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# Colonial nesting in the Great Crested Grebe *Podiceps cristatus* (Linné 1758)

## Research results from a colony on the Dutch IJsselmeer in comparison to other studies on colonial nesting in the species

André Konter

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Travaux scientifiques
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*Podiceps cristatus* (Linné 1758), Fotos: A. Konter
1. Adult Great Crested Grebe, March 2005.
2. Clutch of four eggs, 22.04.2005.
3. Pullus, about two days old, 06.05.2005.

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A. Konter

# Colonial nesting in the Great Crested Grebe *Podiceps cristatus* (Linné 1758)

## Research results from a colony on the Dutch IJsselmeer in comparison to other studies on colonial nesting in the species

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Keywords: Great Crested Grebe, timing, synchrony, settlement, egg laying, egg parasitism, egg loss, clutch size, breeding success, nesting density, behaviour, aggression, competition, habituation.

### Abstract

In a study over five years of aggregated breeding in a population of Great Crested Grebes *Podiceps cristatus* at the Compagnieshaven of Enkhuizen on the eutrophic Dutch IJsselmeer, it appeared that this phenomenon there was imposed upon the birds by the abundance of food coupled with a scarcity of nesting sites. The arrival and the incubation processes of the different pairs were rather asynchronous. From the start of settlement, the grebes used the entire habitat available and later arrivals had to insist to gain access to the site. This led each year to a gradual decrease of distances between neighbouring platforms ending up at minima of 20 cm only and averages of about 2 m. Other studies confirmed the resulting rather long lasting nesting process. However, in very small colonies or in mixed colonies with more aggressive species, the grebes could be more synchronous.

Clutch size at Enkhuizen displayed a seasonal decrease. This trend was only partially confirmed by other studies so that no simple relationship such as early occupancy of breeding sites by experienced birds laying bigger clutches and later settlement of inexperienced grebes laying smaller clutches appeared. In addition, egg loss and parasitic egg laying impacted clutch sizes, especially under adverse weather conditions. Different comparative studies available suggested that the breeding success of colonial grebes could be superior to the one of solitary pairs on the same lake so that aggregated nesting was beneficial.

Fierce territory defence by established pairs was detected as a main cause for the extended building up process of the colony in Enkhuizen. Ethological data provided evidence for a gradual habituation to close neighbours in settled grebes. Especially with clutch initiation, aggression levels fell.

Situating the coloniality of the Great Crested Grebe in a more general evolutionary process, it was found to agree rather well with early stages of aggregated nesting and the definition of the nominal colonial breeder of Siegel-Causey and Kharitonov (1990). Indeed, consequential features of aggregation that allow limiting the associated costs appear to be hardly developed.

## Zusammenfassung

Eine Fünf-Jahres-Studie im Compagnieshaven in Enkhuizen am eutrophen niederländischen IJsselsee über gruppiertes Brüten beim Haubentaucher *Podiceps cristatus* ergab, dass dieses Phänomen den Vögeln dort durch ein reichhaltiges Nahrungsangebot, gekoppelt mit einem Mangel an Bruthabitat aufgezwungen wurde. Ankunft und Brutfortschritt der einzelnen Paare verliefen eher asynchron. Vom Beginn der Besiedlung an besetzten die Lappentaucher das gesamte zur Verfügung stehende Habitat, und später siedelnde Paare mussten ihren Zugang zur Kolonie hartnäckig erstreiten. Das führte jedes Jahr zu saisonalen Verringerungen der Distanzen zwischen benachbarten Plattformen, die am Ende mit minimal 20 cm und im Mittel mit etwa 2 m sehr gering waren. Auch andere Studien bestätigten den sich daraus ergebenden langwierigen Brutfortgang innerhalb der Kolonie. Allerdings konnten in recht kleinen Anhäufungen oder in gemischten Kolonien mit aggressiveren Vogelarten die Haubentaucher mehr synchron sein.

Die Gelegegröße nahm in Enkhuizen saisonal ab. Diesen Trend bestätigten andere Studien nur teilweise, so dass kein einfacher Zusammenhang mit etwa frühem Siedeln erfahrener Paare, die größere Gelege tätigen, oder späterer Ankunft jüngerer Haubentaucher, die weniger Eier legen, gefunden werden konnte. Die Gelegegröße wurde zusätzlich durch Eiverluste und Nestparasitismus beeinflusst, dies insbesondere bei widrigen Wetterverhältnissen. Verschiedene vergleichende Studien ließen den Schluss zu, dass der Bruterfolg von Kolonienbrütern größer als der territorialer Paare auf dem gleichen Gewässer sein könnte, so dass das Zusammenbrüten vorteilhaft für die Haubentaucher wäre.

Das starke Territorialverhalten etablierter Paare war Hauptursache für den langwierigen Besiedlungsprozess in der Gruppierung von Enkhuizen. Ethologische Daten wiesen auf einen graduellen Gewöhnungsprozess der Haubentaucher an nahe Nachbarn hin. Besonders mit Beginn der Eiablage reduzierte sich die Aggressivität deutlich.

Bewertet man das derzeitige Kolonialverhalten der Haubentaucher in einem evolutionären Rahmen, so scheint es sich in einem noch recht frühen Stadium zu befinden, das dem der Definition von Nominal-Kolonien (Siegel-Causey & Kharitonov 1990) entspricht. In der Tat scheinen weiterreichende Anpassungen, die sich mit der Zeit als Konsequenzen aus dem Minimieren der Kosten des Zusammenbrütens ergeben, noch kaum entwickelt zu sein.

## Résumé

Dans une étude sur cinq années portant sur la nidification groupée dans une population de Grèbes huppées *Podiceps cristatus* à l'intérieur du Compagnieshaven d'Enkhuizen au lac eutrophe néerlandais IJssel, il est apparu que ce phénomène était là imposé aux grèbes par une surabondance de proie relative à la pénurie d'habitat de reproduction. L'arrivée et la nidification des différents couples d'oiseaux étaient plutôt asynchrones. Dès le début de la colonisation, les grèbes utilisaient l'entièreté de l'habitat à leur disposition et les retardataires devaient insister pour gagner une place à l'intérieur de la colonie. De ce fait, chaque année les distances entre plateformes avoisinantes se réduisaient au fil du temps atteignant des minima de 20 cm et des moyennes d'environ 2 m seulement. D'autres études confirmaient la longue durée du processus de reproduction qui en résultait pour les groupes. Néanmoins, elles trouvaient une plus grande synchronisation à l'intérieur de petites colonies ou dans des associations de grèbes avec d'autres espèces plus agressives.

La taille des pontes d'Enkhuizen montrait une décroissance saisonnière. Cette tendance n'était que partiellement confirmée par d'autres études de sorte qu'une simple relation entre par exemple une occupation première du site par des couples expérimentés pondant plus d'œufs et un établissement plus tardif de grèbes inexpérimentés ayant des pontes moins importantes ne pouvait être établie. En plus, les pertes d'œufs et le dépôt parasite d'œufs affectaient la taille des pontes, surtout suite à des périodes de conditions climatiques défavorables. Différentes études comparatives suggéraient que le succès de reproduction des Grèbes huppés à l'intérieur des colonies pouvait être supérieur à celui des congénères territoriaux du même lac de sorte que la formation de groupes pouvait être bénéfique.

Le comportement agressif en défense du territoire des différents couples était une cause majeure de la durée étendue que prenait l'établissement de la colonie d'Enkhuizen chaque année. L'étude de données éthologiques détectait un processus d'habituation aux voisins directs des grèbes établis dans le courant de la saison. Surtout après l'initiation de la ponte, le niveau d'agression des couples se réduisait.

En jugeant les colonies des Grèbes huppés par rapport à un processus évolutionnaire plus général, elles paraissent convenir assez bien à un stade peu avancé de nidification groupée qui correspondrait aux colonies de nom de Siegel-Causey et Kharitonov (1990). En effet, les particularités conséquentes de l'attroupement qui permettent de limiter les coûts y associés semblent à peine développées.

# Introduction

Most birds, Aves, are socially monogamous because extensive bi-parental investment has been favoured throughout most of their evolutionary history. Their breeding systems cover a wide array of variable forms, from isolated over colonially and communally to cooperatively and parasitically (Ligon 1999). About 13% of all species nest in an aggregated manner (Lack 1968). Especially in seabirds, gulls Laridae and terns Sternidae, the formation of huge breeding colonies by generally monogamous pairs is not unusual and has triggered a lot of interest in humans. Such aggregated nesting may have different motivations. While a global lack of breeding sites or of prime nesting habitat may force birds to breed together at close range, this may not provide direct advantages or even disadvantages for the breeders. More often however, colonial breeding is not neutral and the nesting community as a whole may be affected in different ways. Protection against predators for the adults, their eggs and their chicks could be enhanced, either by profiting from the advantages in number or from association with more aggressive species. Under such conditions, generally the breeding effort of the entire colony concentrates in a rather short lap of time; breeding is said to be synchronous. Colonies can also function as a kind of information centre for food locations, permitting all inhabitants to take advantage from a food resource that is locally abundant, but unequally dispersed and therefore difficult to spot. Possible disadvantages of aggregated nesting are related to sharing of food resources that could occasionally become scarce, easier detection of the assembled birds by predators, mate infidelity, intra-species brood parasitism, and infanticide. They will not impact all members of a colony equally although, at the level of a population, one may expect the profits to outweigh at least the costs.

Grebes Podicipedidae have become independent of firm land by building floating nests and back-brooding their young. The 22 species of grebes, of which three might be extinct, form at least seasonally monogamous pair bonds (Fjeldså 2004). The monogamy might be genetically conditioned (Ligon 1999). Otherwise, their breeding behaviour ranges from highly gregarious and colonial to extremely solitary and aggressive. While the South-American Hooded *Podiceps gallardoi* and Silvery Grebe *P. occipitalis* or the Palaearctic Black-necked Grebe *P. nigricollis* occupy the colonial end of the nesting spectrum, the Slavonian Grebe *P. auritus*, the Red-necked Grebe *P. grisegena* and all *Tachybaptus*-species are generally fierce defenders of individual territories and they are therefore found at the opposite end. Generally during pair formation, the partners try to isolate themselves and to find a vacant place with no other grebes. Thereafter, the pair attempts to prevent conspecifics from entering the area. This normally leads to territorial spacing of nests which is often associated with individual food exploitation. The nest spacing must however often be balanced against a limited supply of safe nesting sites (Fjeldså 2004).

During the first half of the 20th century, the nominate Great Crested Grebe *P. cristatus cristatus* was known in most parts of its range mainly as a solitary breeder. However, the species also formed colonies and aggregated nesting has been reported to exist since quite some centuries. Following the nearly extinction of the species in major parts of Eurasia late in the 19th century as a consequence of shooting for grebe fur, numbers on most waterbodies were probably too low to trigger colonial associations. Only the introduction of protective measures in many countries allowed a recovery of the species. In the course of the second half of the 20th century, a generally increasing eutrophication of water qualities favoured an increased occurrence of especially cyprinid fish. The parallel explosion in population numbers of Great Crested Grebes may have favoured the appearance of aggregated breeding at many locations. At the same time, anthropogenic pressure on wetlands increased and possibly reduced the surface of the habitat effectively available to the birds. Nowadays, colonies of Great Crested Grebes are reported from all over the species' range, from the UK and the Netherlands to the Caucasian Republics and Russian Siberia. The number of aggregated nests varies from just a handful to several hundreds. In some regions, the Great Crested Grebes appear to switch rather easily from solitary to colonial breeding and vice-versa. But even if grouped nesting occurs, the species seems to retain its reputation of being rather aggressive and pugnacious against conspecifics, especially early in the breeding season when the territories are established. This trait of character seems to contradict the formation of colonies, colonies in the sense humans usually tend to understand them; from true colonial species, we expect cooperative or social components to play a more or less important role. This a priori is not the case in the Great Crested Grebe and we may then ask how a possibly predominantly solitary breeder comes to establish colonies? What brings about the aggregated nesting and how does such a group form? Are ecological reasons taking the lead and are social aspects playing any role? Is individual aggressiveness overcome in time and, if so, how? What could be consequences, advantages and disadvantages of colonial breeding in the Great Crested Grebe? To answer these questions, colony establishment and nesting progress in the species was studied at the Dutch Lake IJssel (IJsselmeer).

The first time a colony of Great Crested Grebes was described in the Netherlands was in 1923 and the site was located where formerly the river IJssel reached the Zuiderzee. After cutting the area from the open sea through the construction of a dam in 1932, the waters more and more sweetened and slowly permitted increased aquatic vegetation growth. Since then, the region has built up a tradition with respect to the occurrence of aggregated nesting in the Great Crested Grebe and in 1978, eleven colonies of Great Crested Grebes holding a total of over 1,000 nests were reported from the area that was now called Lake IJssel (Vlug 1980). One of the today's colonies, located inside a harbour and of easy access, was monitored during five successive breeding seasons, focusing on ecological and behavioural parameters. Research concentrated on arrival patterns, progress of site occupation and spacing of platforms, clutch initiation, clutch completion and variation in clutch size, aggression levels in general and the evolution of the aggressiveness in established pairs in time. Aiming at reaching a common understanding of the phenomenon in the species, the findings were compared to the results of several other studies that have dealt with coloniality in the Great Crested Grebe.

Throughout the study and in agreement with the proceeding of the other researchers, a simple definition of colonial breeding in the species was applied. Colonies consist of densely distributed nesting territories that contain no other resource than nesting sites (Perrins and Birkhead 1983 in Rolland et al. 1998), and the inhabitants have to leave the area for feeding (Wittenberger and Hunt 1985). A distance criterion of on average 10 m or less between nest platforms was used for designating a group as a dense aggregation of nests (Goc 1986). Only later, we will discuss how the breeding aggregations of the species compare to more theoretical definitions of colonies in birds.

# 1 Study area and methods

## 1.1 A short description of Lake IJssel

Lake IJssel appeared in 1932 when a dyke of a length of 29 km was built in the Northern Netherlands to separate a former bay of the North Sea called Zuiderzee from the Waddenzee in order to better protect the coastal line. From then on, the tides no longer regulated the water levels there. In 1975, a second dyke, the Houtribdijk between the cities of Enkhuizen and Lelystad, split the now isolated water surface in two distinct parts, in the north the IJsselmeer or Lake IJssel and in the south the Markermeer. The two lakes remained connected by locks at both ends of the dyke. It is noteworthy that local people, including Dutch ornithologists, even today very often designate by the term Lake IJssel the combination of both subdivided areas. Unless when referring to the articles of others, I will always clearly distinguish between the IJsselmeer and the Markermeer.

Located at the level of the sea, both lakes are mainly supplied with water by the rivers IJssel and Vecht. Two artificial locks permit the exchange of waters with the Waddenzee. The shallow Lake IJssel covers approximately 1,225 km$^2$ and its sandy bottom is rather flat. Its depth is generally comprised between 2 m and 5 m. Especially along the north-eastern shore, extensive sandy shallows, less than 3 m deep, can be found. Some deeper parts in the centre reach 7 m. Today, the lake is mostly used for sailing and surfing and, to a lesser extent, for commercial fishing. Lake Marken (Markermeer) covers an additional 700 km$^2$.

Lake IJssel is eutrophic and has large fish stocks (Piersma et al. 1997). According to Willemsen (1983 in Piersma et al. 1997), the fish biomass per

**Fig. 1:** View of the Footbridge colony on 7 April 2007 with on the right the footbridge, on the left the dam, in the background the restaurant delimiting the area and in between, part of the Bulrush vegetation and the Reed areas.

ha is 300-500 kg. The results of a sampling exercise detected Smelt *Osmerus eperlanus*, representing 56% of total numbers caught and 90% of surface catches, as the dominant species in numbers of the fish community. Bream *Abramis brama* contributed 67% of the fish biomass, but occurred mainly along the bottom (Piersma et al. 1988). Other common species are Roach *Rutilus rutilus,* Ruffe *Gymnocephalus cernuus*, Perch *Perca fluviatilis* and Pikeperch *Stizostedion lucioperca* while Eel *Anguilla anguilla*, Three-spined Stickleback *Gasterosteus aculeatus* and Flounder *Platichthys flesus* occur more seldom. Not surprisingly the diet of the Great Crested Grebes is composed for 85% of Smelt. Ruffe (9.3%) and Perch (4.5%) make up for most of the rest (Piersma et al. 1997). Consequently, the water body harbours good numbers of fish-eating birds during the breeding and the winter season. Before the lake was separated from the sea, emerging macrophytes permitting the construction of grebe nests were largely absent. The gradual reduction in salt content of the waters in time produced the conditions favouring the growth of emerging vegetation. Due to the from the start existing limitations in nesting space, piscivorous birds, even if not particularly colonial, generally formed more or less extended aggregations when breeding.

## 1.2 The study site

The study site itself is located inside the yachting harbour of Enkhuizen, the Compagnieshaven. This city extends in the south-west of the IJsselmeer or at the western end of the Houtribdijk separating the IJsselmeer from the Markermeer. The harbour has a direct access to Lake IJssel that is limited to an opening of some 30 m permitting the boats to enter and to leave it.

The harbour holds three different groups of nesting Great Crested Grebes that are clearly separated by their location. In the west, to the side of the city, the City colony extends. At the northern edge, close to the Buitenmuseum and the boat entrance, is located the North colony. Finally, in the east along a small dam separating the harbour from Lake IJssel, we find the Footbridge colony (Fig. 1) and target of our study. The term colony is applied to these aggregations of breeding grebes in the sense of Goc (1986), who arbitrarily defined a colony in the species as where a group had an average distance of 10 m or less between nest platforms.

As already said, the Footbridge colony was protected in the east by a small and vegetated dam, 320 m long and of difficult access for humans. Inside the harbour, more or less parallel to the dam and in a distance to it of maybe 5 m in the south and 10-15 m in the north, a footbridge ran. The latter, together with a perpendicular quay connecting the dam to the footbridge in the north and a comparable connection by a restaurant closing the surface in the south, prohibited access to the boats to this part of the water surface, where the third group of Great Crested Grebes had chosen to nest.

Before starting the research program in 2003, the area delimited by the dam, the quay, the footbridge and the restaurant was mapped to a 1:100 figure. On the dam side, emergent vegetation could be divided into three vegetated zones. Reed I, about 100 m long, was a stretch of reed *Phragmites australis*, covering some 300 m². The width of the vegetation accessible to the grebes for nesting varied between 1 - 6 m. Especially, the southern half of Reed I, Reed IA (ca. 70 m long), was very narrow and allowed the grebes to enter the vegetation for a maximum of 1-2 m. The northern part, Reed IB, widened more and more, finally reaching about 6m accessible to the grebes. Reed I was separated from Reed II by an open area of 7 m in length. Reed II was 86 m long and covered approximately 350 m². Its width varied between 2 - 6 m. In the southern part Reed IIA (ca. 40 m long), the stands of reed were sparser and the width of the vegetation was generally close to 2 m. Reed IIB was wider and denser. Reed II was followed by 30 m clear of emerging vegetation, except for a small stand of water lilies *Iris ssp*. and some grasses along the shore. Then, the bulrush zone extended for 72 m, covering some 200 m² with *Typha latifolia*. It had a maximum width of 6 m for the first 12 m and of only 2 m thereafter. An open area of some 25 m followed and reached to the quay. The vegetation was cut back by the harbour authorities in every autumn so that the vegetated areas of the colony only changed marginally in shape in the course of the five-year study. However, their quality for nesting was not the same from year to year, mostly as a consequence of winter and early spring weather conditions. Only in 2006, a narrow stretch of some 20 m in Reed IA remained inaccessible to the grebes: during excavation works inside the harbour in early March of that year, sand and mud was deposited there on the dam and completely buried the small line of reeds. The stretch remained affected in 2007.

The footbridge ran alongside the entire nesting area of the Footbridge colony, where the closest platforms were built at a distance of only 1 m and the most distant were at maybe 10 to 12 m. This pathway was also elevated for a bit more than 1 m with respect to the water surface so that the observer had an excellent visibility. In addition, the grebes settled early in the season and started egg laying early, too, so that the new vegetation growth did not obstruct the view to detect newly built platforms and nest contents. Only in late April, a limited number of more remote nests could no longer be checked. The observers could move freely on the footbridge to obtain the best viewing angle using Zeiss 10x25 binoculars. As the nesting grebes had been accustomed for years to the presence of people on the footbridge, mostly boat owners, but also local people, there was no disturbing effect whatsoever of the monitoring program on the breeding of the birds.

Additional indications about the study site can be found in Konter 2005 and 2007:1.

## 1.3 Timing of the study

Data collection was scheduled to happen mostly over weekends, generally starting around mid-afternoon on Fridays and lasting until midday on Sundays, except for 2003 when the weekly program each time covered two days only. Exceptionally, a round of observation could also be organised in the middle of the week or could be extended by adding a public holiday.

In 2002, the site of the colony was visited three times for preparative planning and application of authorizations from the harbour management. In 2003, the first year of the study, a total number of 11 weekends were retained for data collection at the colony. After an initial visit to the site by J. J. Vlug on 27 February, the program itself was executed on 9, 15, 16, 22, 26, 29 and 30 March, 4, 5, 12, 13, 17, 18 and 30 April, 1, 7, 8 and 17 May and 6

June. The author spent a total of 95 hours with the colony, the two other observers involved in 2003 contributed an additional 30 hours.

The timing of the 2004 program was more restrictive from the beginning. In 2003, the new vegetation growth had reduced the visibility on the platforms from early May onwards and, with the start of hatching in late April and its amplification in early May, the number of occupied platforms had diminished quickly after the first May-weekend. It was therefore decided to stop the 2004 program around mid-May. Building on the experience gained in 2003, data collection weekends were also more spaced. The program was run over 4 weekends only on the following days: 31 March, 1, 2, 3, 23, 24 and 25 April, 7, 8, 9, 18 and 19 June. The author spent 64 hours in total with data collection. The contribution of other participants focused on double-checking and the collection of clutch data during an estimated total of 30 hours.

In 2005, it was decided that ethological data should be collected with a different method requiring a greater time effort. The program was scheduled in total over nine weekends mostly covering three days. Most times, two and sometimes three observers were present on 12, 18, 19, 20, 24, 25 and 26 March, 1, 2, 8, 9, 15, 16, 17, 22, 23, 24 and 30 April, 1, 6, 7 and 8 May. Recording by the author took a total of 118 hours and the efforts of the other contributors added an additional 100 hours.

Due to the long lasting winter, the 2006 program was reduced to six weekends run on the following dates: 17, 18, 19, 24, 25 and 26 March, 6, 7, 8, 9, 15, 16, 17, 28, 29 and 30 April, 5, 6 and 7 May. The author spent 86 hours and the other two participants together another 86 hours with the colony.

In 2007, a short program permitted to check colony size, density and nest contents. On the weekends of 7 and 28 April and of 4 May, three observers spent a total of about 100 hours inside the harbour.

## 1.4 Participants in data collection

In 2003, J. J. Vlug, a renowned specialist on grebes, participated actively in the program on most days and contributed with valuable advice at its early stages.

M. Konter was present in all five years on about two thirds of the days. She has a good knowledge of grebes stemming from 10 years of common grebe observations with the author.

G. Laroche, a member of the LNVL's field ornithologists group, was involved in the program from 2004 to 2007. He was present for about 90% of the program days.

The author was present during all observation days with the exception of 27 February 2003 and 12 March 2005 when J. J. Vlug, respectively G. Laroche undertook a quick check of the situation in the colony before the program itself was started for both years.

On all program days, a minimum of two observers/ data collectors were present. All participants received clear instructions on their duties and on how to fulfil them from the author before any recording was started.

## 1.5 Data recorded and methods

### Ecological data

Counts of grebes: - Complete harbour counts: especially early in the 2003 season, at least one complete count per weekend of all grebes present inside the harbour, including birds present at the boat entrance, was executed. The greater distances of the North and the City colonies to footbridges inhibited accurate counts there later in the season when the grebes remained more inside the vegetation. The numbers counted were recorded separately for the three colonies and for birds just outside the harbour. A limited number of complete harbour counts were also performed in 2004 and 2006.

- Counts at the Footbridge colony: at least twice per observation weekend, the grebes present at the Footbridge colony were counted. The counts were organised by subdividing the colony into the stretches Reed IA, Reed IB, Reed IIA, Reed IIB and the Bulrush zone. For each section or zone, the grebes were separated in birds at either side of the footbridge considering that grebes present on the vegetation side of the footbridge probably had already settled whereas those counted at the harbour side were still lacking a platform.

- Traffic of the grebes between the harbour and Lake IJssel: in 2003, the traffic of grebes between the harbour and the lake was regularly recorded for durations of 30 minutes each time. Incoming and outgoing birds were recorded separately and pairs were counted in a different column from individuals.

Mapping of platforms: During each observation weekend, all platforms were registered at least once on a new 1:100 map of the area that already contained in light markings the locations of the platforms from the preceding mapping. If an observation round extended over more than two days, the mapping was always executed twice, occasionally even three times. The quality of each platform was noted down distinguishing between loose heaps, basic platforms and solid platforms and the presence of grebes and their activity (simply present, building, inter-specific and intra-specific competition for the platform, incubating) were recorded. This way of proceeding helped to detect all pairs that held more than one platform at a certain moment in time.

Date of platform start: For platforms that appeared during an observation weekend, their date of initiation was known. Platforms recorded during the first mapping of a year were supposed to have been built on that weekend. For later platforms appearing between two observation weekends, the start of building was estimated by applying the following rules: 1. A solid platform registered for the first time when starting the observations on a weekend was supposed to have been started right in the middle of the end of the previous observation weekend and its day of registration. 2. When the registered platform was basic, we supposed it to have been started two days before its day of registration. 3. When it was only a loose heap, its start of building was said to be the day of its registration.

Start of egg laying and clutch size: All data about egg laying and evolution of clutch size for each single nest were recorded continuously during the presence of observers at the site of the colony. Therefore, often the precise day and for some nests even the precise time of laying of individual eggs was known. A limited number of platforms needed special guarding by an observer in order to come to know their content. The elevation of the footbridge, the short distances to most nests and the limited vegetation growth until the end of the yearly programs generally permitted to easily look inside the nests during change-over or momentary rising of incubating birds. For some nests, clutch initiation was observed. For others, the day of laying of one particular egg in the clutch was known. The clutch initiation date was then calculated based on the asynchrony in egg laying by deducting from the observation date a time interval of 1.5 days (indications about egg laying intervals vary between a bit more than one day and two days in literature) per egg already inside the nest before it received the egg for which the date was known. In the absence of such indications, egg colour in the clutch was used. An egg with a bluish shine was supposed to have appeared during the day it was found. A completely white egg was treated as being one day old. Clutches with all eggs stained could not be dated.

Egg loss: Records of egg loss were either episodic or indirect. Direct observations of egg loss and the causes identified were noted down with precise indication of the nest concerned. Reductions in clutch size from one observation day or weekend to another were obtained by comparison of individual nest data.

Full clutch size and related analyses: For full clutch size, only those nests were considered where egg laying had definitely stopped when the program of the year was ended and where for at least three days no eggs had been added. The knowledge about the story of individual platforms permitted to analyse clutch size with respect to the dates of platform initiation and clutch initiation and with respect to the degree of clumping. With respect to clutch initiation, the data of full clutches were classified in three categories: date of first egg laying before 11 April, in the second decade of April and later. As in 2005, in the night from 8 to 9 April a storm destroyed most of the existing platforms, whether containing eggs or not, related data were analyzed separately. With respect to the start of platform building, full clutch sizes were classified in four categories depending on the date of platform initiation: start of building in March, in the first decade of April, in the second decade of April and later. The analyses concentrated on the reed parts of the colony as the number of platforms in the bulrush were too limited to warrant valid results.

