, it progressed a bit while pivoting its body and turning its head. The second grebe moved to its side and the first slowly lowered its posture. Both ended up with their bodies horizontal to the water surface and facing into the same direction. They relaxed their bearing and preened simultaneously. The courtship ended. After a short interruption, they started a new bout of Stiff Circling during which one grebe dived and passed underneath its partner. It surfaced again and both rose into a Plumb Penguin posture, dancing breast to breast. Then they turned parallel and Swam Parallel while retaining the posture. One partner now dived and the other followed. After surfacing, they started to swim one behind the other in the direction of a short ditch. Their bodies were sloping, their necks extended vertically, the neck feathers raised and the ornamental feathers rather relaxed. At the entrance to the ditch, they hesitated, fully stretched their necks, sleeked their crests and ear tufts, milled around and started to inspect the grasses of the shore. With ticking movements of their heads, they approached the vegetation here and there, bent their necks, lifted some weeds and deposited them again in Ceremonial Building. During the inspection, they remained close together. Occasionally, they inclined their necks for a short preening of the mantle feathers or the breast. Finally, one grebe hopped ashore, Reared


Figure 18: Breast to breast after Bumping, Big Pond, Pebble Island (2010).



Figure 19: Habit Preening after Bumping, Big Pond, Pebble Island (2010).

with Wing Quivering, but it did not Invite. The bird rather quickly returned into the water and both swam one behind the other back to the pond where they started feeding dives. On the next day, a pair, perhaps the same, after displaying on the open water surface entered the same ditch and performed the Bumping Ceremony.

Based on all observations, a complete ceremony of water courtship could start with Advertising that is followed by a diving and swimming approach. The partners meet for a bout of Circling, perhaps change from Stiff Circling to Circling or Plumb Penguin Dancing with Head Turning and Habit Preening. Then they dive or start Parallel Swimming. They move to the shore where they inspect the vegetation and, after Ceremonial Building, they engage in a Bumping Ceremony. Thereafter, the water courtship ends. It can be immediately followed by platform courtship.

4.2.3.2 Courtship in an aggressive context

Besides threatening, attacking or chasing in antagonistic situations, a pair could also choose to display. If a single rival or another pair arrived, the partners often engaged in Low Funnel Circling, then they turned to facing the opponent(s) and swam at it (them) with sloping bodies and necks fully extended vertically. They could also use any other kind of Circling, rise into a Plumb Penguin posture during Circling and swim at the other(s) in this posture. After territorial conflicts, mainland White-tufted Grebes may meet in Triumph Ceremonies as described by Fjeldså (1985): they then mill around in Hunched postures with their heads rather low and their wings more or less lifted. In this study, the corresponding displays of Falkland grebes were most often very short, either because they occurred during a short break in the territorial conflict or because at least one partner wanted to engage in platform courtship. The partners could start all four kinds of Circling as described for water courtship. The displays served to confirm the strength of the pair bond to the partners themselves and they demonstrated their union to the rivals. A few observations are described in more detail below.

On Big Pond, Pebble Island, pair A was resting close to the shore inside some rushes when pair B arrived in swimming. Pair A swam at the encounter of pair B with necks straight and obliquely advanced, one partner behind the other and zigzagging on its way. Both grebes were rather deep in the water with sloping bodies and alternated their head form between pear-shaped and Funnel look. Finally one bird dived and passed its mate below water. It surfaced close to pair B that meanwhile had stopped its progression, but milled around on the spot. The partners B swam together in the Funnel look and immediately rose out of the water for Plumb Penguin Dancing, breast to breast. Pair A retreated in swimming and one partner B dived out of Penguin Dancing into the direction of pair A that dived, too. Pair B resumed Plumb Penguin Dancing. Pair A approached again and also started Plumb Penguin Dancing. While dancing, one or both partners in both pairs could turn briefly towards the rivals. At times, the dancing was interrupted by Funnel Circling and diving. It finally ended when pair B started Parallel Swimming into the direction of the initial resting place of pair A. However, pair A moved parallel to pair B. As it was closer to the shore, it thereby blocked the access and pair B was pushed off. It was forced to progress in parallel to the shore. Having passed the resting place, pair B dived and surfaced only when farther out. Pair A returned to its initial place inside the rushes where both partners intensively preened.

On Swan Inlet Pond III, East Falkland, a third grebe approached a pair resting inside short rushes. It arrived, swimming with sloping body, its neck vertically extended and the ear tufts flared out. It rose into a Plumb Penguin posture and, once rather close, it adopted the Funnel look. In response, the partners flared out their ornamental feathers. With straight necks, they first hesitantly advanced in the direction of the trouble-maker, but then adopted the Funnel look and progressed with ticking movements of their heads. The third grebe dived away and the partners turned to face and milled around in a Hunched posture before going to rest again. After a short time, the third grebe returned and surfaced a bit to the side of the pair. One partner reacted by launching a short Patter attack and the third grebe escaped again in a long dive. The partner slowly moved back to its mate, preening on its way. Upon meeting, no Triumph Ceremony or other courtship followed.

Once, a paired male with a platform approached a second female that Advertised at the border of its territory. Both engaged in Stiff Circling with Wing Raising and Wing Quivering. Suddenly, the female mate showed up. Out of the display, the male launched a sudden Pattering attack at the strange female, chasing it above and under water before returning to its partner.

4.2.3.3 Group courtship

Besides the courtship performed by single pairs, on three occasions groups of five to six Whitetufted Grebes displayed on Big Pond, Pebble Island, in 2010. Most probably, it were three times the same birds. They displayed always rather close to the shore inside a bay of the pond. While all grebes were resting or feeding there, two birds fully stretched their necks, adopted a pear-shaped head and started to mill around. The other grebes joined in quickly and soon the entire group was Parading along the shore. The grebes moved to and fro with extended necks and ticking movements of their heads that were occasionally interrupted by Head Jerking. One or two dived now and then to change their position in the parade. The grebes could stop their progression and then start to move into the opposite direction. At times, the group seemed organized in twos. Then all grebes could stop, pivot a bit on the water surface and a majority of them simultaneously Splash dived. One or two grebes could not dive and these waited for the others to surface. This took a few seconds and all birds were up again, stretching their necks. Then, after remaining motionless for a second, another Splash Dive followed. This could end the displays. In one observation, two birds of the group continued to display and, after a short hesitation, the others joined, too.

In a few observations, two pairs engaged in a kind of mutual courtship. The Circling, Stiff Circling or Plumb Penguin Dancing by one pair attracted the attention of a second pair or, at least of one partner in this pair. With obliquely advanced neck, one grebe swam quickly in the direction of the displaying pair. It was followed in little distance by its mate. One displaying bird turned to facing and swam at the encounter of the other grebe. Both came together quite quickly for a bout of Circling that could even grade into Plumb Penguin Dancing while their respective partners waited in their back a few metres apart. Both then rotated towards their mates and returned to them. The original partners could briefly display together or one or both pairs departed in different directions. In one case, during Plumb Penguin

Dancing by one partner of each pair, one grebe stabbed with its bill at the rival and made it flee.

In the following, two examples for the course of events are given.

On Big Pond, Pebble Island, six grebes were close together inside a bay at little distance from the shore. The Circling of one pair attracted the attention of two other pairs that were at rest or feeding not far away. They approached the displaying grebes with their necks extended and obliquely advanced, showing occasional Head Jerking. Then all engaged in a kind of common Circling or milling around before they pivoted and Paraded one behind the other along the shore. Their necks remained fully stretched and thin, their heads were pear-shaped. On their way, they performed Head Turning and occasional Head Waggling. The progression of the group was not in a straight line and the grebes sometimes slowed down or pivoted. Then all remained more stationary, suddenly froze their bearing for a second and three grebes disappeared in a splashing fold-in-the-middle dive. Up again, all birds fully stretched their necks and seemed to look around. They finally pivoted and engaged in a kind of disorganized Circling and diving that ended with the group dividing again into three pairs. It was unknown whether during the display a change of partners had occurred.

At the pond between Laguna Isla and Laguna Ronda, three grebes engaged in rather parallel and synchronous diving in 2008. They surfaced three or four times, fully stretched their necks vertically and dived again. They remained close together and progressed rather steadily while doing so. Finally, they reached a bay where they stopped for a bout of Circling. The courtship ended and the group fed inside the floating vegetation. A similar behaviour was not observed again.