Parasitic egg laying: Based on all the data about egg numbers recorded, the laying patterns of the grebes were analysed with respect to indications for possible brood parasitism. Eggs were identified as possibly parasitic if an average laying interval for a clutch or an interval between two eggs in a clutch of less than 24 hours was detected or if the addition of late eggs occurred more than 48 hours after laying of the previous egg. Data of 2005 and 2006 were sufficiently detailed for the analysis as nest contents were recorded up to three times per observation weekend.

Incubation time indications: They were all from clutch initiation date to the day of hatching of the first chick.

Hatching information: Information on hatching success was generally scarce in this study, mostly because the families left the harbour once all pulli had hatched, but also because in most years, the program ended before the major hatching periods. For hatching observations, numbers of pulli hatched and numbers of eggs still incubated were noted down continuously. As hatching of an entire clutch took generally longer than the time reserved per observation weekend, hatching information remained mostly partial.

Breeding success: Breeding success could not be assessed at all as for the rearing of chicks, the families left the harbour and mixed up on Lake IJssel with families from other breeding places.

Story of individual platforms: At the end of each year, all data and annotations related to every single platform were assembled to establish their individual chronology of events.

Distances between nests: Based on the registrations on the individual maps, the distance between centres of neighbouring platforms was measured with a ruler for each date. From the value obtained, 40 cm were deducted to cater for the average diameter of a Great Crested Grebe platform so that the distance retained was from edge to edge of two neighbouring constructions.

Clumping of nests: The degree of clumping of a particular nest was expressed by the number of neighbouring platforms located within a distance of three meters from it (Konter 2004). The degree of clumping at a particular spot of the colony corresponded to the number of nests that could be aggregated so that each platform in the group had at least one distance to one other nest in the group equal or inferior to three meters. For the evolution of clumping within a nesting season, the measures were taken based on the nests existing per observation weekend. When expressed more generally, clumping represented the measure at the moment in time when the maximum density for the colony was reached. The latter expression did not consider differences in platform or clutch initiation dates of the different platforms thus clumped. It was rather based on the idea that even if platform or clutch initiation was early when the degree of clumping was less, the final degree of clumping may represent more adequately the settlement pressure on a particular nest or inside a particular stretch.

Recording of the effects of a storm: During one observation weekend in 2005, a storm blew over the colony and the research program was amended so as to get maximum knowledge about its effects. On the afternoon of 8 April, just before the storm came up, a regular mapping of all platforms was executed. In the morning of 9 April, the storm had calmed down. On that day, the situation of the colony was mapped twice, once in the early morning hours before 7 a.m. and once at 2 p.m. For six nests under special observation, details of the reaction of their owners were obtained. Methodological indications about these records are given under Ethological data.

## Ethological data

While some ecological data also pointed indirectly to behavioural aspects in colony establishment, the ethological data described below tried to directly measure aggressive behaviour and changes thereof in the colony. Besides of taking notes of interesting episodes, three different kinds of records were taken.

Number of fights between grebes: All aggressions between two or more grebes in the colony that involved physical contact and observed by chance by the author solely were recorded for each observation day. They were added up for each weekend and divided by the observation time to obtain the average numbers of fight per hour.

Level of aggression in a particular sector: In 2003 and 2004, the numbers of aggressions in a particular sector of the colony, the northern half of Reed II, Reed IIB, were recorded regularly for time periods of 15 minutes each. Intensive threatening, pursuit, under-water pursuit and fight by all grebes present in the section, whether already settled or trying to intrude, were noted down separately. Intense threatening included prolonged directed threatening with extended and lowered neck, threat chasing (a threatening grebe swims slowly and for a very short distance in the direction of one or two other grebes which thereupon change their direction), threatening provoking a reaction by the rival, prolonged facing while threatening and token diving. In a pursuit, a threatening grebe makes a fast and continued pursuing move in the direction of one or two other grebes that escape. In under-water pursuit, the threatening grebe continues the chasing of one or two other grebes with a dive. Fight consists of aggressive physical contact between two grebes. There was no differentiation between short and longer pursuits or between short and more intense fights. In 2004, before starting each bout of observation, the grebes present in the sector were counted. For each observation weekend, the average number of aggressions per category and per observation bout was calculated and a global aggression indicator was deduced in two ways: 1) by simple addition of the average numbers in the different categories, a total aggression level was obtained, and 2) by weighing the different categories of aggression differently, a weighed aggression level was calculated. Intense threatening was weighed 1, the pursuits 2 and fights 3.

Level of aggression in particular pairs: In 2005 and 2006, a method focusing more on changes in the behaviour of individual pairs was applied. During the first weekend of observation in both years, two observers each chose three platforms to be followed simultaneously for the rest of the season. The platforms were located so as to be easily visible all three from a same spot of the footbridge at the same moment in time without being too close. The distance between two neighbouring platforms in a group of three was in the range of 5 m. It could thus be expected that later other pairs would try to establish themselves in between the pairs under special observation or in their direct vicinity. As it was not possible to recognize the pairs of the colony individually, it was assumed that in between two observation bouts and even in between two observation weekends, ownership of the platforms did not change. Early in the season, it could occur that a platform designated for special observation was abandoned and disappeared in between two weekends. Then, either another platform was picked for further observation or observations simply continued with two platforms. On each day, before recording of behaviour was started, the condition of each platform, its content, its distance to the nearest platforms in each direction and the total number of platforms clumped within a distance of 3 m were registered. Start and end times of the bouts of observation were noted down. Their duration, to some extent depending on weather conditions, was always comprised between 30 minutes and 3 hours. Per weekend, the total observation time was always comprised between 6 hours and 10 hours. Good care was taken in order to insure that the timing of data recording provided an appropriate and equilibrated mix of daytime hours covering the day from early morning to late afternoon. The time where none, one or both partners belonging to one platform were present was recorded as was the non-aggressive activity of each grebe (loafing, building, platform courtship, incubation). With respect to the aggressions of each pair, threatening directed at another grebe, token diving, pursuits above water surface, under-water pursuit, fights, an incubating grebe leaving the nest to chase a conspecific and aggressions against Eurasian Coots *Fulica atra* were recorded separately. By simply summing up the records and dividing the result by the number of observation hours, a total level of aggression per pair per weekend was calculated. A weighed level of aggression was obtained by weighing threats 1, pursuits, token diving and leaving of the nest 2 and fight 3; the result was again divided by the number of observation hours. The evolution of the high cost aggressiveness was assessed by deducting total aggression from weighed aggression of the different pairs.

# 2 Ecology of colonial Great Crested Grebes

In the following the ecological data obtained at the Footbridge colony in Enkhuizen are presented and discussed, also in comparison to the corresponding results of other studies. The presentation generally follows the occurrence of events in time throughout a season, starting with the arrival and settlement of the adult grebes and ending with hatching and rearing of the chicks.

## 2.1 Arrival, settlement and occupancy pattern

Local bird populations may arrive in a short time frame at their breeding grounds where they then also settle rather all together, or their arrival and settlement can be more spaced in time. The constraints of the yearly seasons certainly contribute to at least a minimal synchronisation in the migration and in the occupation of breeding territories, especially if the group under consideration nests far north. In central Europe, there is however room for manoeuvre and members of a local population may individually time their nesting. In such a situation, the type of breeding will most affect its process. In colonial species, we would expect a rather synchronous arrival or at least settlement of all group members whereas in solitary breeders, both could spread out in time.

### 2.1.1 Timing of arrival

To detect the migration strategies of the grebes, spot counts of all Great Crested Grebes present inside the harbour were executed in 2003, 2004 and 2006. Table 1 gives an overview of maximum counts per observation period for each of the three colonies and of total numbers of Great Crested Grebes present inside the harbour. It must be stressed that there was a constant coming and going of grebes between the harbour and Lake IJssel and, as a consequence, there was a good deal of fluctuation in the numbers of the birds present inside the Compagnieshaven throughout the day. Therefore, the maximum numbers found present more a trend in time than a real estimation of the total population that had arrived with the intention to settle there. Also, it could not be excluded that, especially early in the season, part of the unsettled grebes frequently switched their presence between the three colonies, so that it made more sense to focus on the total figure for the harbour rather than on the numbers for the single colonies for assessing the timing of arrival.

As shown in Figure 2, in all years a seasonal increase in the total numbers of Great Crested Grebes counted inside the harbour was witnessed. It spread over a period exceeding by far one month. Also, increases in the population of the Footbridge colony could be explained at the utmost only to a very limited extent by birds switching between the three colonies. Differences in the timing appeared when comparing the three years.

**Table 1:** Number of adult Great Crested Grebes present in spot counts at the three colonies inside the harbour of Enkhuizen in 2003, 2004 and 2006.

| Date | | Footbridge | City | North | Total |
|---|---|---|---|---|---|
| 2003 | 9 March | 71 | 25 | 13 | 109 |
| | 15 March | 71 | 17 | 30 | 118 |
| | 23 March | 79 | 25 | 21 | 125 |
| | 30 March | 117 | 54 | 39 | 210 |
| | 4 April | 127 | 64 | 37 | 228 |
| | 13 April | 151 | 45 | 42 | 238 |
| | 17 April | 174 | 59 | 46 | 279 |
| 2004 | 31 March | 77 | 12 | 13 | 102 |
| | 3 April | 99 | 17 | 23 | 139 |
| | 25 April | 175 | 38 | 33 | 246 |
| 2006 | 17 March | 101 | 48 | 15 | 164 |
| | 24 March | 152 | 29 | 25 | 206 |
| | 8 April | 144 | 29 | 48 | 221 |
| | 15 April | 164 | 31 | 36 | 231 |

In 2003, the waters inside the harbour being frozen until early March, an earlier arrival inside the colonies was impossible. Nevertheless, on 27 February J.J. Vlug already counted 60 Great Crested Grebes (14 pairs and 32 individuals) apparently waiting at the entrance to the harbour; 13 of these grebes were still not in full breeding plumage. Once ice free around mid-March, the growth of the harbour population continued then at least until past mid-April. In spite of a milder winter followed by temperatures reaching already 15° C in late March and early April 2004, grebe numbers inside the harbour were quite low until early April, but then increased quickly until mid-April. In 2006 the winter started only really in late February with a drop in temperatures to far below 0°C and these conditions prevailed until mid-March when daytime temperatures reached again positive figures. Immediately, comparably high numbers of grebes were counted and the population further increased quickly until early April. Thereafter, the growth rate became more moderate.

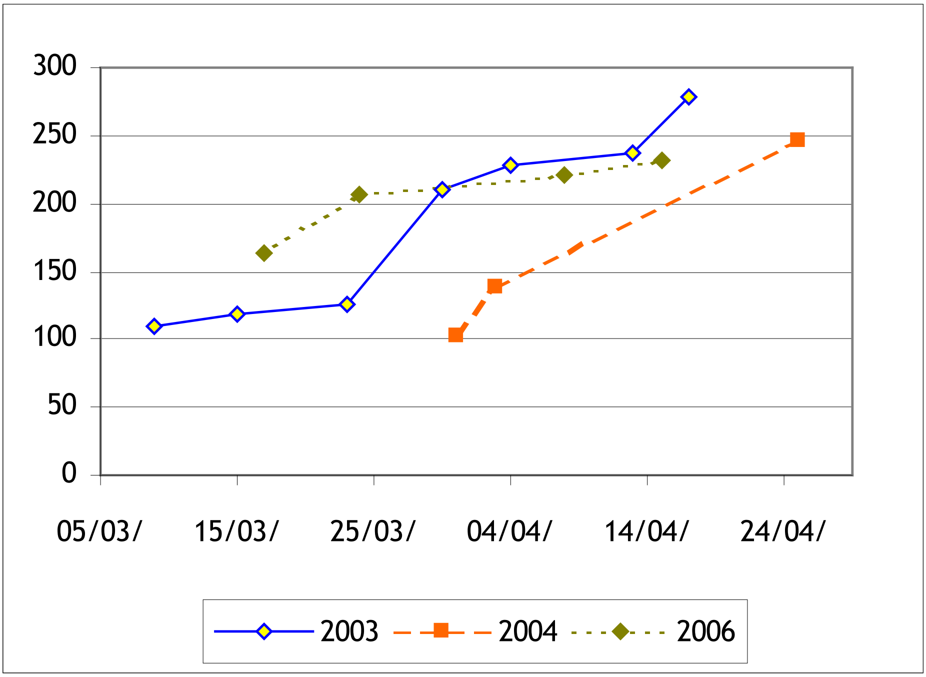

**Fig. 2:** Total number of adult Great Crested Grebes present in spot counts inside the harbour of Enkhuizen.

The data at our disposal only allowed determining when the numbers of grebes present inside the harbour increased. They did not tell us from where these birds came and to what extent local wintering and long distance migration influenced the picture. Indications in literature point at rather important winter populations for the lakes IJssel and Marken that could occasionally perform short distance travels to the nearby sea-coasts if short cold spells occurred. Wiersma et al. (1995) reported August flocks of up to 40,000 moulting birds on Lake IJssel and a winter population for the Netherlands of 14,000 grebes on average. Fjeldså (2004) indicated an average figure of 11,000 birds wintering on the IJsselmeer. Our occasional counts executed when driving over the dam separating Marker- and IJsselmeer between Lelystad and Enkhuizen yielded over 200 grebes on 1st April 2004, 380 grebes on 18 March 2005 and 580 grebes on 24 March 2005. The figures proved that sufficient grebes were present in the vicinity of Enkhuizen to cater for the population growth inside the harbour. Increases in numbers had not necessarily to wait for the arrival of long distance migratory birds. The IJsselmeer however holds many more colonies than just those at the harbour of Enkhuizen. Most of these are more exposed to wind and wave action, so that their inhabitants can only settle later in the season when the new vegetation growth offers enhanced protection. Thus, in the north of Enkhuizen, the colony of De Ven held no platforms when visited on 29 March 2003 although some 50 grebes were hanging around close to it. One week later, 220 grebes were counted and just a handful of copulation platforms were found. In 2005, hardly any platform could be seen there on 23 April while some 50 grebes were counted close to the vegetated area. Only in late April and early May of each year, the grebes settled down there. These limited observations pointed to a high likelihood that breeders arriving early in the season tended to wait within sight of their future breeding site before nesting there became really possible, probably to be among the first settlers and thus to be able to occupy the better sites.

In addition to waiting breeders, generally important numbers of non-breeding grebes could be present on Lake IJssel throughout the breeding season. For instance, on 4 May 2007, when most breeders should have had settled, the count along the entire dam separating the lakes IJssel and Marken still yielded 470 Great Crested Grebes, most of them in groups of 10 to 20 birds.

The building-up in numbers of grebes present at the Footbridge colony is represented in Table 2. In all years, numbers counted showed a sustained increase from mid-March onwards, but then either stagnated or even already came down towards the end of April or in very early May, just before the maximum number of platforms was reached (see 2.1.2 and Table 4). Therefore, the settled population was estimated by multiplying by two the number of platforms started. This deduced population exceeded the birds present during the counts for the respective day from approximately mid-April onwards and this fact provided statistical evidence that the numbers of grebes counted only represented part of the settled population.

**Table 2:** Maximum counts of adult Great Crested Grebes at the Footbridge colony per section and from platform counts deduced population.

| Date | | Reed I | Reed II | Bulrush | Colony | Deduced population |
|---|---|---|---|---|---|---|
| 2003 | 16.03. | 23 | 33 | 24 | 80 | 70 |
| | 23.03. | 19 | 35 | 25 | 79 | 90 |
| | 29.03. | 32 | 36 | 16 | 84 | |
| | 30.03. | 31 | 55 | 31 | 117 | 136 |
| | 05.04. | 42 | 67 | 18 | 127 | 120 |
| | 13.04. | 56 | 75 | 20 | 151 | 150 |
| | 18.04. | 57 | 95 | 29 | 181 | 186 |
| | 30.04. | 58 | 75 | 34 | 167 | |
| | 01.05. | 58 | 93 | 31 | 182 | 236 |
| | 07.05. | 57 | 82 | 38 | 177 | 252 |
| 2004 | 31.03. | 26 | 37 | 14 | 77 | 74 |
| | 01.04. | 30 | 43 | 19 | 92 | |
| | 03.04. | 30 | 47 | 22 | 99 | 90 |
| | 23.04. | 49 | 83 | 35 | 167 | |
| | 25.04. | 59 | 83 | 33 | 175 | 200 |
| | 08.05. | 44 | 63 | 31 | 138 | 226 |
| 2005 | 18.03. | 31 | 54 | 27 | 112 | 52 |
| | 25.03. | 36 | 63 | 29 | 128 | 106 |
| | 02.04. | 38 | 65 | 33 | 136 | 116 |
| | 08.04. | 51 | 75 | 16 | 142 | 126 |
| | 15.04. | 55 | 86 | 24 | 165 | 164 |
| | 24.04. | 53 | 86 | 24 | 163 | 198 |
| | 30.04. | 58 | 86 | 25 | 169 | 210 |
| | 06.05. | 55 | 88 | 23 | 166 | 224 |
| 2006 | 17.03. | 19 | 66 | 16 | 101 | 34 |
| | 24.03. | 37 | 91 | 33 | 161 | 64 |
| | 07.04. | 38 | 81 | 25 | 144 | 122 |
| | 16.04. | 51 | 90 | 23 | 164 | 166 |
| | 28.04. | 49 | 102 | 34 | 185 | 200 |
| | 05.05. | 48 | 119 | 28 | 195 | 230 |
| 2007 | 07.04. | 24 | 51 | 24 | 99 | 60 |
| | 27.04. | 44 | 93 | 52 | 189 | 192 |
| | 29.04. | 53 | 86 | 41 | 180 | 222 |

Figure 3 illustrates this finding for the season 2005. In consequence, a more or less important part of settled grebes must have been outside the colony during the counts and the proportion of such birds could have changed quite substantially in the course of the season. Whereas early in each season, unsettled grebes could make up for any difference between deduced numbers and counts, later, with less unsettled grebes remaining, this was no longer the case. At the end, the counts of grebes failed to provide an accurate idea of the population of the colony, whether settled or not, throughout the settlement process of the birds.

Table 2 indicates separately the grebes counted per section of the Footbridge colony. The counts included all grebes, whether close to the vegetation or on the open water surface in front of a zone. They therefore included as well settled as unsettled birds. The figures display no homogenous evolution over time and in the different sections. This could be explained by the mobility of unsettled grebes and by gradual shifts in the attendance of platforms by the settled pairs. During the March observations of each year, more grebes counted in the vegetated area of the Footbridge colony were in pairs and both partners guarded the chosen nesting site. Later in the season and chiefly after the start of egg laying, settled grebes often left a single mate in the colony, while their partners presumably searched for food on Lake IJssel.

In the course of a day or a weekend, the results of the counts showed a good deal of variation, too. Table 3 illustrates adequately this phenomenon for the weekend of 24 March 2005: not only the numbers per section fluctuated much, total numbers for the colony also displayed similarly important variations.

In spite of all the limitations, the figures for the Footbridge colony at our disposal suggest that in all years, the numbers of Great Crested Grebes present at the Footbridge colony increased from early March until at least mid-April (Table 2). Based on the number of platforms and the deduced minimum number of birds, the population growth of the colony lasted even until early May of each year. In March, a more or less important part of

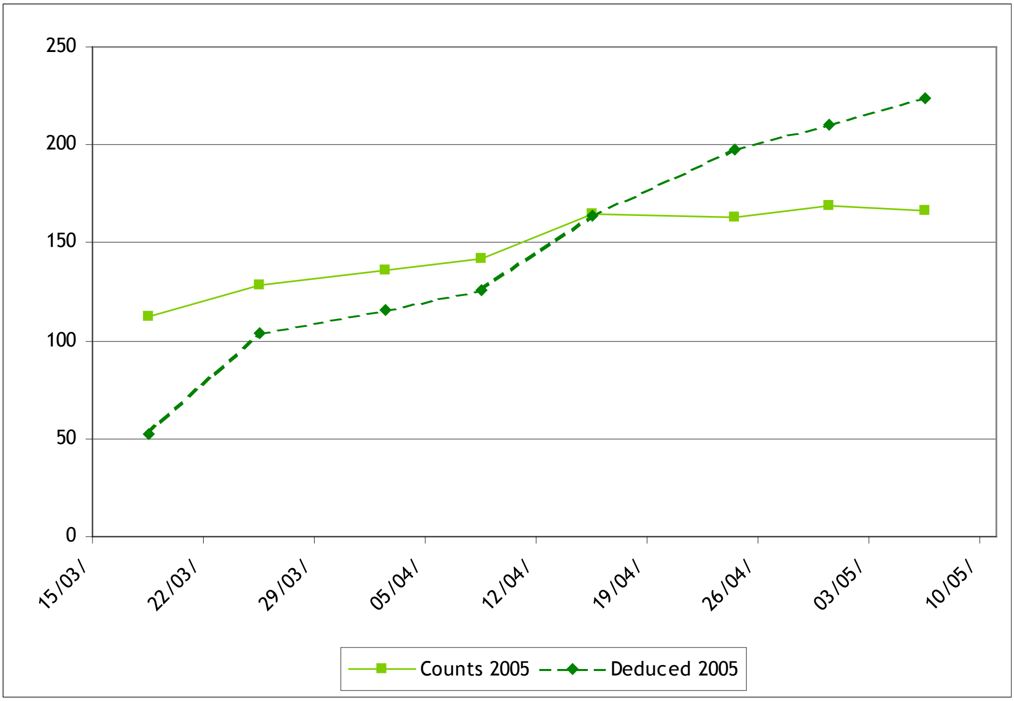

**Fig. 3:** Comparison of the numbers of grebes counted and the minimum population deduced from the number of platforms registered in 2005.

the population counted was yet unsettled. In the course of April, more and more pairs settled down and the figures insinuated a decreasing surplus of unsettled birds so that by early May most, if not all grebes could have found access to the colony. It remained unknown whether the grebes settled down in the order of their arrival or not.

That the arrival of colonial Great Crested Grebes could spread over a rather extended period of time has been reported by other studies. Thus, Leys et al. (1969:2) noticed that in the region of the IJsselmeer before the breeding season really started in spring, the birds concentrated in many places close to breeding sites and their numbers showed a general tendency towards seasonal increases. Koshelev (1981) found the arrival of West Siberian breeders to start in early to mid-May and to last for more than one month. On Lake Sempach in Switzerland, Fuchs (1982) registered the presence of grebe aggregations in front of colonial nesting sites from April onwards while their breeding started only towards late May or June. Only in June, the aggregations had disappeared. In Denmark, Henriksen (1992) witnessed the first arrivals at the breeding site of Lake Braband in late March when the ice melted and numbers increased almost on a daily basis for more than one month.

Generally, early arrival should be favoured as it provides a greater choice of habitats still available for settlement. Therefore, experienced grebes should arrive first to guarantee their access to the best breeding places. Later arriving birds could have less experience, be first-time breeders or their physical conditions could have been adversely affected over winter so that their migration was delayed.

### 2.1.2 Timing of settlement

The settlement process of a new pair started with the appearance of a loose heap that was generally developed into a basic and then into a solid platform receiving eggs. The date of appearance of the loose heap could therefore be considered as the day of settlement.

Except very early in the season, loose heaps were normally few. Mostly their number for the entire colony remained well below ten on any day. Only on 31 March 2004, a day with rather strong winds, 16 loose heaps were found. Grebes were generally able to develop loose heaps rather quickly into basic platforms and to complete a solid platform within a couple of days. Once a pair had gained access to the colony, it was in its own interest to keep platform building progressing in order to establish a firm relationship to the site and to demonstrate its resoluteness to settled neighbours. Occasionally, the weather did not permit a steady progress of platform completion. During such observation periods, more loose heaps could be found. When the meteorological conditions were too bad, loose heaps were often simply abandoned and disappeared soon. Occasionally, loose heaps were abandoned later, either because the opposition of already settled grebes was too vigorous or the place proved to be inadequate.

**Table 3:** Counts of grebes per section at the Footbridge colony during the weekend of 24 March 2005.

| Date | Time | Reed I | Reed II | Bulrush | Total |
|---|---|---|---|---|---|
| 24.03. | 6.30 p.m. | 30 | 53 | 22 | 105 |
| 25.03. | 7.00 a.m. | 32 | 43 | 25 | 98 |
| 25.03. | 5.45 p.m. | 29 | 52 | 35 | 116 |
| 25.03. | 8.00 p.m. | 36 | 63 | 29 | 128 |
| 26.03. | 7.00 a.m. | 23 | 66 | 30 | 119 |
| Average | | 30.0 | 55.4 | 28.2 | 113.2 |
| SD | | 4.74 | 9.24 | 4.97 | 11.82 |

Due to the limited number of loose heaps registered per observation weekend, it seemed more appropriate to assess the progress of settlement in time only considering basic and solid platforms. This permitted an estimation of the number of grebes that should be allocated to the colony. The values would not include grebes that had not yet built and in this sense, it was a real measure of the settlement process. Figure 3 shows for all years rather constant and regular increases of the settled population from some point in March onwards until the first decade of May. Only in 2003, a slight deviation was observed when the numbers of platforms collapsed during the first decade of April, as a consequence of weather conditions: strong winds destroyed all weak platforms. In early April 2005, a storm also tore apiece most of the platforms. But for the next count, settled pairs had rebuilt their platforms and, in addition, new pairs had settled down, so that the effects of the storm remained hidden in the figures of Table 4.

**Table 4:** Counts in time of grebe platforms per section in the Footbridge colony (LH = loose heaps, OP = other platforms, i. e. basic and solid platforms).

| Date | | Reed I | | Reed II | | Bulrush | | Colony | | Total |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | LH | OP | LH | OP | LH | OP | LH | OP | |
| 2003 | 09.03. | 0 | 10 | 0 | 8 | 0 | 1 | 0 | 19 | 19 |
| | 16.03. | 4 | 7 | 0 | 17 | 2 | 5 | 6 | 29 | 35 |
| | 23.03. | 0 | 16 | 1 | 22 | 0 | 6 | 1 | 44 | 45 |
| | 30.03. | 3 | 23 | 3 | 27 | 1 | 11 | 7 | 61 | 68 |
| | 05.04. | 0 | 24 | 0 | 31 | 0 | 5 | 0 | 60 | 60 |
| | 13.04. | 0 | 28 | 0 | 38 | 0 | 9 | 0 | 75 | 75 |
| | 18.04. | 3 | 30 | 2 | 43 | 0 | 15 | 5 | 88 | 93 |
| | 01.05. | 2 | 35 | 1 | 58 | 1 | 21 | 4 | 114 | 118 |
| | 08.05. | 1 | 39 | 3 | 60 | 0 | 23 | 4 | 122 | 126 |
| 2004 | 31.03. | 4 | 9 | 8 | 10 | 4 | 2 | 16 | 21 | 37 |
| | 03.04. | 1 | 18 | 1 | 19 | 3 | 3 | 5 | 40 | 45 |
| | 25.04. | 1 | 30 | 1 | 53 | 0 | 15 | 2 | 98 | 100 |
| | 08.05. | 1 | 35 | 0 | 58 | 0 | 19 | 1 | 112 | 113 |
| 2005 | 18.03. | 1 | 8 | 2 | 12 | 2 | 1 | 5 | 21 | 26 |
| | 24.03. | 2 | 13 | 2 | 28 | 1 | 7 | 5 | 48 | 53 |
| | 26.03. | 0 | 15 | 1 | 28 | 0 | 8 | 1 | 51 | 52 |
| | 02.04. | 1 | 18 | 2 | 28 | 1 | 6 | 4 | 54 | 58 |
| | 08.04. | 2 | 21 | 4 | 32 | 2 | 8 | 8 | 61 | 63 |
| | 17.04. | 2 | 27 | 1 | 40 | 2 | 10 | 5 | 77 | 82 |
| | 23.04. | 1 | 33 | 2 | 48 | 0 | 15 | 3 | 96 | 99 |
| | 30.04. | 0 | 36 | 2 | 52 | 1 | 14 | 3 | 102 | 105 |
| | 07.05. | 0 | 37 | 0 | 57 | 1 | 17 | 1 | 111 | 112 |
| 2006 | 18.03. | 2 | 3 | 3 | 6 | 1 | 2 | 6 | 11 | 17 |
| | 24.03. | 1 | 9 | 2 | 14 | 1 | 5 | 4 | 28 | 32 |
| | 26.03. | 0 | 10 | 1 | 18 | 2 | 4 | 3 | 32 | 35 |
| | 08.04. | 2 | 16 | 2 | 31 | 2 | 8 | 6 | 55 | 61 |
| | 16.04. | 0 | 22 | 0 | 47 | 1 | 13 | 1 | 82 | 83 |
| | 29.04. | 2 | 25 | 2 | 54 | 0 | 17 | 4 | 96 | 100 |
| | 06.05. | 0 | 28 | 0 | 70 | 0 | 17 | 0 | 115 | 115 |
| 2007 | 06.04. | 5 | 6 | 5 | 9 | 3 | 2 | 13 | 17 | 30 |
| | 08.04. | 1 | 8 | 3 | 16 | 0 | 6 | 4 | 30 | 34 |
| | 28.04. | 2 | 25 | 0 | 48 | 0 | 21 | 2 | 94 | 96 |
| | 05.05. | 1 | 29 | 0 | 55 | 0 | 26 | 1 | 110 | 111 |

Possibly in 2007, the grebes were comparably late in settling and the total number of platforms recorded on 6 April was more than 30% lower than in any of the other years at that moment in time. The maximum size of the colony reached in early May showed hardly deviations from the figures obtained from 2004 to 2006. Generally, the settlement process started in March of the different years, essentially varying in dependence of weather conditions. Latest settlers joined in early May so that the entire process spread over a period of six to eight weeks.