4.2.4 Platform courtship in the Falkland Islands

In continuation of water courtship, pairs often swam to the shore or they entered floating vegetation to inspect the nesting or mating possibilities. The partners remained close together, stopping here and there. They grasped some weeds with the bill, elevated their heads, inclined their necks again and deposited the weeds inside some rushes, onto floating Pondweeds, on flat beaches or in excavations on elevated shores. sometimes also simply on the open water surface. This Ceremonial Building could be repeated in turns with short Habit Preening in between. The pairs often milled around and deposited weeds at different places. In 2010, the grebes mostly placed the weeds either directly on land in areas with gently sloping shores or in pond shallows immediately adjacent to the shore that were overgrown with short rushes Juncus sp., sedges Carex sp or grasses Poaceae. The scenes were indicative of an intense search for a copulation place. Ceremonial Building was not seen to be followed by the construction of a real platform. In a few cases, one partner ran ashore, halted in upright posture, and then returned to the water without showing Rearing or Inviting.

Rearing, Inviting and Mounting happened either on a floating platform (Fig. 20-22) as in other grebe species or ashore, on firm ground (Fig. 23, 24), without that a platform was built. If hopping ashore, the White-tufted Grebes could walk a few steps before Rearing and they could again walk a bit before settling down for Inviting. Otherwise, Rearing and Inviting happened in a manner similar to other grebe species.

During Rearing, the Falkland White-tufted Grebe stood upright, high on its feet, with the neck bent downward (Fig. 20). Ornamental feathers were sleeked. Then the bird elevated its breast, raised its mantle feathers and simultaneously guivered with its wings while throwing the downcast head a bit to one side. This was repeated two or three times. The partner either waited in the back of the performer or milled around in the vicinity. It occasionally preened vigorously. Thereafter, the upright grebe settled down for Inviting either on a floating platform (Fig. 21) or on land (Fig. 23). With elevated vent, the tail cocked, the neck kinked forward and retracted, the ornamental feathers sleeked, the bird waited for its mate. Slightly turning its head in this posture and emitting soft calls, it seemed to observe the latter's reaction. If the mate hesitated before mounting, the Inviting grebe could grasp some vegetation and feign to arrange a nesting platform or it further lowered its head. At times, it again jumped onto its feet to Rear anew before resuming Inviting. Finally, the water bird decided to Mount. Uttering



Figure 20: Rearing on a floating platform inside Pondweeds, Bett's Pond, Pebble Island (2008).



Figure 21: Inviting on a floating platform inside Pondweeds with the partner ready to mount in the back, Bett's Pond, Pebble Island (2008).



Figure 22. Mating of Falkland White-tufted Grebes, Bett's Pond, Pebble Island (2008).



Figure 23: Rearing on land, Big Pond, Pebble Island (2010).



Figure 24: Inviting on land, Big Pond, Pebble Island (2010).

soft calls, it either swam to its partner's vent (Fig. 21) or it stepped ashore (Fig. 24), stretched the neck over its partner's back, flared out its ornamental feathers, swung its neck backward to take momentum, (shot out of the water) and jumped onto the back of the elongated grebe for copulation. The mounting bird's body remained obliquely advanced and its neck was extended and kinked forward over the head of its partner (Fig. 22). It finally dismounted upright, running over the mate's head. Occasionally, the inviting grebe rose fast and the mounting grebe was more thrown off than it stepped off.

Post-copulatory display: While the mounting grebe landed in the water with a splash (or without if copulating on land), the partner stood already high on its feet, the body rather vertical, the breast protruding and the folded wings slightly lifted. Its lower neck was folded back, the upper neck kinked sharply forward, so that the chin was above the elevated breast without however resting on it. The ear tufts were flared out. The posture was not unlike the Ecstatic posture of the Red-necked Grebe (Wobus 1964) in the same context. In contrast to the grebe on the platform, the mate held its fully stretched neck vertical. Its head was pear-shaped. If in the water, its breast was elevated and its body was sloping. It could pivot slightly in this posture. Both grebes showed Head Turning. Often, the water bird relaxed its posture quickly and swam away or preened while its partner maintained the Ecstatic posture, looking from one side to the other. It finally relaxed its bearing, arranged the nesting material before leaving a platform or walked back into the water. In one post-copulatory display, both grebes showed a short synchronized preening before separating.

As in other grebes, the platform courtship may be repeated several times in a row with or without a short bout of water courtship in between.