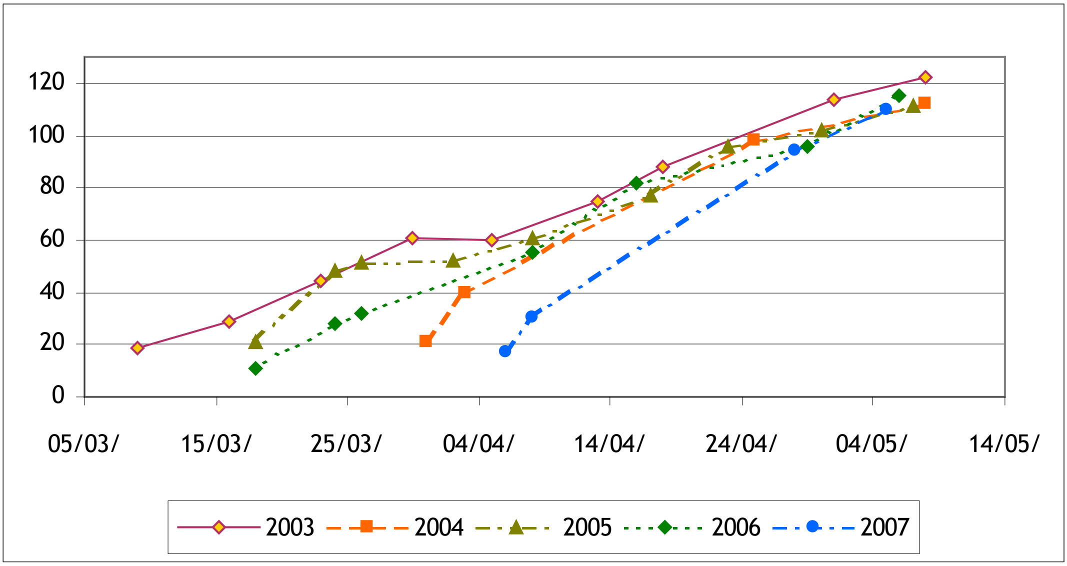

**Fig. 4:** Evolution in the number of basic and solid platforms in the Footbridge colony in 2003-2007.

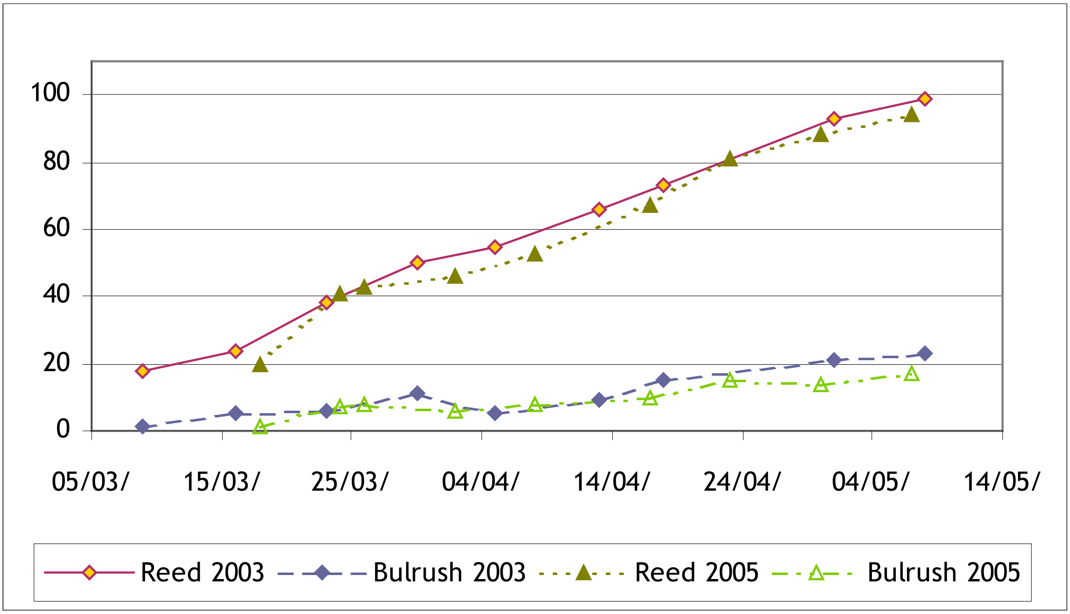

**Fig. 5:** Evolution in the number of basic and solid platforms in the Footbridge colony in 2003 and 2005 distinguishing between Reed and Bulrush platforms.

While the total numbers of platforms for the colony displayed a rather steady and regular growth in time, the picture differed slightly when comparing the different sections of the colony. Especially in the Bulrush zone, from counts in March and in the first half of April, often no real increase in the number of platforms could be deduced. If it nevertheless occurred, it was followed by a rather important drop (as between 30 March and 5 April 2003 or between 26 March and 2 April 2005, Fig. 5). Often, many platforms in the Bulrush appeared comparably late in the season, in the second half of April and early May.

In the Reed zones of the colony, in most of the years there seemed to be a more regular process of settlement although not completely insensitive to periods of bad weather. Thus, in Reed I, platform numbers stagnated or even declined (depending on whether loose heaps were considered or not) in the first half of March 2003, and in late March 2005, no new platforms were registered for about ten days.

According to Simmons (1974), early site attachment would seem to be anticipatory. Given a general shortage for premium sites, there must be a strong competition for good sites and this would also favour early and prolonged occupation of the future breeding areas. A more general scarcity of acceptable breeding sites would lead to colonial nesting. Continuing these reflections, Great Crested Grebes establishing themselves inside colonies should be interested to settle as early as possible. If all birds followed the same strategy, as a consequence, a colony should build up within a short period of time. This was definitively not the case at the Footbridge colony. In other colonies, such as near Yverdon in Switzerland, the settlement of the members of a colony took more time, too, spreading from late April to early July (Berthoud 1963). Moskal and Marszałek (1986) however found colonies to arise almost simultaneously on Lake Żarnowieckie, this in spite of the fact that no lack of nesting habitat could be witnessed. Indeed, reed beds judged suited in direct neighbourhood of the colonies remained unoccupied. Given these differences, it remains to be analyzed whether a more synchronous settlement is simply related to local circumstances, essentially the variation in quantity and quality of the habitat available, or to differences in social attraction in different populations, possibly related to some kinds of benefits.

### 2.1.3 Build-up pattern of the colony and spatial distribution of the nests

**Evolution of distances between nesting platforms:** Two different processes can lead to the establishment of aggregated nesting: either a first platform is built from where settlement spreads out and new platforms are added at rather equal distances at the border of the existing ones or, from the beginning, the platforms are more scattered all over the entire habitat and later platforms appear in between existing platforms. In the first case, we could expect individual pairs to be also socially attracted by conspecifics whereas in the second, a greater reluctance to close aggregation would be displayed and the grouping could be entirely conditioned by the habitat. To test what process was involved at the Footbridge colony, the evolution of average distances between platforms in time was measured.

Whether one considered each section of the colony separately, whether one distinguished between types of vegetation or whether one took the colony as a whole, a general tendency towards a gradual reduction in average, minimum and maximum distances between the nesting platforms of the grebes was apparent in all years (Tables 5-9, Fig. 6, 7). Also SD values developed in the same direction and indicated an ever increasing concentration of individual distances around the average value in the course of the season. The pace of shrinking differed from one year to the next and also between the two types of vegetation and the three sections of the colony. It thereby reflected the difference in the numbers of pairs settled on the same date in different years. In all years, the end average distance was lower in the Reeds than in the Bulrush. When the colony reached its maximum size in early May of each year, the average distance between two neighbouring platforms was comprised between 2.09 m and 2.25 m for the colony as a whole. In the Reeds, the average was slightly less. In the Bulrush, it varied between 2.34 m and 4.16 m and thus displayed a rather high degree of variation over the years.

When going into more detail, isolated values contradicted the general trend of gradual reduction in distances between nests and they needed further explanations.

**Table 5:** Average nearest neighbour distances (m) between platforms of nesting grebes in 2003.

| | **Section \ Date** | | **16.03.** | **23.03.** | **30.03.** | **05.04.** | **13.04.** | **18.04.** | **01.05.** | **08.05.** |
|---|---|---|---|---|---|---|---|---|---|---|
| **2003** | Reed I | Average | 12.24 | 5.49 | 3.81 | 3.53 | 3.10 | 3.02 | 2.64 | 2.37 |
| | | SD | 9.31 | 4.43 | 3.06 | 3.16 | 2.37 | 2.28 | 2.16 | 2.14 |
| | | Range | 2.8-26.9 | 0.9-18.2 | 0.7-10.4 | 1.2-15.4 | 0.3-10.4 | 0.3-10.4 | 0.3-10.4 | 0.3-10.4 |
| | | N | 7 | 15 | 23 | 23 | 26 | 29 | 35 | 39 |
| | Reed II | Average | 4.55 | 3.72 | 2.79 | 2.55 | 2.28 | 2.07 | 1.71 | 1.68 |
| | | SD | 2.82 | 2.27 | 1.31 | 1.31 | 1.19 | 1.18 | 1.08 | 0.95 |
| | | Range | 1.1-13.0 | 1.0-9.8 | 0.8-5.7 | 0.8-5.7 | 0.7-5.7 | 0.5-5.7 | 0.4-5.7 | 0.4-4.6 |
| | | N | 17 | 22 | 27 | 31 | 36 | 42 | 58 | 60 |
| | All Reeds | Average | 6.55 | 4.43 | 3.29 | 3.00 | 2.69 | 2.50 | 2.12 | 2.05 |
| | | SD | 6.30 | 3.37 | 2.21 | 2.21 | 1.63 | 1.57 | 1.42 | 1.38 |
| | | Range | 1.1-26.9 | 1.0-18.2 | 0.7-10.4 | 0.8-15.4 | 0.3-10.4 | 0.3-10.4 | 0.3-10.4 | 0.3-10.4 |
| | | N | 24 | 37 | 50 | 54 | 62 | 71 | 93 | 99 |
| | Bulrush | Average | 13.95 | 11.04 | 5.41 | 13.93 | 6.86 | 3.88 | 2.62 | 2.34 |
| | | SD | 8.70 | 7.92 | 3.71 | 16.20 | 4.93 | 3.90 | 1.74 | 1.26 |
| | | Range | 2.8-22.5 | 2.8-22.4 | 2.7-15.5 | 2.8-41.7 | 1.7-15.4 | 0.9-16.4 | 0.9-8.6 | 0.9-5.4 |
| | | N | 5 | 6 | 11 | 5 | 9 | 15 | 21 | 23 |
| | Colony | Average | 7.65 | 5.20 | 3.62 | 3.68 | 3.06 | 2.67 | 2.18 | 2.09 |
| | | SD | 7.34 | 4.72 | 2.64 | 5.33 | 2.47 | 2.05 | 1.48 | 1.37 |
| | | Range | 1.1-26.9 | 1.0-22.4 | 0.7-15.5 | 0.8-41.7 | 0.3-15.4 | 0.6-16.4 | 0.3-10.4 | 0.3-10.4 |
| | | N | 29 | 43 | 61 | 59 | 71 | 86 | 114 | 122 |

In 2003 in Reed I, the maximum distance increased on 5 April to 15.4 m and provoked even a slight increase in SD (Table 5). The elevated values were a consequence of the rather poor quality of the habitat in major parts of Reed IA. For close to 40 m in length, the reeds hardly offered any possibility of access in depth to the grebes for nest building. One pair trying to build in between two platforms that were at a distance of 15.4 m from each other had to abandon its plan in early April, as it was not successful in durably anchoring its construction. One week later, the same or another pair chose a better place inside the same stretch of Reed IA and again divided the distance of 15.4 m into two values. Between two other platforms at a distance of 10.4 m, it proved impossible to add a platform.

The maximum distance in the Bulrush nearly tripled from 15.5 m to 41.7 m from 30 March to 5 April 2003. At the same time, the average distance more than doubled and reached 14 m, the SD more than quadrupled while six platforms disappeared (Table 5). These platforms were destroyed by strong winds on 5 April. Mainly in the wider parts of the Bulrush located at both ends of the section, two and three platforms survived at distances of twice ±3 m and once 8 m, but in between both groups, a stretch over 40 m long was emptied of all grebe constructions. The latter distance caused all increases in the Bulrush values. In addition, it impacted the aggregated values for the colony as a whole and provoked the sole rise of average colony distances in 2003. Inside the Reed parts of the colony, a corresponding increase of distances was avoided because the platforms there were better protected.

In 2004, the limited number of observation dates provided less occasions for observing drawbacks against a general trend of decreasing distances between nesting platforms (Table 6). Again, the poor quality of a stretch of the vegetation in Reed IA kept the maximum distance between the grebe platforms there high. On 3 April, three distances exceeding 10 m still existed in Reed I and two were in the range of 6 m.

In Reed II, the change of ownership of one platform between 24 April and 8 May caused an increase of the maximum distance. The grebes had been chased by a pair of coots that took over their construction.

**Table 6:** Average nearest neighbour distances (m) between platforms of nesting grebes in 2004.

| | Section \ Date | | 01.04 | 03.04. | 24.04. | 08.05. |
|---|---|---|---|---|---|---|
| 2004 | Reed I | Average | 7.35 | 4.18 | 2.88 | 2.32 |
| | | SD | 3.23 | 3.62 | 2.43 | 2.34 |
| | | Range | 2.1-13.1 | 0.7-13.1 | 0.9-10.6 | 0.3-10.6 |
| | | N | 12 | 18 | 29 | 35 |
| | Reed II | Average | 7.12 | 4.29 | 1.70 | 1.67 |
| | | SD | 6.00 | 2.31 | 0.83 | 0.87 |
| | | Range | 2.0-23.6 | 0.5-9.6 | 0.2-4.4 | 0.2-4.7 |
| | | N | 12 | 19 | 53 | 58 |
| | All Reeds | Average | 7.23 | 4.24 | 2.13 | 1.91 |
| | | SD | 4.75 | 4.23 | 1.66 | 1.65 |
| | | Range | 2.0-23.6 | 0.5-13.1 | 0.2-10.6 | 0.2-10.6 |
| | | N | 24 | 37 | 82 | 93 |
| | Bulrush | Average | 9.05 | 29.78 | 4.39 | 3.54 |
| | | SD | n.a. | 29.31 | 2.98 | 1.89 |
| | | Range | 9.05 | 9.1-50.5 | 1.3-10.0 | 1.3-7.9 |
| | | N | 2 | 3 | 13 | 19 |
| | Colony | Average | 7.31 | 5.58 | 2.46 | 2.19 |
| | | SD | 4.66 | 8.07 | 2.07 | 1.77 |
| | | Range | 2.0-23.6 | 0.5-50.5 | 0.2-10.6 | 0.2-10.6 |
| | | N | 26 | 40 | 95 | 112 |

In the Bulrush, the condition of the vegetation, especially in the central part, prohibited early nesting and the grebes had to wait for the new vegetation growth before being able to anchor the platforms. Therefore, the different values in Table 6 came down comparably late.

In 2005, the evolution of the values in Reed I displayed a sustained decrease and the maximum value reached in early May was much reduced in comparison to the two previous seasons (Table 7). This was a consequence of the improved habitat conditions in the narrow parts of Reed IA where, at the latest with the appearance of the new vegetation growth, platforms could be anchored at more places.

In Reed II, the average distance between the platforms increased between 26 March and 1st April without a change in the number of platforms. But four platforms had slightly changed their position, four platforms had disappeared and four platforms were registered for the first time. While the total length of the occupied area had not changed, the new distribution of the platforms was less in a straight line than previously. Especially for new platforms, the grebes had taken more advantage of the entire width of the vegetation at their disposal. The values of SD and maximum distance increased again between 1st and 8 April. The new platforms registered on 8 April were mostly at short distances (below 2 m) from previously existing constructions. However, one platform had disappeared increasing the distance between the two remaining neighbouring platforms to 7.8 m.

In the Bulrush section, the average and maximum distances and SD values between platforms increased twice in 2005, once between 26 March and 1st April and then again between 8 and 17 April (Table 7). The first increase was a consequence of the destruction of two platforms by strong winds. The second was due to a storm that tore apiece about all platforms in the Bulrush. Both reversals of trends in the sub-division were less apparent at the level of the entire colony.

When considering the evolution of the maximum distance between platforms in the Bulrush in early May, a steady increase from 5.4 m in 2003 (Table 5) to 12.1 m in 2005 appeared. This was a consequence of habitat deterioration over time: indeed, in the centre of the section an area spread out where the already from the beginning narrow vegetation belt decreased in width from one year to the next.

In 2006, average and maximum distances, but also SD values in Reed I suffered from the excavation works in the harbour. These made a stretch of some 20 m inside Reed IA inadequate for nesting and still in early May, the values were adversely affected (Table 8). Except for the maximum distance, the very regular and sustained downward trend of all values in Reed II masked the situation in Reed I at the level of all Reeds. In the Bulrush, too, the downward trend in distances was rather regular, but ceased already by the end of April, no new platforms being added there in May. With respect to the previous year, the quality of the habitat recovered somewhat in its centre and allowed two pairs to settle there.

Though the program in 2007 covered only three weekends, the evolution of nearest neighbour

**Table 7:** Average nearest neighbour distances (m) between platforms of nesting grebes in 2005.

| | Section \ Date | | 20.03. | 26.03. | 01.04. | 08.04. | 17.04. | 23.04. | 30.04. | 06.05. |
|---|---|---|---|---|---|---|---|---|---|---|
| **2005** | Reed I | Average | 11.01 | 5.95 | 4.61 | 3.98 | 3.39 | 2.71 | 2.38 | 2.29 |
| | | SD | 7.45 | 3.42 | 3.46 | 3.37 | 2.96 | 2.01 | 1.34 | 1.34 |
| | | Range | 4.4-23.4 | 2.5-13.5 | 0.9-13.5 | 0.5-13.5 | 0.5-13.5 | 0.5-11.3 | 0.5-5.5 | 0.5-5.5 |
| | | N | 9 | 15 | 18 | 21 | 27 | 33 | 36 | 37 |
| | Reed II | Average | 5.81 | 3.03 | 3.14 | 2.79 | 2.11 | 1.86 | 1.71 | 1.70 |
| | | SD | 3.11 | 1.59 | 1.58 | 1.79 | 1.24 | 1.12 | 1.15 | 1.16 |
| | | Range | 2.6-13.2 | 0.9-6.7 | 0.2-6.9 | 0.2-7.8 | 0.2-5.4 | 0.2-5.4 | 0.2-5.4 | 0.2-5.3 |
| | | N | 14 | 28 | 28 | 32 | 40 | 48 | 52 | 57 |
| | All Reeds | Average | 7.61 | 4.05 | 3.72 | 3.26 | 2.62 | 2.20 | 1.99 | 1.93 |
| | | SD | 6.07 | 2.74 | 2.57 | 2.58 | 2.17 | 1.59 | 1.27 | 1.26 |
| | | Range | 2.6-23.4 | 0.9-13.5 | 0.2-13.5 | 0.2-13.5 | 0.2-13.5 | 0.2-11.3 | 0.2-5.5 | 0.2-5.5 |
| | | N | 23 | 43 | 46 | 53 | 67 | 81 | 88 | 94 |
| | Bulrush | Average | 32.00 | 9.61 | 13.42 | 3.96 | 6.49 | 4.48 | 4.84 | 4.16 |
| | | SD | / | 9.09 | 14.27 | 2.72 | 4.84 | 3.11 | 2.96 | 2.81 |
| | | Range | 32.0 | 2.6-29.2 | 1.8-37.5 | 1.2-8.8 | 0.6-14.8 | 0.6-12.1 | 1.4-12.1 | 1.2-12.1 |
| | | N | 2 | 8 | 6 | 8 | 10 | 15 | 14 | 17 |
| | Colony | Average | 9.13 | 4.88 | 4.73 | 3.35 | 3.14 | 2.54 | 2.37 | 2.25 |
| | | SD | 8.46 | 4.60 | 5.67 | 2.58 | 2.95 | 2.04 | 1.85 | 1.74 |
| | | Range | 2.6-32.0 | 0.9-29.2 | 0.2-37.5 | 0.2-13.5 | 0.2-14.8 | 0.2-12.1 | 0.2-12.1 | 0.2-12.1 |
| | | N | 25 | 51 | 52 | 61 | 77 | 96 | 102 | 111 |

**Table 8:** Average nearest neighbour distances (m) between platforms of nesting grebes in 2006.

| | Section \ Date | | 18.03. | 25.03. | 09.04. | 16.04. | 29.04. | 06.05. |
|---|---|---|---|---|---|---|---|---|
| **2006** | Reed I | Average | 18.55 | 8.50 | 4.33 | 3.59 | 3.02 | 3.04 |
| | | SD | 14.11 | 8.91 | 6.83 | 4.80 | 4.49 | 4.39 |
| | | Range | 4.6-38.2 | 0.9-28.6 | 0.5-29.8 | 0.5-22.2 | 0.5-23.9 | 0.6-23.9 |
| | | N | 3 | 9 | 16 | 22 | 25 | 28 |
| | Reed II | Average | 8.27 | 4.21 | 2.53 | 1.84 | 1.57 | 1.45 |
| | | SD | 6.02 | 3.55 | 1.87 | 1.11 | 0.91 | 0.84 |
| | | Range | 2.8-18.4 | 1.0-17.1 | 0.6-8.4 | 0.5-4.6 | 0.5-4.4 | 0.5-4.6 |
| | | N | 6 | 14 | 31 | 47 | 54 | 70 |
| | All Reeds | Average | 11.43 | 5.64 | 3.17 | 2.39 | 2.02 | 1.90 |
| | | SD | 9.92 | 6.08 | 4.35 | 2.92 | 2.66 | 2.52 |
| | | Range | 2.8-38.2 | 0.9-28.6 | 0.5-29.8 | 0.5-22.2 | 0.5-23.9 | 0.5-23.9 |
| | | N | 9 | 23 | 47 | 69 | 79 | 98 |
| | Bulrush | Average | 29.60 | 11.26 | 7.96 | 4.43 | 3.41 | 3.41 |
| | | SD | 10.89 | 10.18 | 5.48 | 3.47 | 1.82 | 1.82 |
| | | Range | 22-37.3 | 2.6-25.2 | 1.0-16.2 | 1.0-11.0 | 1.2-8.0 | 1.2-8.0 |
| | | N | 3 | 5 | 8 | 13 | 17 | 17 |
| | Colony | Average | 13.85 | 6.52 | 3.75 | 2.69 | 2.24 | 2.12 |
| | | SD | 11.56 | 6.97 | 4.71 | 3.07 | 2.59 | 2.48 |
| | | Range | 2.8-38.2 | 0.9-28.6 | 0.5-29.8 | 0.5-22.2 | 0.5-23.9 | 0.5-23.9 |
| | | N | 12 | 28 | 55 | 82 | 96 | 115 |

**Table 9:** Average nearest neighbour distances (m) between platforms of nesting grebes in 2007.

| | Section \ Date | | 06.04. | 08.04. | 28.04. | 05.05. |
|---|---|---|---|---|---|---|
| 2007 | Reed I | Average | 7.93 | 7.28 | 2.95 | 3.03 |
| | | SD | 6.29 | 6.32 | 2.57 | 3.11 |
| | | Range | 2.6-18.9 | 1.9-18.9 | 0.6-9.8 | 0.4-13.3 |
| | | N | 10 | 11 | 25 | 29 |
| | Reed II | Average | 5.57 | 3.79 | 1.83 | 1.60 |
| | | SD | 3.52 | 1.93 | 0.89 | 0.85 |
| | | Range | 1.7-13.2 | 0.8-8.1 | 0.5-3.9 | 0.4-3.9 |
| | | N | 14 | 20 | 47 | 52 |
| | All Reeds | Average | 6.55 | 5.03 | 2.22 | 2.11 |
| | | SD | 5.03 | 4.31 | 1.74 | 2.08 |
| | | Range | 1.7-18.9 | 0.8-18.9 | 0.5-9.8 | 0.4-13.3 |
| | | N | 24 | 31 | 72 | 81 |
| | Bulrush | Average | 12.50 | 10.60 | 3.21 | 2.62 |
| | | SD | 4.32 | 5.66 | 2.78 | 1.90 |
| | | Range | 6.6-16.4 | 3.0-16.4 | 1.2-12.1 | 0.6-8.3 |
| | | N | 4 | 5 | 18 | 23 |
| | Colony | Average | 7.40 | 5.80 | 2.42 | 2.23 |
| | | SD | 5.19 | 4.84 | 2.01 | 2.04 |
| | | Range | 1.7-18.9 | 0.8-18.9 | 0.5-12.1 | 0.4-13.3 |
| | | N | 28 | 36 | 90 | 104 |

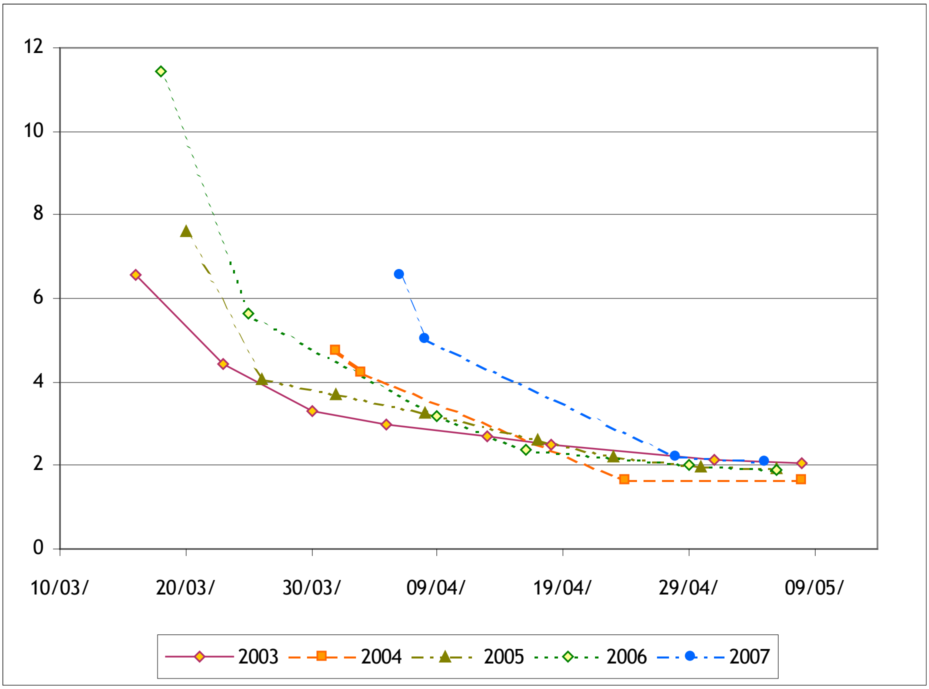

**Fig. 6:** Evolution of average distances between platforms in the Reeds (2003-2007).

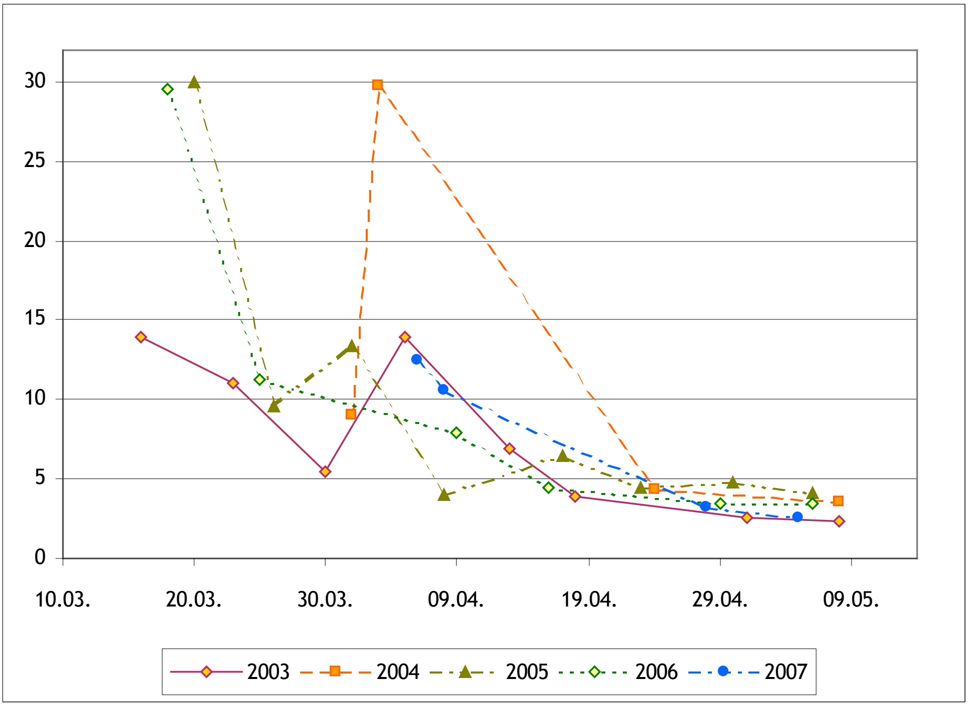

**Fig. 7:** Evolution of average distances between platforms in the Bulrush (2003-2007).

distances confirmed the findings of previous years and a gradual shrinkage of distances in time was observed. Reed IA remained of difficult access. A platform started there on 28 April had to be abandoned later, provoking an increase in average and maximum distances in the section for 5 May.