Copulation on land was common in the Falkland Islands' White-tufted Grebes. On one occasion, a rather curious course of events was recorded. On Big Pond, Pebble Island, after Stiff Circling, a pair for a while searched the shore. It showed interest for a kind of flat and narrow spit of land. One grebe walked ashore, Reared with triple Wing Quivering (Fig. 23) and then entered the spit for another metre. There, it Reared again before settling down. The partner followed ashore and walked until standing directly behind the inviting grebe. With its ornamental feathers sleeked, it bent its body and neck forward over the partner's back (Fig. 24), but it did not mount. Remaining upright, it rather clumsily turned around, also Reared with intense Wing Quivering (Fig. 25) and lay down facing in the opposite direction. The vents of both grebes were touching (Fig. 26). Both remained in this posture with their necks kinked forward. As in Mounting, they lowered their heads for about 10 seconds, apparently pushing their vents together and swaving their heads. Then, the first grebe arched its neck over its back so as to smell at its vent while the partner stood up. Thereupon, the first bird got up quickly and, in a sudden dash, it snapped at its mate. The latter escaped in running, jumping into the water and diving away. It was persecuted for a while by its mate. Fleeing, it reached the opposite shore, where finally both grebes came together again and soon started anew the inspection of the vegetation.

4.2.5 Other behaviours observed

White-tufted Grebes of the Falkland Islands were curious and readily approached if they saw me walking to the shore. If I simply sat down close to the edge of the water and remained quiet, they could come very close to mill around or to rest less than two or three metres away. Often, they uttered a short guttural "gt" or "gat", repeated several times in short intervals. The grebes possibly emit this call if upset. Juveniles were just as curious as adults. Only pairs caring for younger offspring were more prudent. From my observations of mainland birds in Bolivia and Argentina, I cannot recall a similarly unhesitating behaviour. On some occasions, individuals of the form chilensis also approached, but they did so mostly in diving and they always tried to hide as best as they could in between floating or behind emergent vegetation. In more populated areas of Buenos Aires, the grebes took less notice of humans. Nevertheless, they remained always at respectable distance. According to Fjeldså (1981a) and my own observations in 1998, the form *morrisoni* is shy and skulky.

Outside of a nesting context and in the absence of a need for defending an own territory, the form *rolland* was very gregarious. At Big Pond, Pebble Island, three pairs without a platform often rested together. One or both members of a pair could leave the group for feeding. A partner left alone or



Figure 25: One partner Inviting, the other Rearing on land, Big Pond, Pebble Island (2010).



Figure 26: Inviting on land by both partners that push their vents together, Big Pond, Pebble Island (2010).

returning in the absence of its mate stayed in close vicinity of the other pairs while waiting. Once, a grebe that arrived from far initially pattered over the water surface, then it flapped its wings and gained some 2 m in height. It landed quickly and finally settled down at some 10 m from the other grebes where it started to feed. At another occasion, a grebe in a bay was joined by a second bird arriving around the corner. Both moved together and preened now and then on their way. They met without any apparent greeting, but then stayed together to rest. Based on bill size, both were females.

5 Discussion: differences between Falkland Islands and mainland forms

The main purpose of the present paper is to compare mainland and Falkland Islands' Whitetufted Grebes. Already previously, the generally bigger size of the Falkland form was recognized and the measures of Grebes from the islands published by Blake (1977) show no overlapping with those of the subspecies chilensis given by Fjeldså (1981a, 2004) and Storer (in Blake 1977) for wing, tarsus and exposed culmen. Only R. r. morrisoni, averaging slightly larger and with a stronger bill than other mainland populations (Fjeldså 1981a), shows minor overlapping in culmen size, bigger Junín males equalling the sizes of short-billed females from the Falklands. Apart of the size dimorphism, descriptions in literature of chilensis generally do not differ in substance from those of *rolland*. In the field, differences in the plumages appear neither in breeding and non-breeding adults, nor in pulli, nor in immature birds. The continental *chilensis* populations are territorial and pugnacious although they sometimes crowd their territories somewhat together in places with much food, but few optimal nesting areas (Burger 1974, Fjeldså 1985). In morrisoni, the cryptic nest sites are well spaced and multiple-brooded pairs may maintain territories all year round (Fjeldså 1981a). The nominate form from the Falkland Islands is a solitary breeder, too, and monospecific colony formation has not been reported. However, as it may nest close to Silvery Grebes,

it is not excluded that a lack of suitable nesting habitat may lead to aggregated nesting in some places. Also, White-tufted Grebes from the islands seemed less pugnacious against conspecifics in the pre-nesting period than the continental subspecies.