In conclusion and for all the years, the grebes showed a general tendency to take advantage of the entire habitat of the Footbridge colony for settling down early in the season. Later settlers chose places in between existing platforms, thereby contributing to a rather regular reduction of average, minimum and maximum distances over time. SD values followed the same general pattern. The settlement did clearly not spread out from a central point.

**Clumping of platforms:** Even though it was established in the previous section that settlement at the Footbridge colony started with platforms scattered all over the habitat, it was not excluded that some pairs concentrated already early. Earlier in the season when still longer stretches of the colony remained unoccupied, this phenomenon could be measured by the criterion of clumping of platforms. March distances between platforms were mostly far above 3 m in all years, so that counts of platforms grouped at a distance of 3 m and less would a priori indicate a better quality habitat where such clumping occurred. Table 10 displays the measures of clumping over time in the different years. Whereas later in the season clumping was mostly influenced by the scarcity of nesting habitat and simply increased with the number of pairs settling, March clumping seemed more related to habitat features. A graphical presentation of early nest distribution and the progress of clumping in the Footbridge colony for 2003 was published in Waterbirds (Konter 2005). Fig. 8 displays a similar presentation for the year 2005.

In the Reeds, clumping occurred already with the first mappings of platforms in each year. From 2003 to 2006, all together 24 cases of March clumping were recorded. 21 of these concentrations existed in the wider and denser parts of the Reeds. The remaining three groups were located at the begin of Reed IIA where the stands were rather robust, but more scattered.

Inside the Bulrush, the only two nests clumped in the second decade of March 2003 were located right at the start of the section where the vegetation was widest. The first two nests clumped in 2005 were built more in the centre where, for a short distance, two rows of vegetation spread one behind the other. In that year, the begin of the section was in particularly bad shape.

Although no measures of the quality of the habitat were directly performed, for instance by assessing the density of stands per $m^2$ throughout the colony, the entire habitat was inspected visually in the beginning of the season and the major results of this assessment were noted down. With respect to this judgement, it appeared that early clumping of nests occurred in better quality parts of the colony, especially in places where the grebes could enter deeper into the vegetation, while additional places for settlement, possibly slightly less suited, remained yet unoccupied. It could however not be excluded that other factors, such as site fidelity or the presence of other breeding species in the colony also could have impacted early clumping.

In early May of each year, the constant gradual decrease of distances between neighbouring platforms led to a situation where nearly all platforms were clumped and nesting densities inside the colony were extremely high with 13.8 to 17.8 platforms per 100 $m^2$ from 2003 to 2007 (Table 14).

Most other studies about coloniality in the Great Crested Grebe did not touch in substance upon the subject of seasonal evolution of distances between nesting platforms, but rather concentrated on end distances and end densities. Only Koshelev (1985), studying the subject at Tiligul' liman estuary near Odessa, noticed that the formation of a colony started with a more or less simultaneous settlement of several pairs at distances from one another comparable to the situation of solitary breeders. With new pairs settling in between the first platforms, the size of the territories and the distances between neighbouring nesting platforms gradually shrank in the course of the season. It was finally this process that led to the situation of aggregated breeding.

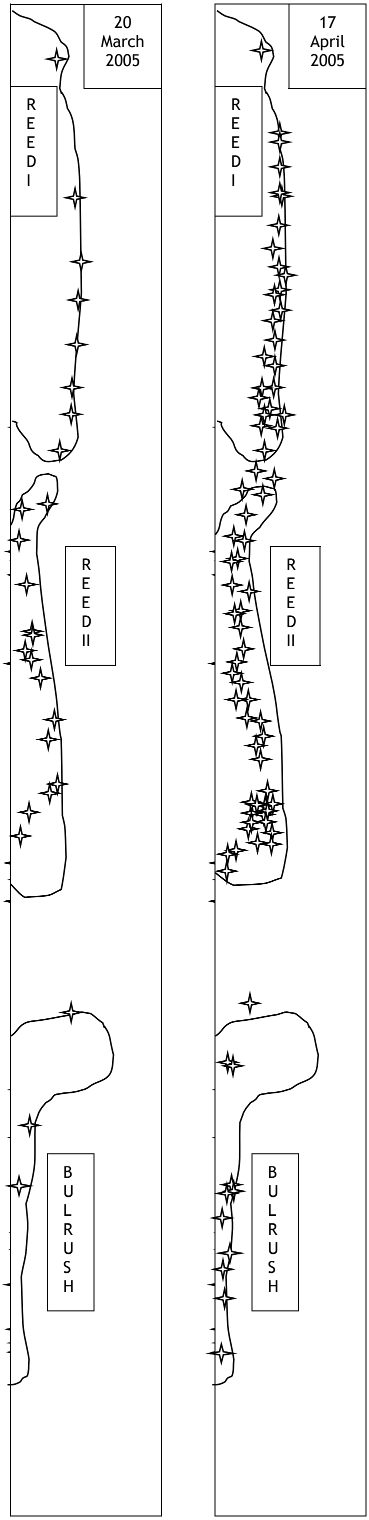

**Fig. 8:** Schematic presentation of the location of the platforms in the Footbridge colony on 20 March and 17 April 2005.

**Table 10:** Numbers of Great Crested Grebe platforms clumped within 3 m with in parentheses the numbers of groups of platforms obtained by applying the 3 m distance criteria.

| Decade | All reeds | | | | Bulrush | | | |
|---|---|---|---|---|---|---|---|---|
| | 2003 | 2004 | 2005 | 2006 | 2003 | 2004 | 2005 | 2006 |
| 2nd decade March | 10 (4) | | 2 (1) | 3 (1) | 2 (1) | | 0 | 0 |
| 3rd decade March | 38 (11) | 6 (3) | 29 (11) | 15 (6) | 4 (2) | 0 | 2 (1) | 0 |
| 1st decade April | 46 (14) | 24 (8) | 39 (8) | 47 (11) | 2 (1) | 0 | 5 (2) | 2 (1) |
| 2nd decade April | 66 (13) | | 60 (11) | 65 (9) | 9 (3) | | 5 (2) | 9 (3) |
| 3rd decade April | 88 (11) | 75 (7) | 81 (11) | 82 (9) | 18 (3) | 7 (3) | 8 (4) | 13 (4) |
| 1st decade May | 94 (11) | 88 (7) | 87 (11) | 90 (6) | 21 (4) | 15 (5) | 11 (5) | 13 (4) |

With respect to end concentrations of colonial nests, the situations encountered on different study sites and even on the same study site in different years could vary greatly. On the German Lake Gothen, minimum distances between platforms were 5 m in 1978 (n=18), but only 1.5 m in 1980 (n=45, Meyer 1992). On the Polish Lake Żarnowieckie, Moskal and Marszałek (1986) studied four different colonies and they obtained distances comprised between 0.5 m and 2 m (n=98), 2 m and 5 m (n=58), 1.5 m and 5 m (n=148) and 0.5 m and 4 m (n=84). Whereas at Lake Gothen, the relationship between nests distances and the numbers of platforms seemed obvious, no clear trend appeared on the Polish lake.

### 2.1.4 Competition for nesting sites and inter-actions with other species

Other nesting species within the colony were rails Rallidae and one pair of Mute Swans *Cygnus olor*. Their nests were mapped at the same time as the grebes' nests were. The two to three pairs of Moorhen *Gallinula chloropus*, the pair of Water Rails *Rallus aquaticus* and the swans built their nests on firm ground and, thus, did not directly compete with the grebes for nesting places.

**Coots:** Due to the inclusion of the nests occupied by Eurasian Coots in the regular mapping of the colony, their date of appearance, their content and their numbers in time were known. Counts of the coots present were not executed regularly and their population size was deduced from their number of platforms. The few counts of coots basically proved that the species was already present at the Footbridge colony when the grebes started to arrive. Nevertheless, in all years they started their settlement later than the Great Crested Grebes (Table 11). Excluding 2003, when a mid-March coot platform disappeared one week later, first coots settled at the earliest towards the end of March or in the beginning of April and it generally lasted until the last decade of April before more coot platforms appeared. In all years except 2007, about 40 or even more grebe platforms existed when the first coots started to occupy their platforms. Due to the late settlement of the grebes in 2007, the early-April number of grebe platforms was comparably low.

**Table 11:** Evolution of the number of coot and grebe platforms in the Footbridge colony in the different years.

| Year | 2003 | | | | | 2004 | | | | 2005 | | | | | 2006 | | | | | 2007 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 09.03. | 16.03. | 23.03. | 30.03. | 08.05. | 31.03. | 03.04. | 24.04. | 08.05. | 18.03. | 25.03. | 01.04. | 08.04. | 07.05. | 18.03. | 25.03. | 08.04. | 15.04. | 07.05. | 07.04. | 27.04. | 05.05. |
| Grebe platforms | 19 | 35 | 45 | 68 | 126 | 37 | 45 | 97 | 113 | 21 | 39 | 52 | 61 | 111 | 17 | 35 | 61 | 83 | 115 | 34 | 96 | 111 |
| Coot platforms | 0 | 1 | 0 | 3 | 8 | 0 | 2 | 2 | 6 | 0 | 1 | 2 | 1 | 6 | 0 | 0 | 1 | 2 | 6 | 2 | 6 | 6 |

The coots also constructed their platforms inside the water and therefore were potential competitors to the grebes for nesting sites. Observations on individual platforms illustrated challenges of property between both species.

In 2003, the ownership of six platforms was eagerly competed between the Great Crested Grebes and the coots and it changed over from coot to grebe or vice-versa several times before one species was able to claim final ownership. In 2004 and 2005, each time five platforms were similarly competed, in 2006 it were seven platforms and in 2007 four platforms. In most cases, it seemed as if the grebes had started the construction of the platform and the general earlier settlement of grebes might be advanced in support of this thesis. According to our assessment, from the total of 27 platforms quarrelled about in the five years of the study, 14 were most likely started by the grebes, eight by the coots and for five, the initiator remained unknown. From the 14 platforms initiated by the grebes, two were so as second platforms and losing them to the coots did not directly harm the grebes. Even so, the grebes defended them and only one second platform changed over to the coots. The defence of the other proved costly for the grebes: although they succeeded in keeping their nest, one only egg was lost in a fight with the rail. From the eleven remaining initial grebe platforms, five were conquered by the coots while the grebes took over six from the eight initial coot platforms. The five remaining platforms with unknown initiator were finally occupied two by the grebes and three by the coots.

Such competition for a platform between both species could last for just one or two days or spread over two or three weeks, with frequent changes of occupants. If a competed platform was occupied by a coot, the grebes threatened from inside the water in front. They never tried to chase the rail by attacking it on the platform and they also remained generally outside pecking distance of the coot. Their threats could however continue for up to 30 minutes and the grebes could resume threatening after short interruptions. When the mate of the rail showed up, it most often readily attacked the threatening grebes, rushing towards them over the water surface. The grebes dived and attacked from below water. Also a coot leaving a competed platform was often harassed with under water attacks. Only twice, a short fight with physical contact occurred between both species. If a coot platform was occupied by the grebes, the coots quite often attacked the grebe on the nest. The latter generally hurriedly left. It cannot be said whether one species was more insisting in this game than the other. This appeared to be more depending on individual pairs, possibly also on whether an alternative site offering less resistance could be found. While in hold of a platform, each species continued building. If the coots were able to elevate the platform sufficiently so that the grebes got problems when trying to jump upon it, they had gained final ownership.

**Table 12:** Total number of coot nests per year and distribution per vegetated area.

| Area | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|
| Reed IA | 2 | 1 | 2 | 2 | 2 |
| Reed IB | 2 | 1 | 0 | 0 | 0 |
| Reed IIA | 0 | 0 | 0 | 1 | 0 |
| Reed IIB | 2 | 2 | 1 | 1 | 2 |
| Bulrush | 2 | 2 | 3 | 2 | 2 |
| Total | 8 | 6 | 6 | 6 | 6 |

In 2006, the scenario experienced deviated slightly from what seemed to be common practise. A pair of grebes, chased from a platform started by it, initiated a new platform in some 2 m distance. The new construction was also immediately claimed by the same pair of coots and the grebes changed for the first platform, where they continued building. Again chased a bit later by the coots, the grebes resumed their work on the second platform. This game continued for more than two weeks before each species definitively occupied one of both platforms.

The competition for nesting sites between both species possibly started to come down in early May of each year when the first grebe families left for Lake IJssel. Their now abandoned platforms could be occupied either by not yet settled conspecifics or by the rails. Later in May, when more grebes left with their chicks for the lake, even more coots could settle down. Thus, on 17 May 2003, two pairs of coots took over the nests of grebes after the successful hatching of the grebes' eggs.

As Table 12 shows, the coot platforms finally spread all over the habitat of the colony. Their numbers remained very limited in all years. The coots did not occupy marginal areas inside the

**Table 13:** Number of grebe platforms in a distance of less than 5 m to a coot platform, shortest and average distance of such grebe platforms to the single coot platforms as in early May of each year.

| Year | Coot platform n° | R1 | R2 | R3 | R4 | R5 | R6 | R7 | R8 |
|---|---|---|---|---|---|---|---|---|---|
| 2003 | Number of grebe platforms =< 5 m | 2 | 1 | 7 | 7 | 5 | 9 | 4 | 1 |
| | Shortest distance to the coot platform (m) | 2.2 | 4.6 | 0.8 | 1.2 | 0.7 | 1.0 | 0.8 | 4.0 |
| | Average distance to the coot platform (m) | 3.5 | 4.6 | 2.1 | 2.4 | 2.8 | 2.6 | 2.8 | 4 |
| 2004 | Number of grebe platforms =< 5 m | 2 | 9 | 6 | 10 | 2 | 2 | / | / |
| | Shortest distance to the coot platform (m) | 1.2 | 0.7 | 1.5 | 1.5 | 0.4 | 2.2 | / | / |
| | Average distance to the coot platform (m) | 2.2 | 2.6 | 2.6 | 3.3 | 2.4 | 3.5 | / | / |
| 2005 | Number of grebe platforms =< 5 m | 3 | 3 | 7 | 2 | 2 | 1 | / | / |
| | Shortest distance to the coot platform (m) | 1.5 | 1.1 | 0.4 | 2.5 | 1.2 | 2.3 | / | / |
| | Average distance to the coot platform (m) | 2.9 | 3.3 | 2.1 | 2.9 | 2.2 | 2.3 | / | / |
| 2006 | Number of grebe platforms =< 5 m | 2 | 4 | 7 | 10 | 2 | 2 | / | / |
| | Shortest distance to the coot platform (m) | 1.3 | 1.8 | 0.9 | 0.9 | 1.1 | 1.5 | / | / |
| | Average distance to the coot platform (m) | 1.5 | 3.3 | 2.8 | 2.7 | 3.0 | 2.4 | / | / |
| 2007 | Number of grebe platforms =< 5 m | 4 | 2 | 6 | 7 | 2 | 0 | / | / |
| | Shortest distance to the coot platform (m) | 1.1 | 1.0 | 0.3 | 0.2 | 1.2 | 10.2 | / | / |
| | Average distance to the coot platform (m) | 1.9 | 1.5 | 2.4 | 1.8 | 1.7 | / | / | / |

colony, but established their platforms in between those of the grebes. To what extent could the aggregated nesting of both species have provided advantages or disadvantages to the grebes?

Table 13 proves that, depending on the location of the coot nests, a more or less important number of grebe nests could surround them at rather low minimum and average distances. Due to the close presence of the aggressive coots, these grebes could have profited from enhanced protection against predators. The coots were however generally later in their settlement so that at least most grebes surrounding their platforms could not have actively searched the neighbourhood of the rails unless their nests appeared each year at exactly the same places.

When comparing the placement of the coot platforms in between years, site fidelity may have occurred to some extent at three locations. Indeed, for three sites, the exact locations of the platforms differed in four years only for a maximum distance of 3.5 m, 4 m and 2m. For the remaining coot platforms, no site fidelity was involved and the grebes could generally not have decided on their settlement place in prediction of a later close coot platform.

Even though, the grebes could have passively profited from the presence of the coots by synchronizing their breeding. Indeed, coots are most pugnaciously defending their territories when on the eggs. In 2003, a first coot clutch with two eggs was registered on 18 April when the grebes had already started 70 clutches, the first having appeared on 30 March. Also in 2006, the first coot clutch with four eggs was noted down on 16 April. Eight days earlier, 23 grebe nests contained one to three eggs. In 2004, one pair of coots was really early and laid a first egg on 2nd April, two days before the first Great Crested Grebe started its clutch. In 2005, both species also started egg laying in early April, the grebes possibly just before the coots as on 2nd April, a coot nest contained two eggs while two grebe nests held three eggs. One week later, the grebes had started 29 clutches, the coots still only one. In 2007, one coot nest contained two eggs on 6 April while one grebe nest contained four eggs and no second grebe had initiated its clutch. Although in some years an individual pair of coots managed to start a clutch early and more or less at the same time as the early grebes, most coots started egg laying much later, during the second half of April. Even most grebe nests directly clumped with coot nests received their eggs first so that at the end, egg laying by both species seemed unrelated.

With a maximum of eight nesting pairs in 2003 and six pairs in 2004-2007, the presence of the coots could probably not really affect the maximum number of grebe platforms in each year. This could have been the case if the coots concentrated their nesting and thereby inhibited the presence of grebes in parts of the habitat. Yet, the platforms of the coots were at rather high distances from each other (minimum distances of 13 m, 23 m, 16.5 m and 15 m in 2003, 2004, 2006 and 2007 respectively). Only in 2005, two coot platforms were at a distance of 4 m, the second lowest distance between two platforms of the species was already 25 m. The distribution of the few pairs of coots all over the Footbridge colony at a moment in time when many grebes had already established themselves rather forced the coots to accept the nearby presence of many Great Crested Grebes.

Threats for the grebes' nesting platforms and their contents could stem from the occasionally high interest the coots showed for the plant material that the grebes had gathered for composing their platform. The coots used parts of the plants for food and they sometimes even did so when the owning grebe was already incubating. The threatening by the grebe could sometimes last for long before the coot was convinced to search for alternative food resources.

Once both species were nesting, neighbouring pairs often stole nesting material from one another, from attended and from unattended platforms. The grebes often did so by diving and stealing more from the base of attended platforms. As a reaction, the victims of such robbery threatened intensively and sometimes engaged in short pursuits.

Coots fighting close to the vegetated areas could endanger the platforms and later the nests and eggs of the grebes. If such opponents came too close to a grebe construction, the owner could intervene by jumping into the fight, too. The coots then, astonished, stopped their aggression for a short moment before resuming with vigour, kicking with their feet, now hopefully moving into a different direction.

As will be illustrated in chapter 2.3.1, coots could not only accidentally cause egg loss to the grebes, they did also actively destroy their clutches.

In the course of each breeding season, the potential roles of the coots with respect to the grebes changed from simple food gatherers to competitors for platforms and at the end to possible predators on their eggs. Not astonishingly, the attitude of the grebes towards the coots changed, too. In March, the settled grebes hardly took notice of the rails that were lingering about searching for food within the limits of the colony. The occasional aggressions of the grebes towards them appeared to be more a displacement activity than to be really directed against the rails. They mainly occurred while the grebes were engaged in intra-specific threatening and other aggressions and an imprudent coot was passing too close. The coots used occasionally the unoccupied grebe platforms for preening. At this stage, the returning grebes appeared to be more patient with the occupants and their threatening was less intense. The more grebes had settled, and especially after they had initiated their clutches, the more their aggressiveness towards the rails seemed to rise. Incubating grebes always threatened and uttered upset calls at coots nesting in their direct vicinity when these passed by for reaching or leaving their nests. The coots were generally not impressed, unless when occasionally attacked under water. The grebes never got really accustomed to neighbouring coots and harsh aggressions between both species were possible at all times. Even in early May, incubating grebes were observed to leave their clutches or their nests with partial hatching to resolutely attack the rails in their vicinity. The precise reasons for such reactions remained unknown. Maybe they were prophylactic to indicate to the coots that the grebes were vigilant and strong enough to protect their nests and even more their clutches.

In literature, many indications for close nesting of grebes and rails can be found. The European grebe species often breed in close vicinity of coots (Blinov et al. 1981, Goc 1989, Konter 2002, 2007:2, Onno 1966, Smogorzhevskiy 1979, Stanevičius 1994). Nest distances between both species can be very low: 70 cm (Kehl 2005), 52 cm (Stark 1969), 50 cm (Engler 1999). Occasionally, their platforms even touch (Jonkers et al. 1987, Perry 2000). In spite of the risks of egg predation by the coots on grebe eggs, it is often pretended that the aggressive defence of its nesting territory by the rail helps to avoid grebe egg loss to other predators. Engler (1999) and Stanevičius (1994) confirmed the earlier nesting of the rail and Blinov et al. (1981) believed that the grebes search for the neighbourhood of the incubating coots. This could explain why often more grebe nests exist in close vicinity of a single coot platform (Blinov et al. 1981, Koshelev 1981, Stanevičius 1994). In the steppe of Baraba, Koshelev (1981) found 15% of the Great Crested Grebe's nests in a distance of less than 7 m from coots. In regions with increased densities of predators, the vicinity of coots or other nesting species could be beneficial to the grebes. This was proven by Goc (1989), who noticed a higher hatching success for grebes associated with coots or Larides than for those nesting away from such species. Especially coots are very aggressively defending their nests against birds of prey and other predators and they often succeed in chasing them away. In addition, birds of prey mostly react to movement: the upset reaction of the coot would possibly deter the attention of the predator from the motionless grebe that could remain unnoticed (Konter 2002).

In the absence of predators, as in Enkhuizen, the rather similar nesting needs of grebes and coots combined with limitations in the nesting habitat available could nevertheless trigger close nesting of both species. Also in Lithuania, on three lakes with surface limitations in nesting habitat, platforms of both species existed in close vicinity (Stanevičius 1994). From the North Irish Lough Neagh, Perry (2000) reported short distances between the platforms of coots and Great Crested Grebes in some areas with limited nesting opportunities. Such conditions would also explain the occasionally vigorous competition for nesting sites between both species. The extent of the shortage in nesting habitat, especially if contrasting with food resources available, would impact the degree not only of intra-, but also of inter-specific competition. Their outcome would generally remain open. Whereas Perry (2000) only mentions coots taking over the platforms of grebes on Lough Neagh, Stark (1969) referred to the Great Crested Grebe as a parasite profiting from the building efforts of the hard working coots. Ulenaers and Dhondt (1991) noticed coots taking over the platforms started by the grebes and Harrison and Hollom (1932) reported two cases where the coots removed the eggs of the grebes to replace them by their proper eggs. If it is generally not sure from the start which species will be the winner in the competition for a platform, in extreme cases, the rivalry could influence the population numbers of the two species at a specific locality. On two English lakes, numbers of coots collapsed between 1927 and 1931 whereas at the same time the population of the Great Crested Grebes increased. On six other lakes investigated during the same period, the rails increased in numbers and the grebes diminished (Harrison & Hollom 1932).

The degree of habitat shortage could not only explain the degree of competition between both species, but also their behaviour towards one another. According to Ryazanova (2002), coots are very tolerant against grebes during their entire breeding cycle. On Lake Potsdam, Kehl (2005) noticed a grebe leaving its clutch unobserved to threaten at the coot incubating at a distance of only 70 cm. Also in Enkhuizen, the potential for aggression remained high during incubation. The need for vigilance by the grebes appears to be justified with respect to the damage the coot can cause to the clutches of the grebes. Harrison and Hollom (1932) reported destruction of grebe clutches by coots from 29 of 83 lakes. In Northern Ireland, Perry (2000) observed the coots to predate on eggs momentarily left unobserved. Coots were detected as the major predator on clutches in a monospecific grebe colony that lost about 50% of the eggs. On Lake Ratzeburg, a coot with five chicks harassed an incubating grebe until it left the nest. Then the rails pecked two eggs to feed on their content (Wenske in Konter 2002). Goc (1989) and Fjeldså (2004) also confirmed the risks for the clutches of Great Crested Grebes deriving from coots. Depending on circumstances, the protection granted by the coots could more than annihilate the damage caused by them to the clutches of the grebes.

It remains to be mentioned that occasionally mixed clutches of grebe and coot eggs occur or that one species incubates the eggs of the other. Harrison and Hollom (1932) reported upon two clutches of two and seven coot eggs incubated by Great Crested Grebes and two additional pairs of grebes incubated mixed clutches. Stark (1969) found two mixed clutches, one incubated by the grebes, the second by the coots.