The courtship activities of Podicipedidae are complex and appear to function in forming, maintaining and strengthening the pair bond. They have an adaptive value in insuring that a bird will mate with an individual of the same species. Similarity may be considered as indicative of a close relationship (Storer 1963). Besides many similarities, the behavioural comparisons based on field observations for the nominate form of the Falkland Islands and on indications in literature for the continental forms a priori revealed quite a number of differences.

In the water courtship, the following possible divergences were detected:

After Advertising, an underwater approach by both partners with turning side by side below the surface was not observed in the Falkland Islands.

The descriptions of Wing Raising (Storer 1967b) and Circling (Fjeldså 1985) do not mention any rising into a Plumb Penguin posture or Plumb Penguin Dancing as recorded in *rolland*. In continuation of Circling, the progression in a Plumb Penguin posture recalls the Circling and Rushing Ceremony of the Titicaca Flightless Grebe *R. microptera* (Fjeldså 1985). Fjeldså considered that this ceremony was the counterpart of the White-tufted Grebe's Bumping Ceremony.

Except for the Approach after Advertising and for the Bumping Ceremony, diving is absent from the displays in the continental subspecies, but occurs in relation to Circling and Parading in the Falkland Islands.

Storer (1967b) reported *chilensis* to skitter across the water with flapping wings and paddling feet, but apparently not in relation to any courtship. Fjeldså (1985) only mentioned a similar behaviour during aggression. His Pattering occurred with folded wings. The grebes in the Falkland Islands used skittering occasionally during the Approach following Advertising. Parallel Swimming is not mentioned for mainland White-tufted Grebes.

Fjeldså (1985) believed Habit Preening to be absent on the continent. It is clearly part of the courtship displays in the Falkland Islands. In comparison to other species, the Habit Preening observed was less ritualized than in most *Podiceps* species and could be close to that of Black-necked Grebes.

Inviting on the open water surface is not reported for the mainland form, but it occurred in the Falkland Islands.

According to Fjeldså (1985), during Advertising the call of *chilensis* is "chorrh". It appears to be quite different from the duck like quacking of *rolland*.

Platform courtship of the three forms could differ in two additional aspects, although Rearing, Inviting, Mounting and Post-copulatory displays are broadly identical in the subspecies:

In the islands' form, mating occurs regularly on land whereas mainland grebes seem to use always a floating platform.

A mating display during which the partners press their vents together is not described for *chilensis*. It is not known to what extend it occurs in the Falkland Islands and whether cloacal contact making insemination possible is established in it.

Two additional differences, one related to the antagonistic behaviour and the other to the placement of nests, were observed:

Chasing in the Swan posture was not reported for continental White-tufted Grebes.

Nests placed on firm ground do not seem to exist in the mainland forms.

Though there seem to be a number of differences between the subspecies, it is unknown to what extent the deviations in size and behaviour are relevant for speciation. The biological concept of a species is based on the idea that two parents belonging to different species, even if closely related, should be unsuccessful in producing fertile offspring. Speciation in birds almost entirely relies on an initial period of geographical isolation permitting to evolve geographical differentiation. After a period of divergence, the barrier may disappear or be crossed again and, if populations come into contact, the criterion of interbreeding is tested. However, when and as long as taxa remain completely separated in space, the criterion of reproductive isolation cannot generally be used (Price 2008). Helbig et al. (2002) proposed to give species status to closely related allopatric taxa if (1) at least one character is fully diagnostic (i.e. it forms a fixed difference between the taxa and differences between the taxa are of the same order as those seen among pairs of sympatric species), or (2) the taxa are statistically distinguishable by a combination of two or three functionally independent characters (colour, body size, vocalization, DNA sequences, ...). In a phylogenetic species concept, monophyly is determined using mitochondrial DNA and the borderline is put at the smallest diagnosable cluster of organisms within which there is a parental pattern of ancestry and descent (Price 2008). Both concepts at the end rely on the idea of reproductive isolation. If the latter cannot be tested directly, the likelihood of successful interbreeding is tested. Indeed, choosing to mate with one's own species is a critical feature of speciation. Bird watchers identify individuals to species based on plumages, behaviours, and vocalizations, size and shape, and so do the birds themselves (Price 2008). In allopatry, two populations would be identified as separate species if diverging sufficiently in one or more character traits.