**Gulls and terns:** In Enkhuizen, gulls or terns occasionally showed up over the colony, but they did not nest there. No acts of predation on either eggs or pulli of grebes were observed. Whereas the protective advantage of association with coots could be limited to solitary breeding grebes, depending on local circumstances, colonial Great

Crested Grebes could be better off if associating with more numerous other breeders, especially gulls and terns. Colonies of Great Crested Grebes are not necessarily mono-specific, and in quite a number of cases, it appeared that the aggregated nesting of the grebes was at least to some extent triggered by their association with Larides that could eventually provide advantages to the grebes. Thus, Meyer (1992) noticed the appearance of a new grebe colony (n=17) on Lake Gothen at the edge of an expanding gull colony holding already some 300 pairs at that moment. A second smaller colony of seven grebe pairs established itself inside a colony of Laughing Gulls *Larus ridibundus*, but it disappeared soon following inter-specific aggressions and silting-up of the area. At the estuary of Tiligul' liman, 90% of the grebe colonies existed in association with breeding gulls and terns. Koshelev (1985) supposed that the gulls and terns provided enhanced protection for the grebes and their clutches because their more elevated constructions offered better visibility and thereby earlier warning from approaching dangers. Monospecific colonies of Great Crested Grebes there experienced clutch losses of 70% and sometimes 100% if anthropogenic disturbances were regular, due to predation by Crows and Western Marsh Harriers *Circus aeruginosus*. According to Blinov et al. (1981), Siberian Great Crested Grebes preferred to nest in colonies of gulls or terns. If these species changed their nesting sites from one year to the next, the grebes followed them. On Lake Menzelinskoe, the Terns once changed their site in the course of the season. The grebes, now left on their own, saw the contents of their nests destroyed by Hooded Crows *Corvus cornix*. On Lake Belukha, the grebes abandoned their clutches when the Terns deserted the place (Koshelev 1981). At Lake Drużno, mono-specific colonies of grebes as well as mixed colonies with Laridae existed. Whereas in the first, the nesting success of the Great Crested Grebes reached only 18%, those pairs associated with gulls synchronised their breeding with the latter and 58% of the nests knew hatching. In addition, simultaneous switches by Laughing Gulls and Great Crested Grebes occurred in the colonisation of areas and local densities of grebes were higher in mixed than in mono-specific colonies. The basis for the close association could hardly be explained by an overlap in nesting requirements of both species and Goc (1986) found it to reflect an active search by the grebes for the vicinity of the gulls.

### 2.1.5 Comparison of occupancy patterns and nesting density between the sections of the colony

This section concentrates mainly on differences in the grebes' timing of settlement between the different zones of the Footbridge colony within one season. It also evaluates the final nesting density achieved per section. Throughout all years, a seasonally variable number of loose heaps were registered in the different sections of the Footbridge colony (Table 4). As their number only impacted the results of the analysis in 2003, they were generally not included in the analyses of other years.

In 2003, the growth in the number of basic and solid platforms in Reed II was very continuous for most of the season and Reed II achieved the highest final nesting density. Reed I knew an elevated early March number of platforms. It was reduced only one week later. Until the end of March, important increases followed. Throughout April and until early May, the growth rate of Reed I platform numbers was rather regular, but inferior to those of the other two sections, especially in late April. The evolution in the Bulrush was generally more erratic. After increases in the number of platforms in March, a complete reversal of the trend occurred during the first decade of April. The important decrease was followed by strong increases in settlement from mid-April onwards. The number of Bulrush platforms was the lowest of the three sections at all times, but the sustained increase late in the season significantly narrowed the gap in terms of density, especially with respect to Reed I. The picture changed when loose heaps were included, in the sense that the mid-March downward trend in Reed I disappeared. This could be explained by the effect of weather conditions that reduced the quality of some platforms from basic to loose heaps. On the opposite, the early April evolution in the section became more erratic and showed even a slight downward movement before increasing again.

The short field program of 2004 probably masked a more irregular settlement pattern by the grebes than observed. In late March, important numbers of platforms existed in both Reed sections, but not in the Bulrush. Reed II sustained a high increase rate for the first two decades of April. Thereafter,

**Table 14:** Evolution of the nesting density (platforms/100 m²) in the sections of the Footbridge colony, including only basic and solid platforms.

| Date | | Reed I | | Reed II | | Bulrush | | Colony | |
|---|---|---|---|---|---|---|---|---|---|
| | | Density | n | Density | n | Density | n | Density | n |
| 2003 | 09.03. | 3.33 | 10 | 2.29 | 8 | 0.5 | 1 | 2.24 | 19 |
| | 16.03. | 2.33 | 7 | 4.86 | 17 | 2.5 | 5 | 3.41 | 29 |
| | 23.03. | 5.33 | 16 | 6.29 | 22 | 3 | 6 | 5.18 | 44 |
| | 30.03. | 7.67 | 23 | 7.71 | 27 | 5.5 | 11 | 7.18 | 61 |
| | 05.04. | 8.00 | 24 | 8.86 | 31 | 2.5 | 5 | 7.06 | 60 |
| | 13.04. | 9.33 | 28 | 10.86 | 38 | 4.5 | 9 | 8.82 | 75 |
| | 18.04. | 10.00 | 30 | 12.29 | 43 | 7.5 | 15 | 10.35 | 88 |
| | 01.05. | 11.67 | 35 | 16.57 | 58 | 10.5 | 21 | 13.41 | 114 |
| | 08.05. | 13.00 | 39 | 17.14 | 60 | 11.5 | 23 | 14.35 | 122 |
| 2004 | 31.03. | 3.00 | 9 | 2.86 | 10 | 3 | 6 | 2.94 | 25 |
| | 03.04. | 6.00 | 18 | 5.43 | 19 | 3 | 6 | 5.06 | 43 |
| | 25.04. | 10.00 | 30 | 15.14 | 53 | 7.5 | 15 | 11.53 | 98 |
| | 08.05. | 11.67 | 35 | 16.57 | 58 | 9.5 | 19 | 13.18 | 112 |
| 2005 | 18.03. | 2.67 | 8 | 3.43 | 12 | 0.5 | 1 | 2.47 | 21 |
| | 24.03. | 4.33 | 13 | 8.00 | 28 | 3.5 | 7 | 5.65 | 48 |
| | 26.03. | 5.00 | 15 | 8.00 | 28 | 4 | 8 | 6.00 | 51 |
| | 02.04. | 6.00 | 18 | 8.00 | 28 | 3 | 6 | 6.12 | 52 |
| | 08.04. | 7.00 | 21 | 9.14 | 32 | 4 | 8 | 7.18 | 61 |
| | 17.04. | 9.00 | 27 | 11.43 | 40 | 5 | 10 | 9.06 | 77 |
| | 23.04. | 11.00 | 33 | 13.71 | 48 | 7.5 | 15 | 11.29 | 96 |
| | 30.04. | 12.00 | 36 | 14.86 | 52 | 7 | 14 | 12.00 | 102 |
| | 07.05. | 12.33 | 37 | 16.29 | 57 | 8.5 | 17 | 13.06 | 111 |
| 2006 | 18.03. | 1.13 | 3 | 1.71 | 6 | 1 | 2 | 1.35 | 11 |
| | 24.03. | 3.40 | 9 | 4.00 | 14 | 2.5 | 5 | 3.44 | 28 |
| | 26.03. | 3.77 | 10 | 5.14 | 18 | 2 | 4 | 3.93 | 32 |
| | 08.04. | 6.04 | 16 | 8.86 | 31 | 4 | 8 | 6.75 | 55 |
| | 16.04. | 8.30 | 22 | 13.43 | 47 | 6.5 | 13 | 10.06 | 82 |
| | 29.04. | 9.43 | 25 | 15.43 | 54 | 8.5 | 17 | 11.78 | 96 |
| | 06.05. | 10.57 | 28 | 20.00 | 70 | 8.5 | 17 | 14.11 | 115 |
| 2007 | 08.04. | 3.01 | 9 | 0.29 | 19 | 3.00 | 6 | 4.00 | 34 |
| | 28.04. | 9.02 | 27 | 13.71 | 48 | 10.5 | 21 | 11.28 | 96 |
| | 05.05. | 10.02 | 30 | 15.71 | 55 | 13.00 | 26 | 13.04 | 111 |

it levelled off. In Reed I and in the Bulrush section, increases throughout April and until early May were less important, but regular.

In 2005, more irregular patterns were observed. In both Reed sections, the numbers of platforms were comparable by mid-March. During the early third decade of March, Reed II experienced tremendous increases in platform numbers, followed by a short period of stagnation before resuming a more regular upward trend in early April that lasted until early May. In Reed I, the evolution was more regular throughout the season and it levelled off towards the end of April. March settlement in the Bulrush was very limited and platform numbers only increased in the course of April. The evolution remained comparatively fluctuating.

In 2006, mid-March settlement in all sections remained limited and differences in relative numbers of platforms developed later. Reed II followed a sustained growth pattern in April that was even accelerated in May. Reed I and the Bulrush displayed comparably regular, but moderate increases of platforms throughout the settlement period.

In 2007, the data collected did not warrant a more detailed discussion.

In all years, the settlement process intensified earliest in Reed II and latest in the Bulrush. Also, the evolution was generally more erratic in the Bulrush than in the other sections. Comparing initial and final densities achieved during the five years of the study, these were always by far highest in Reed II and lowest in the Bulrush. In Reed I, the values of the density remained intermediate to that of both other sections throughout one season. The differences registered pointed at differences in the initial quality and the seasonal evolution of the habitat, not only between vegetation types, but even more generally between the sections.

## 2.1.6 Differences in settlement between years

The previous section concentrated on differences in settlement between the different subdivisions of the Footbridge colony within the same year. If we have a look at platform numbers at comparable dates in different years (Table 4, Fig. 4, 9, 10), we notice that the growth patterns also differed in between years within the colony as a whole as well as per types of vegetation or per sections.

The entire colony (Fig. 4) held already some 20 platforms in the first decade of March 2003 and 61 at the end of the month. In 2005, a similarly sustained settlement process as in 2003 existed during the second half of March, however towards the end of the month it came to a stand still: the number of platforms was eventually about 50. In none of the other years, such high numbers of settled grebes could be counted in March. In 2004, during the first three weeks of April, platform numbers increased rapidly and mostly made up the difference in total numbers when compared to other years. The short 2004 program may have hidden a more erratic evolution than displayed. Also in 2006, settlement was viscous in early March, but once started, it progressed rapidly for the rest of the season. In 2007, the number of platforms was very low in early April, thereafter it rose quickly. In all years, from mid-April onwards, platform numbers displayed quite uniform upward trends. In early May in 2006, a considerable increase in the total number of platforms exceeding by far the rates of the other years thus late in the season was realized.

An analysis per vegetation type summed up the figures of Reed I and Reed II. Differences in the evolution of platform numbers in total Reeds (Fig. 9)

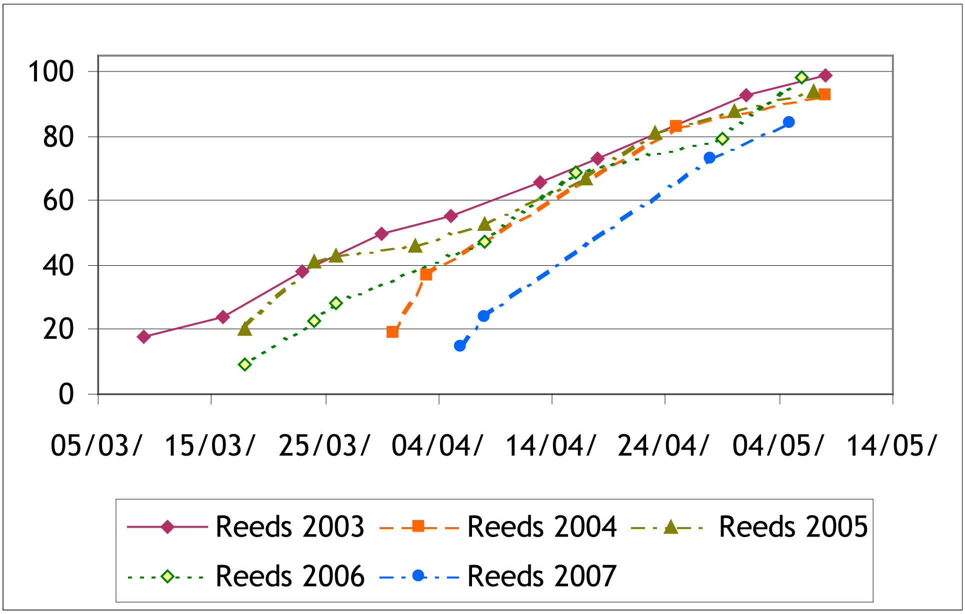

**Fig. 9:** Basic and solid platforms in the reeds (Reed I and Reed II combined) 2003-2007.

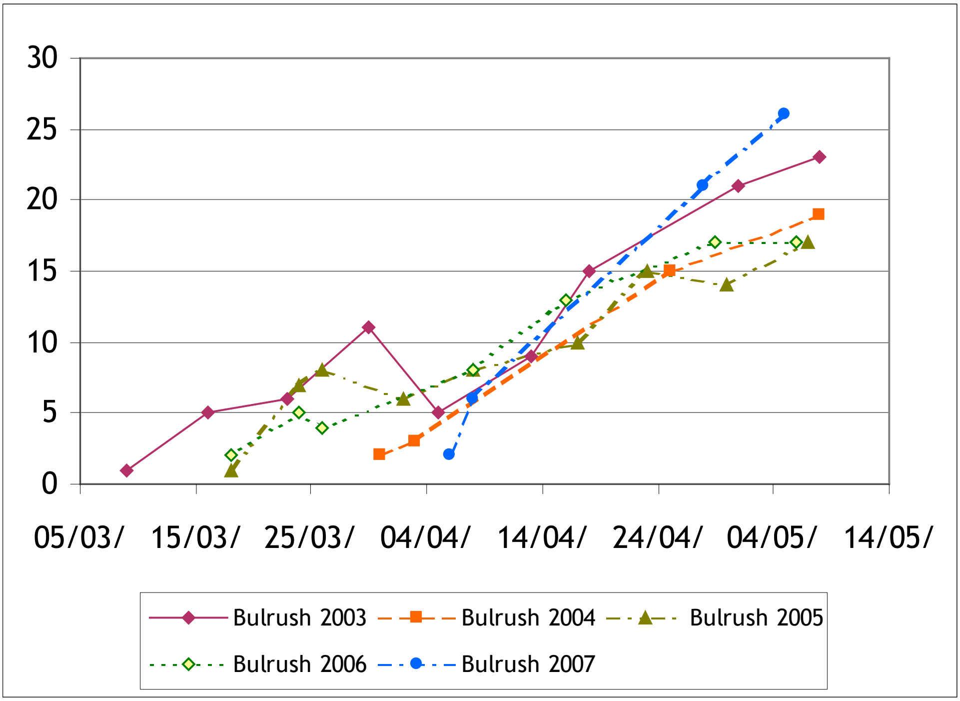

**Fig. 10:** Basic and solid platforms in the bulrush 2003-2007.

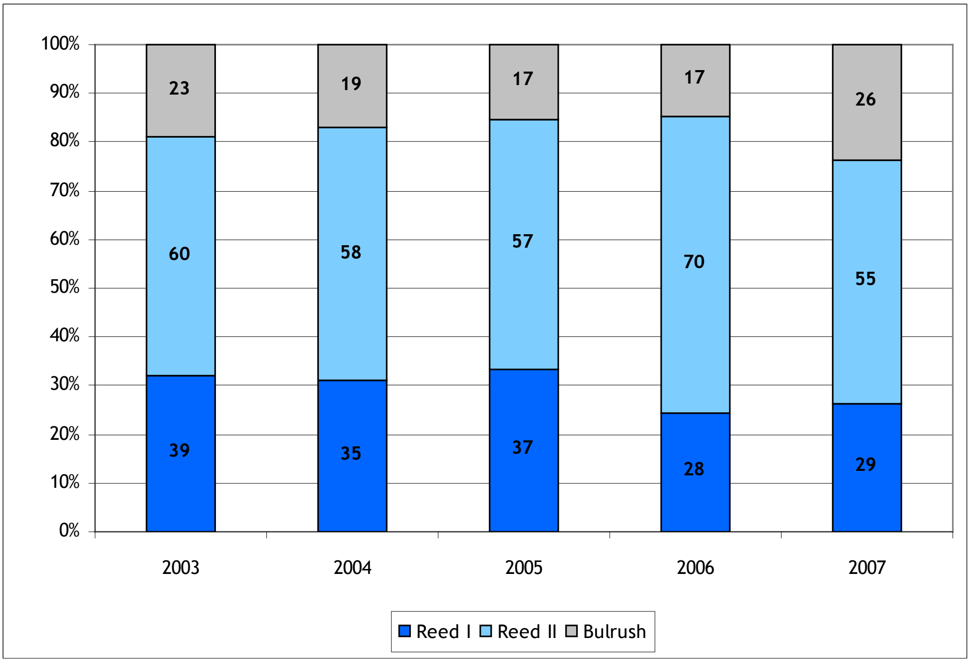

**Fig. 11:** Distribution of basic and solid platforms in the Footbridge colony between the different sections in early May (2003-2007).

in between years were comparable to those noticed for the colony as a whole. The intensification of settlement occurred at varying times in each season, but in time rather continued increases of total Reed numbers of platforms were recorded. A later start of the settlement process was generally combined with an intensified progress, so that in early May of each year the size of the breeding population was rather identical.

In the Bulrush (Fig. 10), platform numbers remained normally low until early April. If March settlement was more intense (years 2003 and 2005), it was also subject to trend reversals that reduced the number of existing platforms again. The bulk of the platforms in the section always appeared starting with the second decade of April of each year and the increase in numbers continued until early May. In contrast to the Reeds, the late evolution of the settlement process remained unpredictable and the final size of the breeding population was very variable.

The relative contribution of each section to the maximum population of the colony in each year (Fig. 11), revealed a constant increase in the percentage of platforms located in Reed II for four years. The absolute number of platforms there remained however rather stable for three years. It increased much in 2006 and dropped equally drastically in 2007. The Bulrush section held an ever decreasing number and percentage of platforms for four years before completely reversing the trend in 2007. Reed I contributed a rather stable part of platforms to the overall picture, except for 2006 and 2007 as a result of partial destruction of the habitat there. A priori, in 2006 the grebes prevented from settlement in Reed I could have triggered most of the increase in platform numbers in Reed II. In 2007, the decreasing number of platforms in Reed II was to a large extent compensated by higher numbers in the Bulrush zone.

Other studies also noticed fluctuations in timing or differences of site occupation patterns from one year to another in colonial Great Crested Grebes. Goc (1986) reported delays of up to ten days between breeding seasons of different years on Lake Drużno. They were apparently unrelated to the weather conditions. On Lake Braband, Henriksen (1992) recorded differences in the timing and the settlement progress of the grebes that could at least partially be explained by atmospheric conditions in the years concerned. On Lake Żarnowieckie, one patch of vegetation held 56 well dispersed nests in 1980, but 84 concentrated nests in 1981 (Moskal & Marszałek 1986). Perry (2000) noticed that the numbers of platforms at each colony on Lough Neagh and their distribution fluctuated in between the years. He recorded a strong correlation between the numbers of Black-headed Gulls nesting at a particular place and the size of the associated grebe's colony: the larger the aggregation of gulls, the greater the number of nesting grebes. Most studies however provided few details about settlement processes in general. They were therefore not in a position to establish whether the occupation pattern of a particular colony was repeated from one year to the next or not. Except for the influence of climate on the timing of settlement and the correlation between the settlement of gulls or terns and the Great Crested Grebes at some locations, other authors provided no insight.

### 2.1.7 Nesting habitat and weather conditions

It is generally assumed that birds occupy prime habitat first. Prime habitat must be defined in the context of the local environment where it is characterized by superior physical or biotic properties serving the needs of the breeding birds better than other habitat available, especially providing safer nesting for the adults and their clutches. The quality of a habitat is not stable in time and it might even depend on population numbers or the presence of other breeding species. For instance vegetation growth can transform less suited habitat in prime habitat.

Over the five years of the study, the quality of the Footbridge habitat was not measured. However, for each day of observation, a general assessment of the habitat conditions was performed and particular attention was given to areas that displayed deviations from the more general features observed. Similarly, only basic indications about the meteorological conditions were noted down. This way of proceeding did not allow monitoring all meteorological changes, especially those that certainly occurred in between observation weekends. The following analysis, therefore, builds on empirical evidence.

**Nesting habitat:** Differences in the quality of the nesting habitat existed from several points of view. First, the widths of the three vegetated areas differed, second the open areas of water in front of the areas differed in size and in their exposure to wind action, third, the density of stands was generally not uniform, even within one section, and, fourth, the early condition of the vegetation differed depending on winter survival, at least between the two types of vegetation.

Looking at the width of the vegetation accessible to the Great Crested Grebes, Reed I was only one or two meters deep for over two thirds of its total length. In Reed II, the minimum width was about two meters, but for more than two thirds of the length of that stretch, the grebes could effectively enter the vegetation for up to six meters. In the Bulrush, a width of about only two meters covered five sixth of the length of that section. Generally, platforms in the narrow parts of the colony were supposed to be more vulnerable as they had to be built closer to the water front and, thereby, there was less vegetation between the anchored construction and the open water to serve for wave braking. A vegetation width dependent analysis of nesting densities (Table 15) failed however to detect such differences as sole argument for the quality of the nesting habitat. In early April, nesting density could be higher in the narrower vegetation parts as well as in the wider parts of the colony and in between years, the order could change. In early May, most often the theoretically more vulnerable narrower parts were the most densely populated. Vegetation width was but one criterion for assessing the suitability of the habitat.

The quality and the density of the stands themselves were others. They were not uniform over the entire colony. Differences existed per vegetation type and per section, but also within sections. Denser stands could contribute to revalorizing the quality of narrower parts of the reeds whereas some wider parts had rather spaced stands. Inside the bulrush, the density of the vegetation was more uniform. *Typha* was generally rather dense close to the dam and more spaced further away.

The main differences between the vegetation types were apparent early in the season. Whereas generally the old stands of *Phragmites* survived the winter in good shape and allowed settlement already from early March onwards, this was not the case in the *Typha*. There, the new vegetation growth annihilated most early differences in the quality of the habitat and it was needed before the bulk of settlement could take place. Before it appeared, most platforms could not be anchored efficiently to the vegetation. In the Reeds, the re-growth of the vegetation mainly contributed to improve nesting conditions in the narrow parts with spaced stands.

With respect to wind exposure, differences inside the habitat were judged minor for three directions from where the dams offered protection and from where most of the time the wind blew. Only to the side of the harbour itself, wind and wave action could have affected the sub-divisions differently. In most parts along the footbridge, boats were anchoring most of the time and they acted as a kind of shield against the winds. This shielding was most effective if the boats anchored very close to the vegetation, in other words, if the footbridge

**Table 15:** Nesting density (nests/100 m²) in early April and in early May according to the width of the vegetation.

| Section | Width | Length | April 2003 | April 2004 | April 2005 | April 2006 | April 2007 | May 2003 | May 2004 | May 2005 | May 2006 | May 2007 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Reed IA | 1-2 m | 70 m | 10.0 | 9.1 | 7.3 | 5.5 | 3.6 | 14.5 | 14.5 | 16.4 | 8.2 | 10.9 |
| Reed IB | 2-6 m | 30 m | 6.8 | 4.7 | 5.8 | 6.3 | 2.6 | 12.6 | 10.5 | 10.0 | 10.0 | 9.5 |
| Reed IIA | ±2 m | 40 m | 9.1 | 7.3 | 9.1 | 11.8 | 7.3 | 19.1 | 16.4 | 18.2 | 21.8 | 19.1 |
| Reed IIB | 2-6 m | 46 m | 12.9 | 5.0 | 8.3 | 8.3 | 4.6 | 17.5 | 16.7 | 15.4 | 19.2 | 14.2 |
| Bulrush (1) | 6 m | 12 m | 2.7 | 4.0 | 1.3 | 4.0 | 4.0 | 6.7 | 9.3 | 6.7 | 8.0 | 12.0 |
| Bulrush (2) | 1-2 m | 60 m | 2.4 | 2.4 | 4.8 | 5.6 | 2.4 | 14.4 | 9.6 | 10.4 | 8.8 | 13.6 |

was close to the vegetated area. This was the case in all parts of Reed I and Reed II, but not in the Bulrush. There, the increasing distance of the vegetation to the footbridge reduced the protection by anchoring boats and the winds could develop more easily higher waves on the increased water surface. In addition, two broader channels ending at the footbridge and allowing the boats to move inside the harbour gave onto the Bulrush.

**Weather conditions:** Weather conditions impacted the nesting progress of the grebes in two ways. First, conditions over winter dictated to a large extent the quality of the habitat early in the season. Second, once the time for settlement had arrived, it influenced the pace of its progress.

During winter 2002/2003, the harbour surface was frozen. When the ice thawed, virtually no emerging vegetation was left in the Bulrush area whereas inside the reeds, the ice had caused only minor damage to the old above water vegetation. As a result, the bulrush was inadequate for nesting before the new growth offered protection and stability for nest construction while early nesting in the Reeds was possible. The old stands of *Typha* survived the next winter in better condition. Thus, in 2004 the Bulrush area was more adequate for platform construction already when the grebes arrived. The 2005 Great Crested Grebes' settlement was preceded by a long period with low temperatures, ice and snow. It left the Bulrush zone in better conditions than in 2003. Nevertheless, its quality for nesting purposes was greatly reduced with respect to 2004. In the Reeds, many stands were cut half way up over the water surface due to the winter snow loads. This did not hamper the grebes excessively. They had to remove some of the broken stands obstructing their movements inside the vegetation and these were easily integrated into the platform constructions. Also the year 2006 was marked by a late spell of winter weather that left the bulrush in a shape comparable to 2005. The reeds remained in rather good conditions. In 2007, the mild winter lasted until long into March. Only in Reed II, the quality of the vegetation was deteriorated and the surviving old stands were often more spaced than in previous years.

The grebes seemed to be generally ready for settlement somewhere in March. Their exact timing depended much on the weather, on temperatures and wind speeds. As long as the temperature remained very close to 0° C or the winds were stormy, the grebes were reluctant to start their constructions. In 2003, the surface of the Compagnieshaven was covered with ice until early March and prohibited anterior settlement. The following rise of temperatures to 3-4° C at night and occasionally 10° C during the day attracted first settlers. The settlement process progressed rather steadily, in line with the general tendency towards weather improvement noted until the end of April. In 2004, mid-March weather was still harsh, and the grebes were generally later in their settlement. In 2005, following bad early March conditions, the weather improved by mid-March and triggered the start of the grebes' settlement. Late March and early April conditions were unstable with partially strong winds that hampered a steady progress in platform construction. A storm during the night of 8 to 9 April finally destroyed most nest-platforms, The process of settlement had to restart from scratch. The wind remained strong until mid-April and temperatures were partially very low for the season, so that the numbers of platforms remained below those of corresponding dates in previous years. Only during the second half of April, the wind calmed down and temperatures and numbers of platforms rose quickly. After a rather mild winter, a drop in temperatures to far below 0°C occurred in late February 2006 and lasted until mid-March when daytime temperatures reached again positive figures. Thus, the first platforms of the grebes appeared also towards mid-March. Until early April, the weather remained very changing, with occasional heavy showers, partially strong winds and days with light night frost. Although many pairs initiated their platforms, their constructions progressed slowly. In 2007, the favourable early March weather was interrupted for about two weeks by a spell of cold and windier conditions. Although during some previous years, the weather had been worse at this point in time, the grebes appeared to delay their settlement immoderately.

Koshelev (1985) and Meyer (1992) agreed that the habitat conditions on one same lake could differ from one section to another and in between years. Thereby, they influenced nest initiation and subcolony sizes section-wise. With respect to platform building, Renevey (1988) noticed that on ponds associated with Lake Neuchâtel, the growth of reeds was about two weeks earlier than on the lake itself. As a consequence, nesting there started also about two weeks earlier. On the Danish Lake

Braband, spring arrival of the grebes varied in between years depending largely on the duration of winter conditions in the region and the period of ice break-up on the lake (Henriksen 1992). On Lake Menzelinskoe, Blinov et al. (1981) calculated that the mass arrival of breeders could differ by one week in between years.

On eutrophic lakes in South Lithuania, the grebes could choose between different vegetated areas. Under such conditions, Stanevičius (1994) proved that structural differences of the reed beds were most important. The grebes built in parts with denser vegetation and thereby achieved better protection against high waves. The morphological restrictions of grebes' locomotion however limit the density and the shallowness of stands that are still suited. On Lough Neagh, Perry (2000) noted that the nesting process of the Great Crested Grebes was affected especially by the wind vectors and the water level fluctuations. The prevailing direction and the strength of winds influenced colony size through the exposure of platforms to wave action. He found a relationship between the geographic location of colonies and the variation in the quality of the preferred nesting habitats of the grebes. In contrast to the findings at the Footbridge colony, Perry believed that the grebes preferred to nest inside the bulrush because it regenerated earlier than the reed and grew to maturity faster. Thereby, it provided earlier and greater protection from predation and inclement weather.

The examples emphasized the dependence of the definition of prime habitat on timing and local conditions that each year anew are predominant for prefixing the settlement process of the local populations. Inside the Compagnieshaven, the Footbridge colony must be considered as a prime habitat as it offered enhanced nesting conditions when compared to the North and the City colonies: it was less exposed to wind and wave action and its width accessible to the breeders was less limited. Within the Footbridge colony, stands

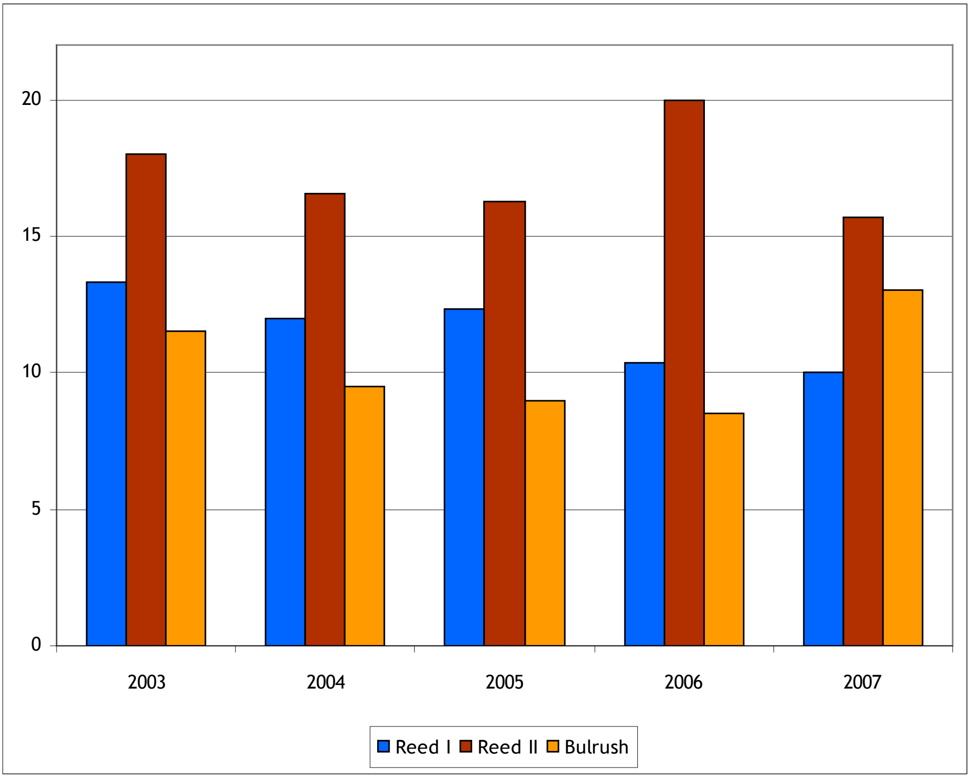

**Fig. 12:** Final nesting density achieved in Reed I, Reed II and the Bulrush zone in 2003-2007 (platforms/100 m²; 2006 density in Reed I corrected for the reduced surface available, 2007 uncorrected).

of reeds in wider vegetated parts of the colony and in the lee of anchoring boats could be considered as prime habitat already early in the season. At other locations, other emerging water plants proved more favourable so that one vegetation type would not be generally more convenient for nesting than another. Structural and other features of the habitat could be at least as important.

In addition, changes in the quality of a habitat in the course of the season occur. Inside the Footbridge colony, early in the season, some reed parts were better suited for nesting than others while most bulrush parts had to wait for the new vegetation growth. This became obvious when comparing the two vegetation types. The mostly narrow bulrush, unprotected from anchoring boats, was only sparsely settled in early April when the nesting densities inside the reeds were already partially high (Table 15). In time, the new vegetation growth transformed most parts of the Footbridge colony into local prime habitat. Thus, by early May of each year, the nesting densities in the sub-sections became more similar.

## 2.1.8 Final nesting density

The maximum number of settled grebes at the Footbridge colony was found during the first decade of May of each year (Table 14) and the related nesting densities in the sections of the colony are representad in Fig. 12. The deduced average nesting density for the five years was 11.52 platforms/100 m² in Reed I (range 10.6-13.0, SD=1.1), 17.14 platforms/100 m² in Reed II (range 15.7-20.0, SD=1.5), 10.20 platforms/100 m² in the Bulrush (range 8.5-13.0, SD=1.8) and 13.55 platforms/100 m² for the colony as a whole (range 13.1-14.4, SD=0.6). Within each section, the figures displayed a lot of variation. At the level of the colony as a whole, the variation was less important.

In different studies, the following end nesting densities were reported (per 100 m²):

- 1.7 platforms on Lake Gothen in 1978 (n=18), but 4.3 platforms in 1980 (n=45) in one colony; 3.8 platforms in 1980 (n=17) and 0.8 platforms in 1983 (n=8) in a second colony. There, the nesting density was very much reduced as a consequence of the combined effect of the reduction in the number of settlers and the higher water levels that increased the vegetated area accessible to the grebes by 120% in 1983. A third colony had a density of 1.4 platforms (n=20) and a fourth of 3.3 platforms (n=5, Meyer 1992).
- On Lake Żarnowieckie, four different colonies ended up with densities of 2.1 (n=98), 1.6 (n=58), 0.3 (n=56) and 0.8 platforms (n=56) respectively in 1980 and of 0.42 (n=20), 0.4 (n=15), 0.7 (n=148) and 1.2 platforms (n=84) respectively in 1981 (Moskal & Marszałek 1986).
- Near Potsdam, the density was 4.6 platforms (n=32) on Lake Zern and 1.0 platforms (n=50) on Lake Werbelin (Litzbarski & Litzbarski 1983).
- On the Northern Irish Lough Neagh, 1,827 breeding pairs were recorded in 1998 and they contributed to a nesting density of 0.2 platforms inside reeds and of 0.4 platforms inside bulrush. The density inside the reeds was about the same as the one reached inside reeds on the Swiss Lake Neuchâtel (Perry et al. 1998).
- A more detailed study that subdivided the borderline of Lake Neuchâtel into sectors yielded densities of 0.72 (n=42), 0.35 (n=206), 0.34 (n=107), 0.18 (n=25), 0.22 (n=359), 0.08 (n=207), 0.13 (n=147), 0.04 (n=28) and 0,10 platforms (n=205) respectively. In some sub-sectors, densities were higher and reached 0.95 (n=76) and 1.1 platforms (n=51, Renevey 1987).

The densities display a great deal of variation between sites, but also between years. In time, part of these differences was explained by changing nesting conditions. In space, part of the differences might be explained by differing methodological approaches of the authors. Indeed, when defining the reference area of the habitat for the calculation of the density, two options appear: either, the basis is a coherent, unbroken stretch of vegetation available to the grebes, whether entirely occupied or not, or it is limited to the area effectively occupied by the nesting birds and unoccupied parts are not included. None of the studies consulted gave clear indications on how it defined the underlying surface area, so that, at the end, it remained open to what extend the figures of different studies were comparable. Also, in colonies of more difficult access, we cannot be sure that the densities obtained were maximum densities. The limited number of visits to most sites may in many cases have failed to identify the in time highest settled population. It is also not sure to what extent platforms without eggs were included in the counts as these could theoretically be second platforms of grebes having initiated their clutches. In Enkhuizen, the birds used the entire vegetation for nesting so that the densities calculated for the Footbridge colony were at the same time related to the surface of the habitat available and the surface effectively occupied. The regular mapping of the nests also always clearly identified the owners of the platforms. The end densities obtained for the colony during the five years of the study were all comprised between 13 and 15 platforms per 100 m². These figures proved to be far above the densities obtained at other sites where the highest density was 4.6 platforms (n=32) on Lake Zern. Even if considering the limitations of comparability insinuated by possible differences in methodology of the various studies, the nesting densities of the Footbridge colony must have been close to the upper limits of densities so far realized by the species. Unavoidably, the question pops up of whether such close breeding can be achieved exclusively by habitat features or whether attraction by conspecifics could be involved. Before trying to answer, let us first analyze possible consequences of the aggregated nesting.

## 2.2 Timing of egg laying, clutch size and incubation time

Over most population densities, intraspecific competition diminishes the fitness conferred upon a habitat's occupants (Rodenhouse et al. 2003 in Johnson 2007). Density dependent consequences could therefore already affect the breeding process of colonial birds. They may impact clutch initiation, its size and the incubation times. Beyond, they might even relate to the survival chances of adults if these had to invest disproportionably in the season's offspring. The latter effects are difficult to measure and we concentrate in the following on possible direct drawbacks during the progress of breeding.

### 2.2.1 Time span from platform building to egg laying

We would normally expect birds to proceed rather quickly from settlement to clutch initiation. If the nesting habitat is in short supply, it could nevertheless be that it is occupied before its condition allows safe nesting, so that it could take some time from the start of platform building to the start of egg laying. Assuming that experienced Great Crested Grebes settled first to occupy the better sites, they should also be the first to initiate their clutches. Due to the improving condition of the habitat in time, later settlers would need less time before

**Table 16:** Time span from platform building to egg laying by decades and vegetation areas in 2003.

| Decades | | 2003 | | | |
|---|---|---|---|---|---|
| | | **Reed I** | **Reed II** | **Reeds** | **Bulrush** |
| March | Mean days | 20.2 | 22.2 | 21.3 | 30.0 |
| | SD | 11.5 | 10.5 | 11.0 | 9.5 |
| | Range | 2-49 | 2-38 | 2-49 | 17-42 |
| | n | 24 | 29 | 53 | 10 |
| D1 April | Mean days | 9.4 | 14.2 | 12.7 | 20.0 |
| | SD | 5.7 | 10.3 | 9.2 | / |
| | Range | 2-17 | 2-29 | 2-29 | / |
| | n | 5 | 11 | 16 | 1 |
| D2 April | Mean days | 7.6 | 6.4 | 6.7 | 4.7 |
| | SD | 4.8 | 8.3 | 7.4 | 5.2 |
| | Range | 3.-13 | 1.30 | 1.-30 | 1-15 |
| | n | 5 | 13 | 18 | 6 |
| D3 April | Mean days | 4.8 | 6.6 | 5.8 | 3.5 |
| | SD | 2.6 | 3.1 | 2.6 | 1.8 |
| | Range | 4-7 | 4-12 | 4-12 | 2-6 |
| | n | 4 | 5 | 9 | 6 |

laying their first egg. Thus, habitat constraints could contribute to a rather synchronous nesting progress of pairs settling at more or less the same moment in time inside the same habitat. To test these ideas, the timing from settlement to clutch initiation of individual pairs in the course of each season was analyzed.

In 2003, for 53 platforms started inside the reeds in March, the average time span between the appearance of a platform and the laying of the first egg was 21 days (range 2-49 days, SD ± 11.0). For some late March arrivals, platform building and egg laying occurred practically in one shot and it took the birds just two to five days to build a platform and lay a first egg. For 16 platforms started in the first decade of April, the average time span was reduced to only 13 days (range 2-29 days, SD ± 9.2). In the second decade of April, 18 platforms were started and received their first egg on average within seven days (range 1-30 days, SD ± 7.4). In the third decade of April, it lasted a mean of six days (range 4-12 days, SD ± 2.6, Table 16). Throughout the season, the average time span from platform building to egg laying and the related range and SD data decreased. But only for platforms started during the third decade of April, range and SD figures were low. Prior, the SD left much room for differences in the settling and nesting strategies of individual pairs. Comparing the two Reed sections, it appeared that the average time span between the appearance of a platform and the laying of the first egg came down already to below ten days in Reed I during the first decade of April whereas it remained at two weeks in Reed II. Thereafter, the average durations for both sections were more comparable, yet in Reed II some pairs needed much time from their start of platform building to clutch initiation.

The evolution in the bulrush (Table 16) was comparable to that of the reeds. Per decade, the average time span between the appearance of a platform and the laying of the first egg decreased from 30 days to 20 days, to 4.7 days and to 3.5 days with similar reductions in SD and range figures. The average time span in the bulrush was much higher than in the reeds for the third decade of March, reflecting the fact that the bulrush vegetation was better suited for nesting later in the season. During the second and third decade of April, the bulrush time spans, range and SD values dropped drastically and to much below the corresponding values of the reeds. Late settlers inside the bulrush were thus prompter to initiate their clutches than conspecifics in the reeds.

In 2005 and in comparison to 2003, mean days from platform start to egg laying were generally much lower for the third decade of March, mostly as a consequence of the later settlement of the grebes in

**Table 17:** Time span from platform building to egg laying by decades and vegetation areas in 2005 and 2006.

| Decades | | 2005 | | | | 2006 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Reed I | Reed II | Reeds | Bulrush | Reed I | Reed II | Reeds | Bulrush |
| D3 March | Mean days | 11.2 | 14.8 | 13.5 | 9.0 | 20.8 | 15.0 | 17.2 | 21.7 |
| | SD | 5.1 | 7.0 | 6.5 | 1.4 | 7.9 | 7.8 | 8.2 | 6.6 |
| | Range | 5-21 | 4-28 | 4-28 | 8-10 | 5-30 | 4-30 | 4-30 | 13-29 |
| | n | 11 | 20 | 31 | 2 | 9 | 15 | 24 | 4 |
| D1 April | Mean days | 8.6 | 5.3 | 6.6 | 3.3 | 8.2 | 8.7 | 8.7 | 8.3 |
| | SD | 5.5 | 3.8 | 4.7 | 1.5 | 2.4 | 5.7 | 5.2 | 7.8 |
| | Range | 2-20 | 1-15 | 1-20 | 2-5 | 6-12 | 2-23 | 2.23 | 2-17 |
| | n | 8 | 13 | 21 | 3 | 5 | 21 | 26 | 3 |
| D2 April | Mean days | 4.3 | 4.6 | 4.5 | 4.4 | 7.4 | 4.8 | 5.6 | 9.4 |
| | SD | 4.0 | 3.8 | 3.8 | 3.3 | 5.2 | 4.0 | 4.6 | 3.3 |
| | Range | 2-15 | 1-15 | 1-15 | 2-13 | 2-17 | 3-17 | 2-17 | 4-12 |
| | n | 10 | 12 | 22 | 10 | 9 | 15 | 24 | 5 |
| D3 April | Mean days | 4.7 | 3.8 | 4.5 | 4.0 | 5.7 | 4.4 | 4.7 | 6.7 |
| | SD | 2.8 | 3.1 | 2.8 | 1.4 | 3.3 | 3.3 | 3.0 | 1.5 |
| | Range | 2-10 | 1-9 | 1-10 | 3-5 | 4-7 | 3-13 | 3-13 | 5-8 |
| | n | 6 | 6 | 12 | 2 | 3 | 10 | 13 | 3 |

that year (Table 17). Thereafter, inside the reeds the mean days displayed a rather continued decrease from one decade to the next. In the bulrush, the average time span was already in March at nine days only and the values remained for the entire season below the figures of the reeds; after a fast drop in the first decade of April, they showed slightly increased values in the second and third decade of April. As for 2003, the range and SD figures came down in time, but they left room for variation in the timing of platform building and egg laying of individual pairs.

The results of 2005 must be considered with prudence as they were biased by the consequences of the storm in the night of 8 April. All the platforms destroyed during this night that did not already contain eggs prior to the storm could not be considered for the time span analysis and this fact also contributed to reduce the upper limit range figures for platforms started in March and in early April. In addition, grebes close to egg laying when losing their platforms, subsequently probably quickly built a new platform, possibly at a slightly different place. The reduced time span needed before this new platform received the first egg was then included in the analysis. Finally, some grebes able to rebuild their platforms at their initial location might have been physically in a position to delay their egg laying and they may have done so to gain time for repairing their platforms.

In 2006, the average time span between the appearance of a platform and the laying of the first egg in the third decade of March was again much increased and showed values comparable to 2003 (Tables 16, 17). In spite of a later settlement, egg laying did generally not proceed quickly. In the reeds, the mean days remained below the values of the bulrush. The time span came down very much during the first decade of April for all sections of the colony. The reductions were continued in the second and third decade of April, except for the Bulrush section. Overall, range and SD figures generally declined in the course of the season, but they left enough room for individualized timing.

The mean time span from the start of platform building to the appearance of the first egg (Fig. 13) and the associated range and SD values were highly variable in the course of one season and between different sections of the vegetated area. The analysis didn't detect much synchronisation in the nesting of the grebes. The increased synchrony in the course of a season was much a consequence of in time improved habitat conditions and possibly of changes in the behaviour of earlier settlers once they were incubating. No sign of active synchronisation efforts by the grebes themselves could however be detected.

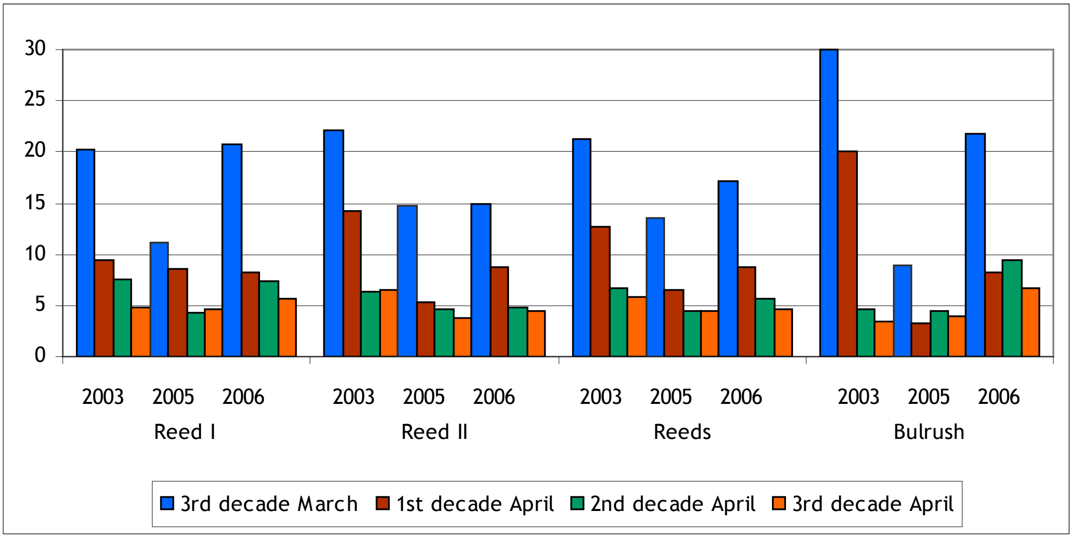

**Fig. 13:** Evolution of the average time span from platform building to first egg laying in 2003, 2005 and 2006 in the different sections of the colony.

Most other studies provided little information about the timing from settling to egg laying of individual pairs. Leys et al. (1969:2) noted that at the Houtribsluizen, nest building was possible in some cases within a week and such nests could then even contain up to four eggs. Platform initiation spread out in time for the colony as a whole. Blinov et al. (1981) found nest construction to last for three to seven days, but no time span from the end of platform construction to first egg laying was indicated. Both studies failed in comparing the evolution of the timing in the course of the season.

### 2.2.2 Synchrony in egg laying

In the previous section, it was concluded that the arrival, settlement and nesting progress of the grebes as a whole was rather asynchronous for the Footbridge colony. The general reduction of the pre-laying period observed in time might nevertheless have led to a rather synchronous egg laying by the different females. Range and SD figures of the time span from platform construction to first egg laying would then mainly reflect differences in timing of settlement by the different pairs. Therefore, the timing of egg laying was analyzed independently from the start of platform building.

The start of egg laying by individual pairs extended from 30 March to 18 May (49 days) in 2003. Disregarding both extreme dates, when only two clutches were started, first egg laying still extended over 33 days. In 2005, first egg laying occurred from 1 April to 4 May (33 days) and in 2006 from 3 April to 6 May (33 days). In all three years, individual pairs spread their start of egg laying over a bit more than one month.

A statistical measure of synchrony was performed for the three years by calculating a mean first clutch laying date for the colony and its associated SD (Table 18). Thereby, the time interval in which most of the laying occurred was determined. In 2003, the mean first clutch egg laying date for the colony was 19 April (SD ± 10 days), the majority of laying occurring between 9 and 29 April. In 2005, the date was 15 April (SD ± 8 days) and in 2006, it was 17 April (SD ± 9 days). In spite of the possible biases in the 2005 figures as a consequence of the storm, the findings were in line with those of the two other years. The major clutch initiation period spread in all years over about 2 ½ weeks and this could be considered as loosely synchronous.

In all the years, differences between the two Reed sections were minor and in line with the findings for the reeds and for the colony as a whole (Table 18). The average clutch initiation dates did not differ markedly between the reeds and the bulrush, except for 2003 when this date was about one week later for the bulrush, most probably a consequence of the negative effects the winter conditions had on the Typha. The latter section generally displayed a greater synchrony than the reeds, especially in 2003 and 2005, with SD values about 3 days shorter (Table 18). We believe however that such improved synchrony was less a consequence of aggregated nesting than of the quality of the habitat. Early settlers in the bulrush were not in a position to stabilize their constructions sufficiently for secure egg reception before the new vegetation grew. In all years, the first clutches in the bulrush were on average about one week later than in the reeds and this explained most of the reduced SD values there.

The degree of synchrony did not increase if restricted areas of the colony were considered. For example in 2003, the first egg in the colony appeared on 30 March. Nine additional nests within 4.5 m of this nest received their first egg

**Table 18:** Average clutch initiation date in different years for different zones of the Footbridge colony.

| Year | 2003 | 2005 | 2006 |
|---|---|---|---|
| **Reed I** | 16.04. ± 10 days | 15.04. ± 10 days | 16.04. ± 8 days |
| **Reed II** | 18.04. ± 10 days | 15.04. ± 8 days | 17.04. ± 9 days |
| **All Reeds** | 17.04. ± 10 days | 15.04. ± 9 days | 17.04. ± 9 days |
| **Bulrush** | 25.04. ± 7 days | 16.04. ± 6 days | 19.04. ± 8 days |
| **Colony** | 19.04. ± 10 days | 15.04. ± 8 days | 17.04. ± 9 days |

on 5 April (3), 13 April (2) and 1 May (4). Seven of these nine platforms already existed on 30 March. The other two platforms appeared one around 10 April and one at 18 April and they received their first egg on 13 April and on 1 May, respectively. In this very limited area, the laying of the first egg was spread over a whole month. Another nest received its first egg on 30 March 2003. At that moment, the closest existing nests were 8.5 m, 5 m, 2 m and 6.5 m away and they received their first egg on 13 April, 18 April and 1 May. The examples proved that neighbouring pairs were not more synchronous in egg laying than any two pairs chosen at random.

In total, the colony was at the utmost very weakly synchronous in its clutch initiation. The analysis of first egg laying dates provided no evidence that colonial nesting *per se* synchronized laying, neither in the Footbridge colony as a whole, nor at the level of the sub-divisions. On the contrary, the efforts undertaken by settled pairs to prevent newcomers from settling contributed to an extended laying period.

Many studies on colonial nesting in the Great Crested Grebe concentrated on synchrony in clutch initiation. Their findings were however not uniform. Moskal and Marszałek (1986) stated that colonies arose almost simultaneously on Lake Żarnowieckie. They thought that the synchronization of egg-laying was probably caused by physiological and habitat conditions: the inner motive power of the grebes commanded a point in time from where on their body became prepared to reproduction and then the birds simply waited for the appropriate vegetation growth and started their nesting all together. No reason was however provided for the 5-10 days later breeding of solitary grebes on the same lake. Koshelev (1985) found synchronous breeding only to occur in smaller colonies (10-30 nests) on Tiligul'liman estuary. In bigger colonies or in colonies built in dense vegetation, egg laying was extended and it could last for 2-3 months. Koshelev explained the extended laying period partly by the loss of clutches as a consequence of the actions of waves and wind. Including replacement or second clutches in such an analysis however falsifies the results and at the end the period really covered by first egg laying on Tiligul'liman estuary remained unknown. Koshelev (1977) had previously investigated the breeding of the grebes at Lake Menzelinskoe. There, 35 nests of one colony holding 60 nests were examined on 3 June 1974: 25 nests were at different stages of incubation, in five nests chicks were hatching, in four nests egg-laying was on-going and one platform was freshly built. A smaller colony with ten nests held only two nests with eggs (three eggs each) on 6 June, but on 5 July all nests had hatched completely. The examples provided evidence for clutch initiation to spread over about one month in the bigger colony and to cover only about one week in the smaller one. On Lake Amstel, on 14 June 1967 van IJzendoorn (1967) found 66 nests in different colonies, all at different stages of incubation within each concentration. Some nests contained no eggs at all, others held 1 to 4 eggs, and even in each colony one clutch of 5, 6 or 7 eggs was registered. In other nests, only remains of eggshells were found. The data proved that there was little synchronisation between the different pairs. On Lake Drużno, Goc (1986) discovered that the main egg laying period spread over 35 days in the seasons from 1976-80, except for 1978 when it spread over 55 days (possibly due to lower water levels). However, in mixed colonies with Laridae, the grebes synchronized their breeding with that of the gulls. They initiated their clutches at an earlier stage and were more synchronous. In the Třeboňsko Biosphere Reserve, Voldánova et al. (2000) found a mean first egg laying date of 2 June (± 18 days) for colonial grebes. Whereas their laying occurred about two weeks later than that of solitary breeders (20 May, ± 21 days), it was similarly asynchronous. At the Houtribsluizen, Leys et al. (1969:2) concentrated not on synchrony in egg laying. Their data provided nevertheless evidence for a rather asynchronous egg laying effort by the different pairs. In 1967 first nests with eggs were found on 29 April when the colony held 36 platforms. The number of platforms reached a maximum with 165 platforms on 3 June when still 19 nests held only one egg.

It seems reasonable to state that experienced grebes become physiologically prepared for reproduction at around the same moment in time in each year. The constraints of the habitat then often contribute to an apparent synchrony of their breeding. For true synchrony in first-egg laying of colonial Great Crested Grebes, most studies, similarly to the findings of the Footbridge colony, provided little evidence. If clutch initiation was more concentrated, factors extraneous to the grebes themselves appeared to be responsible. Especially, the direct synchronisation of breeding with Larids indirectly provoked a greater fine tuning of egg production by the grebe females of the same colony. The aggregated nesting of the Great Crested Grebes per se could then rather cause delays in clutch initiation for at least some pairs as a result of intraspecific competition for nesting space. Moskal and Marszałek (1986), while admitting the roles of the birds' physiology and the habitat condition, beyond believed that the synchrony they observed was not entirely fallacious and that it could rely to some extent on the grebes' preferences as it might increase the chances of survival for adult birds. Consequently, coloniality would actively contribute to synchronisation. If this was true, it presupposes that the habituation process to close nesting in the population would not need to go through a long period of reductions in mutual aggressive behaviours. Such a population could either have evolved genetic changes favouring a more social behaviour or it may have learned how to cope best with breeding aggregations in order to take full advantage of its possible benefits.