In the case of Rollandia rolland, geographical isolation of the nominate form possibly exists since some 10,000 years and this period of time may have been enough to develop sufficient differences between the subpopulations. The distance of at least 500 km over open sea that separates the Falkland Islands from continental South America appears to prevent regular contacts between the subspecies. Reports about the continental forms showing up in the islands are exceptional. Thus, A. Henry (pers. communication) recorded a R. r. chilensis in the company of a R. r. rolland at Cape Dolphin, East Falkland, on 29 October 2005. In spite of the possibly occasional presence of continental birds in the islands, so far no common courtship or breeding and no offspring of intermediate or small size (as we could expect from a mixed mating) was recorded. Although this could be partially due to the lack of observers in the islands, based on our current knowledge, we have to assume a rather complete separation in space between the Falkland White-tufted Grebe and its mainland relatives.

As a consequence, the biological species concept cannot be used directly to determine a degree of assortative mating. Instead, we have to assess in how far identified differences in appearance and behaviour (that might need cross-checking with new observations in mainland subspecies) are diagnostic for speciation. Besides size dimorphism, a priori, three additional differences could be far reaching enough to prevent interbreeding of the subspecies.

The first concerns the placement of the nest. Burger (1974), O'Donnel and Fjeldså (1997) and Fjeldså (1981a, 2004) confirm that the mainland forms built floating nests away from the shore. Storer (1967b) is less precise and in one passage he writes of "two males which appeared to have nests approximately 5 m apart on a grassy island in the lake" without however insisting that the platforms were not floating. The nominate form regularly places its nest on firm ground. Especially the nests built underneath the bank of a pond or ditch and resembling cavity nesting could be problematic for the mainland forms.

The second difference could be a consequence of the first. On platforms located underneath the elevated bank and even on most platforms built on islands of Tussock Grasses, copulation is technically impossible or very difficult as the available space for mounting and for dismounting is too restricted. As such nesting platforms cannot be used for copulation, a second "platform" is needed. Storer (1963) considered that platform behaviour varies little in between grebe species and that interspecific differences are not of an adaptive value in preventing the formation of mixed pairs as pairs were formed prior to the start of this behaviour. The building of a second platform for copulation in itself is not abnormal for grebes. In the absence of suitable floating vegetation, this may have led to the development of copulation on land that nowadays occurs commonly in the Falkland Islands. It remains yet unknown whether the observation of a kind of common inviting by two White-tufted Grebes that thereafter push their vents together was an accidental event or whether it could occur more regularly. In the second case, it could also be critical for speciation and it could have evolved following platform courtship ashore. Mounting on a rigid underground puts a greater burden on the back of the inviting bird. It is then of advantage to replace at least reverse mounting and mounting by the male without insemination by a display with less risk of injury. It is questionable whether a mainland White-tufted Grebe could follow a twice as heavy Falkland partner ashore and the differences in weight might be another barrier to copulation on firm ground.

The possible obstacles to reproduction discussed so far only come into effect after two partners have achieved a good degree of acquaintance so that their pair bond is quite firm.. Therefore, their value as an argument for a split might be more debatable and the hurdle to mating not entirely insurmountable. The last argument concerns however the very start of pair bonding activities, namely Advertising. There, the calls used by continental and Falkland Islands' White-tufted Grebes seem to differ greatly. In North-American Aechmophorus grebes this call serving to attract an unpaired conspecific was identified as essential for assortative mating between Western A. occidentalis and Clark's Grebes A. clarkii (Nuechterlein 1981a) and contributed a major argument to the decision for a split of the two grebes formerly considered as colour morphs (AOU 1985).

Other differences encountered could be of lesser importance. If at some time in the future a more widely sympatric distribution of the subspecies was given, selective pressures could favour an accentuation of even these behavioural differences (Storer 1963). However, as the ritualization in the courtship of *Rollandia rolland* is poor in comparison to other grebe species, the subpopulations could react generally with greater flexibility or plasticity to them. A closer look at what has happened when two recognized grebe species that had evolved out of a common ancestral stem occurred again in sympatry may be helpful in this sense.