## 2.2.3 Clutch size, variation in time and space

The clutch size of birds is known to vary in between pairs and years. Even average figures for a population are not stable in time and may differ in the course of one season or from one year to the next. The following two sections analyze how clutch size evolved at the Footbridge colony and at other sites with aggregated nesting of Great Crested Grebes.

### 2.2.3.1 Clutch size variation in between years and between locations

The mean full clutch size for the Footbridge colony as a whole varied between 3.67 eggs and 4.19 eggs in the five years under review (Table 19). Summing up the data of the five years, an average clutch size of 3.94 eggs (N=452, SD±0.2) was obtained. Compared to the average over five years, the 2003 and 2007 mean clutches were low whereas the 2006 figure was high. The lowest yearly average clutch represented 87.6% of the highest average clutch. In each year, for 65% to 87% of first clutches, the full size was known, so the chances for biased results by a limitation in figures were reduced A priori, there were no obvious explanations for the lower 2003 and 2007 and the higher 2006 figures.

In 2003, with an average of 3.76 eggs per nest in the reeds and 3.73 eggs in the bulrush, the clutch size showed no significant differences between vegetation types. This changed for the next four years, when the average full clutch size was each time much higher inside the reeds (Table 19). In the bulrush, the average clutch size remained comprised between 3.53 eggs and 3.75 eggs, except for 2007 when it fell to a low 3.30 eggs. Over the years, a tendency for clutch reduction was apparent. On the contrary, in the reeds the average clutch size increased for three successive years, reaching 4.32 eggs, before dropping in 2007 to the level of 2003. On average for the five years, the colony held 4.00 eggs in the reeds and only 3.59 eggs in the bulrush. It is noteworthy that in the bulrush, in all five years, only four clutches or 5.6% (n=72) held five eggs and none held more than five eggs. In the reeds, a total of 75 nests or 19.8% (n=379) contained five eggs or more. The higher percentage of clutches with five eggs and more inside the reeds explained the differences between both vegetation types. One possible reason for the big clutches that occurred exclusively inside the reeds could reside with conspecific brood parasitism. The track will be explored later.

In the sections of the reeds, variations of mean clutch size in between years were also observed

**Table 19:** Mean first full clutch sizes per colony section in 2003-2007 (n) and mean of all years (SD).

| | 2003 | 2004 | 2005 | 2006 | 2007 | Average (SD) |
|---|---|---|---|---|---|---|
| **Reed I** | 3.77 (37) | 4.07 (28) | 4.00 (31) | 4.17 (24) | 3.63 (19) | 3.93 (±0.20) |
| **Reed II** | 3.75 (53) | 3.96 (45) | 4.33 (49) | 4.39 (51) | 3.77 (43) | 4.05 (±0.27) |
| **All Reeds** | 3.76 (90) | 4.00 (73) | 4.20 (80) | 4.32 (75) | 3.73 (62) | 4.00 (±0.23) |
| **Bulrush** | 3.73 (20) | 3.75 (12) | 3.53 (15) | 3.53 (15) | 3.30 (10) | 3.59 (±0.16) |
| **Colony** | 3.75 (110) | 3.96 (85) | 4.09 (95) | 4.19 (90) | 3.67 (72) | 3.94 (±0.20) |

(Table 19). Except for 2003, when both Reed sections held average clutches of similar size, and 2004, when the clutch size in Reed I exceeded the one in Reed II by 0.11 eggs, from 2005 onwards, Reed II held the higher average clutch. It exceeded the one of Reed I by up to 0.33 eggs.

The results point at possible differences in the micro-habitat of the sections of the colony that might have attracted birds with different characteristics. An indirect explanation for the variability in clutch size might to some extent be provided by the density dependence analysis of section 2.2.4 below.

Mean clutch sizes of colonial Great Crested Grebes varied widely between sites as the following data show: 2.92 eggs (n=840, Perry 2000) at Lough Neagh (N. Ireland), 3.5 eggs (n=241,Voldánova et al. 2000) at the Třeboňsko Biosphere Reserve (Czech Republic), 3.6 eggs (n=111, Leys et al. 1969:2) at the Houtribsluizen (Netherlands), 4.03 eggs (Lawniczak 1982 in Perry 2000) at Milicz (Poland), 4.1 eggs (n=50, Bukacińska et al. 1993) at Lake Łuknajno (Poland), 4.32 eggs (n=107, Berthoud 1963) at Yverdon (Switzerland), 4.49 eggs (n=313, Moskal & Marszałek 1986) at Lake Żarnowieckie (Poland), 4.58 eggs (n=114, Blinov et al. 1981) at Lake Menzelinskoe (Siberia). On average, these sites produced together a clutch of 3.54 eggs (n=1776). Without Lough Neagh where the mean value was extremely low, this average was 4.10 eggs (n=936).

At other locations, the mean clutch sizes also showed variation in between years:

- 4.65 eggs (n=156) at Lake Żarnowieckie in 1980 and 4.33 eggs (- 6.9%, n=157, Moskal & Marszałek 1986)
- 4.48 eggs (n=53) at Lake Menzelinskow in 1976 and 4.66 eggs (+4.0%, n= 61, Blinov et al. 1981)
- Goc (1986), in his study on Lake Drużno covering the years from 1975 to 1980, noted variation in clutch size between years, between 3.8 and 3.4 eggs (-10.5%) in mixed colonies, and between 3.5 and 3.13 eggs (-10.6%) in mono-specific colonies.

The average clutch size of colonial Great Crested Grebes varied also in other studies with vegetation type or location of individual aggregations on the same body of water:

- 4.38 eggs inside reeds (n=81) and 4.28 eggs inside bulrush (n=76) at Lake Żarnowieckie (Moskal & Marszałek 1986)
- 4.78 eggs (n=60) in one colony and 3.88 eggs (n=30) in a second on Lake Menzelinskoe (Blinov et al. 1981)
- 3.8 eggs in mixed colonies and 3.13 eggs in mono-specific colonies on Lake Drużno in 1978 (Goc 1986)
- 4.20 eggs (n=5) in one colony and 4.08 eggs (-2.9%, n=26) for a second colony inside denser reed on Lake Łuknajno (Bukacińska et al. 1993).

Before assessing the differences in clutch sizes indicated in other studies, it is necessary to point at differences in the way the data were collected. Due to the difficulties of access to most colonies, the aggregations were generally either visited by boat or by wading into the vegetation. This must have caused tremendous disturbances with the nesting birds. The grebes most probably quickly abandoned their incubation duties and thereby offered occasions for egg predation. To limit the perturbation for the breeders, normally few visits to colonies were undertaken, so that it was not sure that all clutches included in the calculations were final. More often, probably all nest contents registered were included to determine the average clutch size.

The examples listed here point nevertheless at variable average clutch sizes in colonial Great Crested Grebes, in time and in space. As for solitary nesters, clutch size would be influenced by the features of the habitat itself, climatic conditions, changes in food availability, the presence of predators, the association with other breeding species, the vegetation types used for nesting, the experience of the breeders, the nesting density, the geographic latitude of location of the site and possibly other factors. The impact of each single factor might however differ depending on whether territorial or aggregated nesting is concerned. In comparison, the average clutch sizes found at the Footbridge colony could lie within a normal range for colonial nesting.

**Table 20:** Average full clutch size of the Great Crested Grebes in relation to the date of first egg (in parentheses number of clutches).

| Date of first egg | | Before 11 April | SD | 11-20 April | SD | After 20 April | SD |
|---|---|---|---|---|---|---|---|
| 2003 | Reed I | 3.92 (12) | 0.51 | 3.58 (12) | 1.08 | 3.50 (11) | 0.93 |
| | Reed II | 4.33 (9) | 0.50 | 3.77 (22) | 0.87 | 3.50 (18) | 0.72 |
| | All Reeds | 4.00 (21) | 0.54 | 3.85 (34) | 0.94 | 3.67 (29) | 0.79 |
| 2004 | Reed I | 4.25 (4) | 0.50 | 4.25 (12) | 0.45 | 4.09 (11) | 0.70 |
| | Reed II | 4.33 (3) | 0.58 | 4.14 (22) | 0.56 | 3.50 (16) | 0.82 |
| | All Reeds | 4.29 (7) | 0.49 | 4.18 (34) | 0.52 | 3.74 (27) | 0.81 |
| 2005* | Reed I | 4.87 (8) | 0.83 | 3.82 (11) | 0.75 | 3.80 (10) | 0.42 |
| | Reed II | 5.46 (13) | 1.45 | 3.95 (20) | 0.91 | 3.58 (12) | 0.67 |
| | All Reeds | 5.24 (21) | 1.26 | 3.90 (31) | 0.84 | 3.68 (22) | 0.57 |
| 2006 | Reed I | 4.38 (8) | 0.74 | 4.00 (4) | 0.82 | 3.90 (10) | 0.57 |
| | Reed II | 4.69 (16) | 0.79 | 4.44 (18) | 1.10 | 3.67 (15) | 0.72 |
| | All Reeds | 4.58 (24) | 0.78 | 4.36 (22) | 1.05 | 3.76 (25) | 0.66 |

* Clutches still incomplete and destroyed by the storm on 8 April were not considered.

### 2.2.3.2 Clutch size variation within one season

It is generally assumed that young breeders produce full clutches containing less eggs than experienced breeders. As experienced Great Crested Grebes were expected to settle and breed earlier in the season, for nests with later laying dates smaller clutches should have resulted. Against this background, the evolution in time of the full clutch size was analyzed at the Footbridge colony. Subdividing the few clutches laid inside the Bulrush in each year into different laying periods left however too few data in each time category, so that an analysis of clutch size per first-egg laying date was limited to the Reed sections of the Footbridge colony.

In Reed I, in all years from 2003 to 2006, the average clutch size decreased in time within the same season (Table 20). The extent of the reduction was quite changing. Thus, from 2003 to 2006 the size declined on average by 10.8% (range 0-21.6) between clutches started before 11 April and those started from 11 to 20 April. Excluding the figures of 2005 that were biased by the effects of the storm on 8 April, the average variation was -5.8% (range 0– 8.7). Between clutches started in the second decade of April and those started later, the decrease was on average 2.3% (range 0.5-3.8). The total clutch size reduction within one season was 10.7% in 2003, 3.8% in 2004, 22.0% in 2005 and 11.0% in 2006, or on average 11.9%, respectively 8.5% (range 3.8-11.0) when the year of the storm was not considered.

In Reed II, a seasonal decrease of clutch size occurred, too. Clutches started from 11 to 20 April declined on average by 12.3% (range 4.4-27.3) or, not considering 2005, by 7.5% (range 4.4-12.9) in comparison to those started before 11 April. Between clutches started from 11 to 20 April and later clutches, the reduction was on average 12.6% for the four years and 13.7% (ranges 7.2-17.3) without 2005. The total clutch size reductions within one season were 19.2%, 19.2%, 34.4% and 21.7% respectively, or on average 23.6% for the four years and 20.0% if 2005 remained unconsidered.

Comparing both Reed sections, it appeared that the reductions of clutch size were more important in Reed II, especially later in the season. Globally, seasonal clutch size reduction was confirmed for all Reeds (Table 21). Average clutch sizes were highest if initiated before 11 April and lowest if initiated after 20 April. Clutches initiated in the second decade of April were generally intermediate in their number of eggs. The seasonal decreases were very variable from one year to

**Table 21:** Average variation in time of full clutch size inside the reeds in 2003, 2004 and 2006 in relation to the date of first egg.

| Periods | Before11 April to 11-20 April | 11-20 April to After 20 April | Total variation |
|---|---|---|---|
| Average Variation | -3.7% | -9.7% | -13.0% |
| Range | -2.6 to -4.8 | -4.7 to -13.8 | -8.2 to -17.9 |

**Table 22:** Average full clutch size of the grebes in the reeds in relation to the date of platform start (in parentheses number of clutches).

| Date of platform start | | In March | SD | 1-10 April | SD | 11-20 April | SD | Later | SD |
|---|---|---|---|---|---|---|---|---|---|
| 2003 | Reed I | 3.72 (18) | 0.83 | 3.88 (8) | 1.25 | 3.75 (4) | 0.50 | 3.60 (5) | 0.55 |
| | Reed II | 4.00 (26) | 0.76 | 3.91 (11) | 0.83 | 3.38 (8) | 0.92 | 3.29 (7) | 0.76 |
| | All Reeds | 3.89 (44) | 0.79 | 3.89 (19) | 0.99 | 3.50 (12) | 0.80 | 3.42 (12) | 0.67 |
| 2004 | Reed I | 4.38 (8) | 0.74 | 4.20 (10) | 0.42 | 4.00 (6) | 0 | 4.00 (4) | 0.82 |
| | Reed II | 4.17 (12) | 0.58 | 3.86 (7) | 0.38 | 3.70 (10) | 0.67 | 3.75 (4) | 0.50 |
| | All Reeds | 4.25 (20) | 0.64 | 4.06 (17) | 0.43 | 3.81 (16) | 0.54 | 3.88 (8) | 0.64 |
| 2005 | Reed I | 4.23 (13) | 1.10 | 4.00 (7) | 0.58 | 3.40 (5) | 1.34 | 3.67 (3) | 0.58 |
| | Reed II | 4.90 (21) | 1.34 | 4.33 (12) | 0.89 | 3.67 (9) | 0.87 | 3.75 (8) | 0.46 |
| | All Reeds | 4.65 (34) | 1.25 | 4.21 (19) | 0.79 | 3.57 (14) | 1.02 | 3.73 (11) | 0.47 |
| 2006 | Reed I | 4.11 (9) | 0.93 | 4.20 (5) | 0.84 | 4.29 (7) | 0.49 | 3.00 (2) | 0 |
| | Reed II | 4.59 (17) | 0.80 | 4.22 (18) | 0.94 | 3.91 (11) | 1.30 | 4.00 (2) | 0 |
| | All Reeds | 4.42 (26) | 0.86 | 4.22 (23) | 0.90 | 4.06 (18) | 1.06 | 3.50 (4) | 0.58 |
| 2003-2006 | Reed I | 4.04 (48) | 0.92 | 4.07 (30) | 0.82 | 3.91 (22) | 0.73 | 3.64 (14) | 0.61 |
| | Reed II | 4.41 (76) | 0.94 | 4.12 (48) | 0.84 | 3.69 (38) | 0.98 | 3.62 (21) | 0.57 |
| | All Reeds | 4.27 (124) | 0.93 | 4.08 (78) | 0.82 | 3.77 (60) | 0.89 | 3.63 (35) | 0.60 |

the next. One reason could have been that the analysis simply maintained the three identical time intervals for all four years whereas the birds exposed some variation in the yearly timing of their breeding effort, especially depending on weather and habitat conditions. Thus, in 2004 when clutch initiation was generally rather late, only few clutches were started in the first decade of April and their average size was close or equalled clutches started during the second decade of April. By distinguishing in the second decade between early and late clutches and by deducting early clutches from the second decade to add them to the first decade, the picture changed slightly. The Reed I first decade average increased to 4.29 eggs (N=7) while the second decade mean clutch decreased to 4.22 (N=9). In Reed II, the mean first decade clutch increased to 5.50 eggs (N=8) and the second decade mean became 4.00 eggs (N=17).

While a general tendency for seasonal clutch size reduction was confirmed, the reason could only be guessed. It was thought to be triggered mainly by decreasing breeding experience of pairs with later clutch initiation. Even though their egg laying was late, could the pairs concerned nevertheless have settled early?

Settled grebes waited for a variable amount of time before initiating their clutches. The previous review of seasonal clutch size variation did not consider the date of settlement by the pair, but only the date of clutch initiation by the female. Repeating the exercise and taking the start of platform building as point of reference, a general tendency for a gradual clutch size reduction in time remained obvious (Table 22).

On average for the four years, clutch size decreased from 4.27 eggs for platforms started in

**Table 23:** Average full clutch size in the reeds in relation to the date of platform start and time span from platform start to clutch initiation in 2005 and 2006 (in parentheses number of clutches).

| Date of platform start | | In March | 1-10 April | 11-20 April | Later |
|---|---|---|---|---|---|
| Time span 2005 | < 6 days | 3.67 (3) | 4.25 (8) | 4.00 (12) | 3.71 (7) |
| | 6-10 days | 4.20 (10) | 3.86 (7) | 3.67 (3) | 3.50 (2) |
| | > 10 days | 4.95 (19) | 4.00 (3) | 2.67 (3) | / |
| Time span 2006 | < 6 days | / | 4.38 (8) | 4.20 (10) | 3.50 (2) |
| | 6-10 days | 4.83 (6) | 4.33 (9) | 4.20 (5) | / |
| | > 10 days | 4.30 (20) | 3.75 (4) | 3.50 (4) | / |

March to 3.63 eggs for platforms started after 20 April (-15%). For the two Reed sections, globally the same trend appeared, however individual years did not necessarily support a seasonal clutch size decrease. Especially in 2006, the trend was completely reversed in Reed I, showing increasing clutch sizes for first and second decade of April platforms.

Based on the pooled results over four years, one could conclude that early settlers laid the biggest clutches. This is in agreement with the thesis that experienced birds that lay the biggest clutches should settle early. As they should also readily initiate their clutches, a combination of early settlement and early clutch initiation should be most beneficial to clutch size.

Refining the analysis for all reeds for 2005 and 2006 by combining the date of platform initiation and the duration of the pre-laying period (Table 23), it appeared that early settlers in March laid not necessarily the bigger clutches. Early settlers and quick layers in 2005 had indeed the on average lowest clutches of all March settlers. For them, it seemed advantageous to wait for longer as with increasing settling period the clutch size increased, too. March settlers waiting for over ten days produced the on average by far biggest clutches of the year (up 16.5% in comparison to the second biggest average of Table 23). As chapter 2.3.2 will prove, storm damage and nest parasitism might have been the main causes of this unexpected evolution. For settlers in April, clutch size evolved again as expected and they had the biggest clutches when starting their clutches within five days.

In 2006, no platforms started in March received quickly a first egg. March settlers waiting between six and ten days before initiating their clutches had the on average biggest clutches of the year, exceeding the second biggest average by 10.3%. March settlers waiting for over ten days and April settlers waiting for less than ten days produced clutches of comparable size. For April settlers, delaying clutch initiation by more than ten days or starting their platform after 20 April meant on average smaller clutch sizes.

The analysis provided evidence that early settlement and quick clutch initiation were advantageous. In the highly competitive environment of a colony, the strongest competitors should be able to impose themselves best and, therefore, they should reach better fitness gains than weaker rivals. Experience will certainly contribute to the strength of individuals and it also helps to avoid needless energy expenditures that would not help their fitness. The strongest grebes of the new generation could also achieve early access to the breeding habitat. Their lack of experience risks however to increase their pre-egg-laying period and this would explain the gradual decreases in clutch size in each settlement window.

In other studies, no examples relating clutch size to settlement date and/or pre-laying period could be found. They all concentrated on clutch size variation in relation to the dates of egg-laying. At Yverdon, the average clutch size in April was 5.5 eggs (n=2), in May it was 4.08 eggs (n=50), in June 4.36 eggs (n=42) and in July 4.92 eggs (n=13, Berthoud 1963). Except for April, when the sample size of only two nests might not have been representative, clutch size steadily increased in the course of the season. At the Dutch site of Houtribsluizen, in the course of the breeding seasons 1966 to 1968, the average clutch size first increased from 2.23-2.5 eggs in May to 2.7-3.1 eggs in June. For July and August clutches, it again decreased to 2.0-2.3 eggs (Leys et al. 1969:2). As this study noticed that on average every breeding pair laid 2.5 clutches in the course of one year, it is very likely that July and August nests contained only second or even third clutches. Therefore, first-clutch size might not have decreased within one season. On Lake Łuknajno, Bukacińska et al. (1993) observed an increase of the clutch size in the season in colonial birds whereas it decreased in solitary birds. At Lough Neagh, a steady seasonal increase of clutch size was also noted: the mean April clutch size was 2.6 eggs (n=287), in May it was 2.99 eggs (n=433) and in June 3.4 eggs (n=120, Perry 2000).

On Lake Drużno, Goc (1986) noticed a seasonal decrease in clutch size in four years (1976-1978, 1980), but in 1979, an initial slight downward trend was reversed later and late clutches held again about the same number of eggs as early clutches. The size decrease between mid-April and mid-June clutches was about one egg at maximum. From Lake Menzelinskoe, Blinov et al. (1981) reported a mean clutch size of 4.6 eggs (±0.2, n=21) in May 1976 and of 4.4 eggs (±0.1, n=32) in June 1976. In 1977, the May average figure was 5.0 eggs (±0.1, n=38) and the June figure 4.1 eggs (±0.2, n=23).

The examples showed that when comparing different sites, the evolution of seasonal clutch size could be quite variable: some colonies recorded seasonally decreasing, others seasonally increasing clutch sizes. A priori, no simple relationship such as early occupancy of breeding sites by experienced birds laying bigger clutches and later settlement of inexperienced grebes laying smaller clutches that could hold true under all circumstances appeared. Bearing however in mind the limitations of data collection observed in other studies, the apparent increases of clutch sizes could also have been triggered by increasing percentages of full clutches in the data. It seems logical to pretend that an early check of nest contents will find many clutches that are just started. A later check has then a better chance of finding more nests where egg laying is complete. Yet, depending on local conditions, it cannot be excluded that even for experienced birds, it could be beneficial to initiate their clutches later or to start breeding early in the season with a smaller clutch and to proceed later in the season with a second bigger clutch. If for instance spells of inclement weather early in the season risked destroying clutches, losing a small clutch would be energetically less costly. At the same time, the laying of a small clutch could lead to the raising of a first early brood if no nest destruction occurred, while still leaving enough time for a second brood of regular size. Also, it might not always be true that nests of first breeders hold fewer eggs, even if inexperienced grebes might lay reduced clutches. Depending on circumstances, their nests could be more vulnerable to conspecific brood parasitism that would increase their clutch size. Even early nests of experienced grebes could receive parasitic eggs that would explain their bigger clutch sizes. However, we would expect them to be better able to avoid nest parasitism than younger pairs. At the end, no unambiguous rule evolved. But at least for the Footbridge colony, where the data were very accurate, it was highly likely that the evolution of the clutch size could be explained by differences in the breeding experience of the pairs involved. Depending on the particular characteristics of each colony, it could occasionally be beneficial for older birds to follow a more complex strategy.

Before concluding this chapter, it has to be mentioned that clutch size might not only be expressed as a number of eggs, but also as a volume of eggs. At the Footbridge colony, no egg biometric data were recorded because it was judged that this would disturb the colony too much and related changes in the grebes' behaviour could have called in question other results of the study. Other authors have dealt with egg biometry and their findings are presented in the following.

Bukacińska et al. (1993) calculated an egg volume index $V=lb^2 \times 0.52$ where b represented the egg breadth and l the egg length. The total clutch volume was larger in colonies (154.8 ±41.4 $cm^3$) than in solitary nests (133.1 ±52.3 $cm^3$). The volume differences however simply represented the differences in egg numbers and the mean volume indexes per egg were quite comparable with 37.8 ±5.3 $cm^3$ in colonial and 37.7 ±4.0 $cm^3$ in solitary breeders. In colonies, at sites close to open water, the egg volume was especially small and eggs were more elongated. As with clutch size, the clutch volume increased in colonial breeders in the course of the season. Comparing colonial four-egg and five-egg clutches revealed significant mean egg volume differences. With 39.1 ±2.4 $cm^3$, the bigger clutches held also the bigger eggs. As colonial clutch size increased within the season, one could conclude that egg size did so, too.

Voldánova et al. (2000) recorded an egg volume of 36.9 ± 2.5 $cm^3$ in colonial and of 38.2 ± 3.3 $cm^3$ in territorial Great Crested Grebes. Egg length (54.6 ±1.7 mm) and breadth (36.36 ±1.0 mm) in colonial breeders were also inferior to the values of solitary breeders (55.1 ±1.8 mm, 36.9 ±1.3 respectively). All in all, clutches of colonial pairs were initiated later, they held fewer and smaller eggs. Fjeldså (1973) observed that young Horned Grebes *P. auritus arcticus* laid eggs of smaller size than experienced females. Assuming that this was also true for Great Crested Grebes, one could conclude that the formation of colonies at the Třeboňsko Biosphere Reserve was mainly a consequence of the aggregation of inexperienced birds possibly unable to defend an own territory.

Goc (1986) defined the egg volume $V = (0.947 \times \Pi \times lb^2)/ 6000$. He found no permanent egg size (dimensions and volume) differences depending on nest location and the differences observed between breeding seasons did not reach the level of statistical significance. The average values found over four years were 36.69 cm$^3$ for egg volume, 36.77 mm for egg breadth and 54.73 mm for egg length (n=1,143). The mean length and breadth of the eggs decreased however within the breeding season leading to a decrease in the mean volume of 2-3 cm$^3$. In addition, some late clutches were characterized by egg sizes below the range figures of early eggs. A seasonal egg-size decrease was also found by Mielczarek (1980 in Goc 1986).

### 2.2.4 Nesting density and clutch size

The settlement process as observed at the Footbridge colony exposed the grebes to quite some stress related to the defence of their platform and the immediate surroundings. The birds invested a more or less important part of their energy reserves in aggressive behaviours. Under such circumstances, one could expect not only delayed egg laying, but also clutch sizes to suffer. Inside a same colony, the nests established at the densest parts could then suffer most and their full clutch sizes could be lower than those of nests in less densely populated parts. Moreover, under high nesting densities, grebes could expose their eggs to greater risks of loss during interferences with neighbours. They might also risk brood parasitism on their own clutches while leaving them unobserved. Birds at greater distances from foreign nests or clumped with less neighbours might be better able to allocate energy resources to egg production. To what extent nesting density could have impacted clutch sizes at the Footbridge colony was measured by calculating for each year and for different degrees of clumping, the average full clutch size (Table 24, Fig. 14). The degree of clumping of a particular nest was again determined by the number of neighbouring platforms within three meters.