Within the family of Podicipedidae, there are a number of cases where, following a period of geographic isolation, two closely related species merged again at least part of their breeding distribution areas. In the following examples, all three endemic populations probably arose out of geographic isolation of stocks of the more widespread close relatives (Collar & Stuart 1985, Fjeldså 1984). All three were recognized as separate species with relatively small populations.

The Atitlan Grebe *Podilymbus gigas* of Guatemala was flightless and almost twice the weight of its close relative, the Pied-billed

Grebe *P. podiceps*, but otherwise quite similar in colouration (Hunter 1988). Possibly hybridization contributed to the extinction of the Atitlan Grebe (BirdLife International 2004, Hunter 1988).

The Rusty or Alaotra Grebe *Tachybaptus rufolavatus*, endemic to Lake Alaotra, Madagascar, and probably almost flightless, differed from the African Little Grebe *T. ruficollis capensis* by its pale eye, pale rufous-washed neck and dark under parts (Hawkins et al. 2000). In the course of the 20th century, the African Little Grebe became widespread on Madagascar and its hybridization with the endemic species may have played a role in the extinction of the Alaotra Grebe (BirdLife International 2004, Voous & Payne 1965).

At present, the endemic Madagascar Grebe *T. pelzelnii* declines in numbers whereas the African Little Grebe becomes more and more widespread on the island and it may hybridize with the Madagascar Grebe (Clotuche 2000, Collar & Stuart 1985).

In all three endemic species, hybridization with the widespread close relative possibly occurred. This insinuates that after their period of geographic isolation, behavioural and other differences apparently deviated not sufficiently to prevent mixed pair formation. However, in all three cases nothing is known about the breeding success of mixed pairs and about the fertility of possible hybrids. In addition, changes in the respective habitats of the endemic species impacted their global reproductive success and they were identified as prime reasons for the population declines. Interbreeding, if at all, possibly occurred only later when the small endemic populations were already collapsing and we might speculate whether hybridization had occurred to a relevant degree if population numbers had been stable.

Another example with so far a different outcome is provided by the North American Western and Clark's Grebes. In spite of their similar appearance and their largely sympatric occurrence, their mating is assortative (Konter 2009, Nuechterlein 1981b, Nuechterlein & Buitron 1998, Ratti 1979) although more recently, the numbers of grebes with intermediate character features may have increased (Konter 2009, 2011b). Similarly, sympatric Junín Flightless *P. taczanowskii* and Silvery Grebes developed character displacement rather than convergence on Peruvian Lake Chinchaycocha and their example shows that sympatric species segregate into ecological niches (Fjeldså 1981a, 1981b, 1983).

In the above examples, although hybridization may have occurred, in no case its extent alone was able to lead to a fast melting of two closely related species of grebes. Their later sympatric occurrence appeared to rather reinforce differences and we could expect a similar scenario for Falkland Islands' and mainland White-tufted Grebes.

Based on the size dimorphism between continental R. r. chilensis and the nominate form, several authors had already speculated that both might be distinct species (Fjeldså 1981a, Woods & Woods 1997) or at least did not exclude this possibility (Fjeldså & Krabbe 1990, O'Donnel & Fjeldså 1997). The present investigation adds behavioural differences of which at least one appears diagnostic. The study contributes thereby further supporting arguments for two separate species. The continued allopatry of the island and the continental forms might help to consolidate existing differences. In order to strengthen the present judgement, the behavioural differences found should be crosschecked by investigations in mainland Whitetufted Grebes. Size dimorphism could be tested by additional measurements of a greater set of grebe skeletons and skins available in all existing museum collections. Of greater value could be the sequencing of regions of the mitochondrial genome to investigate the phylogenetic relationships between the different forms of Rollandia rolland. In case that the outcome would not contradict the present conclusion, Fjeldså's and Krabbe's (1990) proposal for naming should be retained: the island form should be called Rolland's Grebe Rollandia rolland and the continental forms Whitetufted Grebe Rollandia chilensis. From the start, the population size of Rolland's Grebe would however be small and, thereby, the new species exposed to a greater risk of extinction. It would be classified as vulnerable and perhaps require an enhanced protection.

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