**Table 24:** Average full clutch size in the colony in relation to clumping (in parentheses number of clutches).

| Section | Degrees of clumping | 2003 | 2004 | 2005 | 2006 | 2007 |
|---|---|---|---|---|---|---|
| Reed | 0 clumped platforms | 4.00 (2) | 4.33 (6) | 4.40 (5) | 3.80 (5) | 3.33 (3) |
| | 1-2 clumped platforms | 3.69 (10) | 4.06 (16) | 4.14 (22) | 3.70 (10) | 3.39 (18) |
| | 3-4 clumped platforms | 3.71 (34) | 3.86 (27) | 4.21 (28) | 4.27 (22) | 3.91 (35) |
| | >4 clumped platforms | 3.89 (38) | 4.07 (32) | 4.20 (25) | 4.42 (38) | 4.17 (6) |
| Bulrush | 0 clumped platforms | 4.00 (1) | 4.33 (3) | 3.60 (5) | 3.67 (3) | / |
| | 1-2 clumped platforms | 3.40 (10) | 3.56 (9) | 3.44 (9) | 3.55 (11) | 3.20 (5) |
| | 3-4 clumped platforms | 4.00 (11) | / | 4.00 (1) | 3.00 (1) | 4.00 (3) |
| | >4 clumped platforms | / | / | / | / | 2.50 (2) |
| Colony | 0 clumped platforms | 4.00 (3) | 4.33 (9) | 4.00 (10) | 3.75 (8) | 3.33 (3) |
| | 1-2 clumped platforms | 3.57 (20) | 3.88 (25) | 3.94 (31) | 3.62 (21) | 3.30 (23) |
| | 3-4 clumped platforms | 3.78 (45) | 3.86 (27) | 4.21 (29) | 4.22 (23) | 3.92 (38) |
| | >4 clumped platforms | 3.89 (38) | 4.07 (32) | 4.20 (25) | 4.42 (38) | 3.75 (8) |

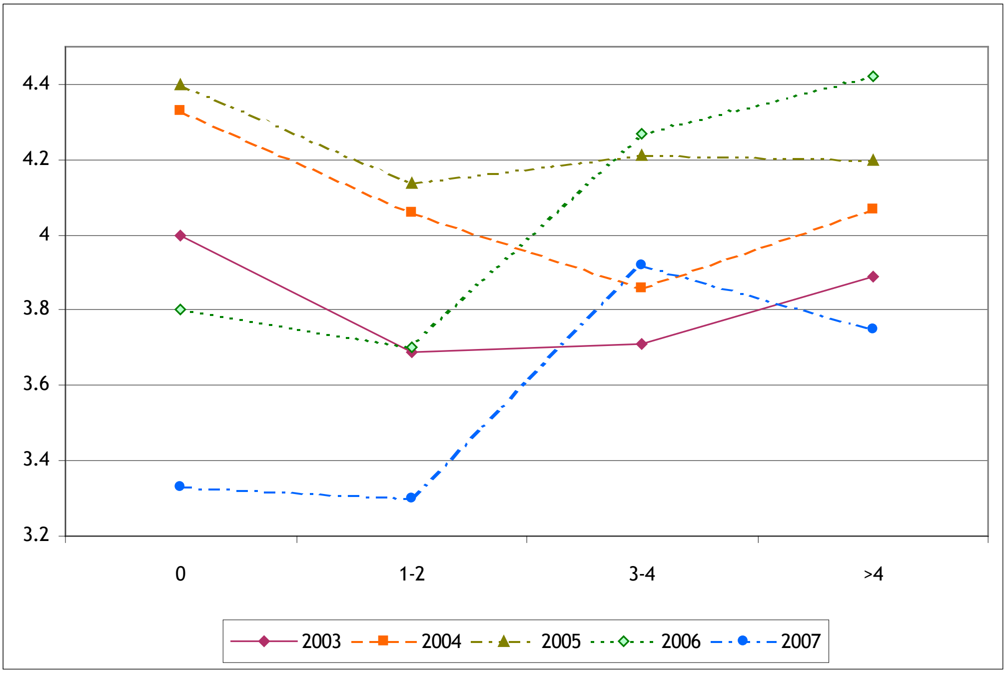

**Fig. 14:** Average clutch size in relation to degree of clumping for the entire colony.

In the Reed zones, nests not at all subject to clumping held the on average highest clutches in 2003, 2004 and 2005. In all three years, nests clumped with 1-2 other platforms experienced declines of comparable magnitude in average clutch size when compared to nests that were not clumped. With a further increase of clumping, no uniform trend subsisted. The patterns observed in 2006 and 2007 differed completely. In both years, the nests most heavily clumped recorded the highest clutches and nests clumped at degrees 0 or 1-2 had markedly lower average clutches. Considering the five years of the study, no clear correlation between degree of clumping and average clutch sizes could be detected.

In the Bulrush zone, the number of data was limited and clumping was less marked than in the reeds. Excluding there from the analysis those degrees of clumping where the content was known only for one nest, two degrees remained for comparison from 2003 to 2006. In 2003, a substantial increase in clutch size occurred with increasing nesting density. From 2004 to 2006, the average clutch size decreased to very variable extents with increasing degrees of clumping. In 2007, clutch size first increased with clumping, but then it collapsed when the number of neighbouring nests exceeded four. No general rule could be derived from the data.

Equally, the mean clutch size for the colony as a whole showed rather erratic movements with respect to the degree of clumping and when comparing different years.

Unfortunately, no other study analyzing the evolution of the clutch size in comparison to the nesting density of the Great Crested Grebes was available so that all lessons had to be drawn from the example of the Footbridge colony. There, the degree of clumping in itself could not explain any trend in clutch size. Though some indications for a reduction of clutch size with increasing population density were found, these effects could possibly be either at least partially counterbalanced or avoided. The strongest competitors should have been able to avoid densely populated sectors of the colony so that clutch size should have been biggest with the lowest degrees of clumping. However, and as we will further analyse in a later chapter, parasitic egg laying may have contributed to increase clutch sizes especially in denser parts of the colony where more occasions for brood parasitism should have existed. Independently from nesting density, some pairs might have been better able to cope with aggregated nesting in general than others. These would react less to close settling conspecifics and thereby save energy. In some cases, individual pairs may have maintained a low degree of clumping because they were investing much energy in the protection of their surroundings to the detriment of their clutch size. A limited number of weaker competitors may have been pushed more to the edges of the habitat where, due to the quality of the area, they remained more isolated. In addition, the asynchronous settlement process of the colony contributed to in time unequal increases of clumping for different platforms that, depending on the nesting progress of the already established pairs, might have affected clutch sizes differently.

As dominant pairs push others to concentrate in poorer habitat, density of birds there is likely to be higher (Bernstein et al. 1991 in Johnson 2007). Therefore, high nesting density per se implies lower clutch sizes. The grebes aggregating there are not only in poorer condition themselves, they are also subject to increased density-related stress. Counterbalancing effect, such as nest parasitism, or features of the habitat may however mask the tendency.

## 2.2.5 Exceptionally small clutches

Nest content was considered to be exceptionally small if the size of the full clutch did not exceed two eggs. From 452 nests where the full clutch was recorded, 19 or 4.2% held a maximum of two eggs. Inside the reeds, such clutches summed up to a total of 13 in all five years. For four of them, all started in March, the pre-laying period was extremely extended and clutch initiation occurred 20 to 33 days after the start of platform building. Two out of three other platforms started in the first decade of April, waited 13 and 21 days before receiving a first egg. The third, started late in the first decade, received a first egg after five days. Three of the remaining platforms appeared in the second decade of April and they waited for 15, 7 and 2 days before their clutches were initiated. For three platforms with small clutches in 2007, no information on the duration of the pre-laying phase was available.

**Table 26:** Total number of full clutches with one or two eggs (small clutches) in the bulrush in relation to clumping 2003-2007.

| | **Number of clumped platforms** | | | |
|---|---|---|---|---|
| | **0** | **1** | **2** | **>2** |
| Small clutches | 1 | 2 | 2 | 1* |
| Total clutches | 18 | 26 | 42 | 71 |
| % of small clutches | 5.6 | 7.7 | 4.8 | 1.41 |

*clumped with 5 other platforms

If we considered the same 13 nests with respect to their degree of clumping, it appeared that nine were clumped with at least three other nests and three with two other nests (Table 25). The remaining nest was already started towards mid-March 2003 at a place with rather poor stands of reed and it had the nearest neighbour at 3.65 m, possibly as a consequence of the reduced quality of the habitat in this area. Its clutch of two eggs was initiated a bit more than one month later.

In the bulrush, a total of six small clutches were counted (Table 26). For three of them, platform building was started in March, but clutch initi-

**Table 25:** Total number of full clutches with one or two eggs (small clutches) - number of full clutches with more than five eggs (big clutches) in the Reeds in relation to clumping 2003-2007.

| | **Number of clumped platforms** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **0** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
| Small-big clutches | 1-1 | 0-0 | 3-1 | 6-2 | 0-2 | 1-1 | 0-6 | 1-2 | 1-2 |
| Total clutches | 19 | 20 | 48 | 61 | 51 | 35 | 35 | 19 | 11 |
| % of small clutches | 5.3 | 0 | 6.3 | 9.8 | 0 | 2.9 | 0 | 5.3 | 9.1 |
| % of big clutches | 5.3 | 0 | 2.1 | 3.3 | 3.9 | 2.9 | 17.1 | 10.5 | 18.2 |

ation occurred 26, 31 and 39 days later. One platform was started on 12 April and received its first egg already two days later. Another platform was started on 23 April and waited six days before the clutch was initiated. Again, no corresponding information was available for the only small clutch of 2007. The six small clutches were recorded in nests that were clumped with no (n=1), one (n=2), two (n=2) or five (n=1) other nests.

Finally, practically all 19 small clutches recorded throughout the duration of the study, either had extended pre-laying periods and/or the nests were built inside parts of the colony that were more densely populated. Clutch initiation could exceptionally follow platform building quickly if the construction was not started early in the season. It seemed therefore judicious to pretend that such clutches stemmed either from inexperienced females and/or were a direct consequence of nesting density.

At Yverdon, from 132 clutches only 1.5% or two small clutches of 2 eggs each were recorded (Berthoud 1963). At Lake Menzelinskoe in 1974, five nests or 8.4% of the clutches in a first colony (n=59) and 30 nests or 11.5% of the clutches in a second colony (n=260) held only two eggs. In 1976 all 35 clutches inside the first colony from 1974 had more than two eggs. In 1977, one nest or 4% of 25 clutches in a colony received two eggs. In all years, no full clutch with a single egg was found. Summing up all the data, 36 clutches or 9.5% were small (Blinov et al. 1981). On Lake Żarnowieckie, Moskal and Marszałek (1986) recorded 1.3% or two small clutches in 1980 (n=156) and 3.2% or five small clutches in 1981. Four of these full clutches held a single egg, another three had two eggs. None of the studies further investigated the characteristics associated with these small clutches.

## 2.2.6 Extraordinary big clutches

Clutches of more than five eggs were considered to be extraordinary big. Throughout the study, no such clutches were found inside the Bulrush section. Inside the reeds, a total of 17 full clutches (3.8%, n=452) with more than five eggs were laid. In 2003 and in 2007, the maximum clutch size recorded was five so that all clutches exceeding five eggs concentrated from 2004 to 2006.

Eleven of the nests or 65% were started in March. On average, these received their first egg after 15 days. The maximum time span to clutch initiation was 26 days. Only with two platforms, clutch initiation occurred within ten days (after 4 and 6 days). Four additional nests receiving more than five eggs were built in the first decade on April; their clutch initiation happened after on average seven days. Two platforms started in the second decade of April waited for 3 and 4 days. In summary, later platform start led to reduced pre-laying periods.

15 of the 17 clutches or 88% occurred in nests clumped with at least three other nests and even ten or 59% in nests clumped with at least six additional nests (Table 25). One additional nest holding a full clutch of six eggs was located inside a narrow part of Reed I where the structure of the habitat did not allow a high degree of clumping. This nest had only two other nests within 3 m and its nearest neighbour distance was 2.3 m. The platform was started already on 25 March 2005 and received its first egg on 5 April. Its laying was disturbed by the storm on 8 and 9 April 2007. Due to the destruction of major parts of the colony at that moment, the nest might have been subject to parasitic egg laying. The remaining platform was started on 20 March 2005 and received its first egg on 15 April, about one week after the storm. The next nest was at a distance of 3.9 m. Where the platform was located, the stands of reeds were very spaced and thereby inhibited the construction of other platforms in close vicinity.

Most of the 17 big clutches occurred at rather densely populated parts of the colony. Their platforms were generally started early and the pre-laying period was generally not short. It decreased with later platform start. As big clutches were associated with high nesting densities, they could have been more vulnerable to brood parasitism and there were good chances that they were mostly a result of more than one female laying into the same nest.

At Yverdon, from 132 clutches, eight held six eggs (6.1%) and one had seven eggs (0.8%, Berthoud 1963). At Lake Menzelinskoe, Blinov et al. (1981) recorded a total of 37 clutches with six eggs (9.8%, n=379), but only one clutch (0.3%) with seven eggs. From Lake Żarnowieckie, Moskal and Marszałek (1986) reported 24 clutches of six eggs (7.7%, n=313), ten clutches of seven eggs (3.2%), three clutches of eight eggs (1.0%) and each time one clutch with nine, ten and eleven eggs (1.0%) inside colonies. No clutch of a solitary pair had more than seven eggs and the authors speculated that at least clutches exceeding seven eggs were probably laid by several females. At the Gooimeer, van der Poel (2000) noticed that three clutches out of 55 held more than 5 eggs and he speculated that such "supernormal clutches" were produced by more than one female. Unfortunately none of the studies further investigated the circumstances that led to the high numbers of eggs. On bodies of water with one or few pairs all occupying extended territories, clutches of more than five eggs are exceptional. These appear to be strongly associated with more aggregated types of nesting where egg parasitism could be involved. Relatively inexperienced pairs and/or those established at more densely populated parts would be most vulnerable.

## 2.2.7 Parasitic egg laying

To test the idea that big clutches may have been laid by more than one female, the data collected in 2005 and 2006 were analyzed with respect to egg laying patterns and possible brood parasitism. The data available for the other years were not detailed enough for this purpose. As in 2005 a storm early in the egg laying period destroyed most of the platforms, the effects of this event were considered separately.

The storm in the night of 8 to 9 April 2005 reduced all but a handful of platforms, whether containing eggs or not, to floating heaps. For six pairs established in the Reed sections that recuperated at least one egg out of the water, the females exhibited an irregular laying pattern. One of these nests was controlled on 17 April and 5 eggs were recorded. Assuming a regular laying interval of two days between two eggs (which is already rather at the upper limit), the clutch should have had these five eggs on 14 April and therefore must have been complete on 17 April. On 22 April, the nest held six eggs; so the last egg had a good chance of being parasitic. Another of the nests held only three eggs on 15 and 17 April, but five eggs on 22 April. Again, the last two eggs might stem from a different female. A pair that had saved one egg out of four on 9 April had again two eggs on 15 April, three eggs on 17 April and five eggs on 22 April. At least three eggs were added to this clutch after a laying interval of over 48 hours. Brood parasitism cannot be excluded although in this particular case, the clutch might have been complete with four eggs before the storm occurred and resuming laying could have needed some additional time. A fourth nest contained six eggs on 15 April, none with a bluish shine as is the case for freshly laid eggs. On 17 April, it held even seven eggs. The addition of eggs two to six to this clutch took an average maximum time interval of 24 hours which is really low, possibly already under normal conditions too low for such a laying effort by only one female. It is more than doubtful whether one single female can maintain such a fast egg production pace in a stress situation for five consecutive days. Another platform experienced a comparable evolution: it contained two eggs on 8 April, one egg on 9 April and six eggs on 15 and 17 April. Curiously, its clutch was increased to eight eggs on 22 April. Again, there were strong indications for parasitic egg laying. One pair that saved three eggs on 9 April had its nest content unchanged on 17 April. After 22 April, two eggs were added possibly by brood parasitism.

A replacement clutch initiated on 15 April had two eggs on 17 and 22 April, but four eggs on 30 April. Another pair cared for four eggs on 15 April and also on 17 April. On 22 April, the nest counted six eggs. One nest contained two eggs on 15 April, three eggs on 17 April and four eggs on 22 April. A fifth egg turned up on 30 April. In all three cases, the irregular laying patterns gave strong indications for brood parasitism.

A further clutch in the reeds held four eggs on 15 April. Assuming a laying interval of about 1.5 days, all eggs could have been laid by one single female with clutch initiation around 10 April. The nest received a fifth egg during the day of 16 April and a sixth egg in the course of the following night. The last one ended up in the water on 17 April. On 6 May, after a first pullus had hatched, still five eggs remained in the nest. One of them was white, an unmistakable sign that it was rather freshly laid.

In the Bulrush zone, only one nest had a questionable laying pattern in 2005. The clutch contained three eggs on 17 and 22 April, but four eggs on 30 April.

In total, the observations gave strong indications for parasitic egg laying of at least 16 eggs for only these eleven nests. Five of the full clutches were finally extraordinary big, holding three times six, seven and eight eggs. Another four of the nests had a full clutch of five eggs, which is still above the average full clutch size. The last two nests had both four eggs. In 2005, a total of ten extraordinary big clutches were recorded. At least half of them were the product of eggs received from two or more females. Even for the eleven full clutches of five eggs in 2005, the analysis suggested brood parasitism in at least four cases.

Besides the stories of individual nests, figures on a global level also indicated possible nest parasitism. Thus, the average full clutch size inside reeds for laying initiated before 11 April exceeded five eggs in 2005 (Table 20). The second best mean figure obtained in 2006 was 4.58 eggs. It was lower by 0.66 eggs or 12.6% in spite of the fact that for the whole year the average clutch size inside reeds in 2006 exceeded the one of 2005 (Table 19). In addition, with a mean of 5.08 eggs, the nests with egg recuperation contained 0.88 eggs more than the average for all reeds in 2005 (Table 19). Ten of these nests received a minimum of 15 parasitic eggs. By deducting these from all eggs inside reed nests with clutch initiation before 11 April 2005, 21 nests containing 95 eggs or a mean of 4.52 eggs per nest were left. The detected brood parasitism reduced the clutch size as laid by one single female by 0.72 eggs or 13.7%. The circumstances created by the storm proved to be particularly favourable to parasitic egg laying.

Continuing the analysis of laying patterns for clutches started after 12 April 2005, another five nests were detected where brood parasitism might have been involved. In three cases, one egg was added and in two cases, two eggs were added to the content of nests after a laying interruption of three days and more. The full clutches came finally up to four, three times five and six eggs. At the end, at least 60% of extraordinary big clutches in 2005 were subject to parasitic egg laying. For the remaining 40%, brood parasitism could not be proved, but it could not be excluded either. Even for full clutches of five eggs, in seven cases or 64%, egg laying by more than one female seemed evident.

In 2006, seven early clutches in the Reed zone received one egg after a prolonged laying interruption. In three cases the exact duration of the interruption was of 10, 11 and 13 days. In the other cases the minimum durations were of 3, 5, 7 and 15 days. Two of these clutches with platform initiation in March were at the end extraordinary big. Three additional clutches initiated towards mid-April also received a parasitic egg. In two nests two eggs were added after laying interruptions of 6 and of minimum 12 days. Both at the end contained seven eggs. The third nest doubled its content to six eggs after an interruption of minimum 13 days, so that all three pairs concerned had to cater for extraordinary big clutches. In the Bulrush section, two early nests also received each one late egg.

A total of seven extraordinary big clutches were recorded in 2006: at least five of them or 71% were subject to brood parasitism. Another 13 nests received five eggs, with laying by two females occurring in at least three nests or 23%.

Summing up the data of both years, 19 nests with extraordinary high egg numbers were recorded. Parasitic egg laying occurred in at least eleven cases or 58%. For an additional 24 clutches with five eggs, brood parasitism was proved in ten cases. Therefore, it seemed highly likely that clutches with more than five eggs in general were laid by more than one female and even for clutches of five or less eggs, brood parasitism cannot be excluded.

Eggs of different species, even if closely related, have differing characteristics. Therefore, inter-specific nest-parasitism is rather easily proved. Blinov et al. (1981) found one Great Crested Grebe egg in a nest of a Little Gull *Larus minutus* and a second one in the nest of a Tufted Duck *Aythia fuligula*. They also recorded one egg of a Slavonian Grebe in the nest of a Great Crested Grebe. Otherwise, they thought nest parasitism, especially intra-specific, to be unusual. Fjeldså (2004) thought that brood parasitism is probably rare in territorial species of grebes, even if these sometimes form colonies.

Intra-specific brood parasitism is however not simple to detect, but has to be investigated methodologically. At Tiligul'liman estuary, Koshelev (1985) concluded that under high nesting density, intra-species aggression rises sharply and leads to birds leaving the nests and their clutches unobserved. Thus, opportunities for predation on the eggs, but also for nest-parasitism are created. Henriksen (1996) studied conspecific brood parasitism in the Great Crested Grebe by checking daily the content of 51 nests. Four of them received parasitic eggs, but no foreign egg appeared in complete clutches. At the site of his study, Lake Braband, 30% of the females lost their nest as a consequence of climatic conditions before clutch completion. Some of them might then have deposited eggs in the nests of other members of their species.

Lyon and Everding (1996) thought that nesting density might be an important factor for the occurrence of brood parasitism. They proved a high frequency of conspecific brood parasitism in the colonial Eared Grebe *P. nigricollis californicus*. In densely packed nests, there are constant interactions with numerous threats and chases between neighbouring pairs that offer opportunities for parasitic egg laying in unobserved nests. In their study, a significantly higher proportion of parasitized nests lost eggs than did nests that were not parasitized. Of 50 eggs that disappeared from parasitized nests, 43 disappeared after parasitism first occurred, one before it occurred and six on the same day the parasitic egg was laid. The authors concluded that such partial loss could either be due to egg rejection by the hosts that were able to detect brood parasitism or to the removal of eggs by the parasites in order to prevent the detection of their act. Whereas the parasites have an easy task in avoiding the removal of their own egg by themselves, the owners of the nest would have to recognize the parasitic egg so that they could withdraw the undesired egg. In many colonial birds, there is much inter-clutch variability in egg coloration, maculation and form that could contribute to egg recognition and the identification of parasite eggs (Deeming 2002).

It is not known to what extent the Great Crested Grebe has at the current stage evolved strategies often associated with conspecific brood parasitism. As the species is still largely territorial, behavioural adaptations favouring egg dumping in foreign nests or its avoidance by the owners possibly are still largely missing. Brood parasitism might therefore be limited to situations of extremely high nesting densities or sudden loss of platforms during the process of egg laying. Egg recognition and the removal of foreign eggs could not be developed so that brood parasitism simply leads to increased clutches for parasitized nests. Depending on circumstances, parasites themselves could face lower own clutches, for instance if their platform is lost during laying. Even if Great Crested Grebes are indeterminate layers, it remains open in how many cases a full "normal" own clutch is achieved by the parasite. Egg survival shows a diminishing return with increasing egg position in the laying sequence. This pattern results from the hatching asynchrony and the strong laying-order-dependent starvation within broods (Lyon 1998). It seems therefore that the Great Crested Grebes have not yet integrated a more general strategy of brood parasitism in their nesting behaviour at the Footbridge colony. Indeed, in many cases parasitic eggs were added after clutch completion so that the chances for survival of their hatchlings to independence were low. The examples provided by Henriksen (1996) already pointed at a more elaborate behaviour in this sense.

It also has to be mentioned that, even if all eggs in a particular nest are laid by one female, it is by no means sure that they have all been fertilized by the same male. Aggregated nesting and high bird densities result in more opportunities for extra-pair copulation than exist for non-colonial species (Ligon 1999). Such extra-pair copulations have been personally observed in the Black-necked and the Silvery Grebe. At Enkhuizen, no such case was directly recorded in the Great Crested Grebes. Early during settlement however, occasionally platform courtship was performed with changing partners. During these mountings, cloacal contact did however not occur.

## 2.2.8 Incubation times

The data collected at Enkhuizen permitted to calculate exact incubation times for some platforms and to see whether the durations differed. For the analysis, it had to be born in mind that egg laying in the Great Crested Grebe is asynchronous and that this asynchrony is repeated in hatching with mean intervals of 1.2 to 1.8 days (Henriksen 1995).

For a total of 57 nests constructed inside the Reed zones of the colony from 2003 to 2006, a precise incubation time from first egg laying to first hatching was known (Table 27). The data of the year 2005 were split into two categories as incubation in nests affected by the storm might have been subject to an altered incubation pattern. The eight nests concerned were considered separately. For the 49 remaining platforms, incubation times in the different years lasted on average between 24.42 (2005, n=12, only clutches started after the storm) and 26.64 (2003, n=13) days, with a mean

**Table 27:** Incubation times in different years.

| Zone | Year | Average (days) | Range | N |
|---|---|---|---|---|
| Reeds | 2003 | 26.64 | 24-29 | 13 |
| | 2004 | 25.00 | 23-27 | 8 |
| | 2005 | 25.55 | 23-28 | 20 |
| | *- 2005 only nests not affected by storm* | *24.42* | *23-26* | *12* |
| | *- 2005 only nests affected by storm* | *27.25* | *25-28* | *8* |
| | 2006 | 25.81 | 23-28 | 16 |
| | All years without nests affected by storm | 25.51 | 23-29 | 49 |
| Bulrush | 2003-2006 | 26.83 | 24-29 | 6 |

of 25.51 days for all years taken together. The difference in mean figures between highest and lowest values was 2.22 days or 8.3%. The range of individual incubation times was from 23 to 29 days, a difference of six days or 20.7%. Clutches in 2005 affected by the storm had a higher average incubation time (27.25 days, n=8) and a higher minimum incubation time (25 versus 23 days) than later clutches in that year or clutches in other years. Most probably this was a consequence of the incubation interruption caused by the storm.

In order to find an explanation for the over two days difference in mean yearly incubation times and of six days between lowest and highest individual incubation times, the durations of incubation were analysed by grouping them according to different criteria. With respect to clutch initiation dates, those clutches started in the first decade of April of all years were incubated for on average 26.00 days (range 24-28, n=26), those started in the second decade for 24.87 days (range 23-29, n=15) and those started later for 24.80 days (range 23-27, n=5). These results pointed to a reduction of incubation times for later clutch initiation dates. Not only the mean duration declined in time. Also no incubation duration of 23 days only was recorded for clutches started before 10 April and if started after 20 April, the first egg took a maximum of 27 days to hatch. With respect to the degrees of clumping, the differences were not significant and they also did not show a clear trend: nests not clumped or clumped with one nest were incubated for a mean 26 days (n=7), those clumped with 2 or 3 other nests were incubated for 25.33 days (n=15), those clumped with 4 or 5 other nests were incubated for 25.43 days (n=14) and those clumped with more than 5 nests were incubated for 25.83 days (n=11). Also with respect to timing from platform initiation to clutch initiation, mean incubation durations were rather similar: 25.13 days for up to one week (n=8), 25.18 days for between one and two weeks (n=11) and 25.78 days for longer durations (n=23).

The only explanation found for the differences in incubation time resided in higher temperatures later in the season that could have contributed to a seasonal reduction of the duration. During egg neglect or change-over of incubation duties between the mates, higher atmospheric temperatures will slow down the cooling of the eggs. It is however doubtful if the generally short incubation interruptions as observed at the Footbridge colony would be enough to explain a difference of over two days in incubation averages. Differences in incubation behaviour as were observed in the different pairs of the colony were more likely to explain the variation. Indeed, some birds were directly sitting for long incubation spells on their first egg. Others left their first, and sometimes even their second egg unobserved, covered or uncovered, for prolonged periods. Exceptionally, a nest containing three eggs remained not incubated for longer. Unfortunately, the incubation behaviour of individual pairs during the days directly after clutch initiation until clutch completion was not measured, so that a direct relationship between the duration of the incubation and the breeding behaviour of each pair could not be established.

Inside the bulrush, the incubation time could be identified for only a total of six nests for all years taken together. Their pooling produced a mean incubation duration of 26.83 days, about 1.22 days longer than for all nests inside the Reeds.

The lowest bulrush incubation time was 24 days (Table 27). For the bulrush, exclusively data for nests with early clutch initiation were available. This could explain the relatively longer incubation times there.

In literature, incubation time indications for each egg vary between 24 and 29 days (Onno 1966, Cramp & Simmons 1977, Ulfvens 1988). In Poland, Hànzák (1952) found the shortest period to be 22 days. Lomholt (1974) registered 28 days for five eggs in an incubator. The findings of Enkhuizen were generally in line with the indications in literature. It could not be established whether solitary or colonial breeding could have an influence on the duration of incubation.

## 2.3 Egg loss

Egg loss in grebes may result from several factors. Besides climatic hazards, clutch destruction and infertility of eggs for whatever reasons can cause reductions of nest contents before pulli hatch. The next two sections analyse the major causes for egg loss in colonial Great Crested Grebes and they demonstrate how the birds can at least partially counter the resulting negative effects.

### 2.3.1 Egg loss and its causes

At the Footbridge colony, egg loss was observed in all years. The data available showed variable patterns when comparing different years or sections of the colony (Table 28). Excluding the storm year 2005, a mean of 17.4% of the nests suffered egg loss. In 2005, 35.7% of all nests knew egg losses. The percentage could have been higher if more platforms contained already eggs when the storm occurred. Except for 2005, relative egg loss was higher in the Reed zones than in the Bulrush zone.

From a total of 190 eggs lost in the five breeding seasons, the reason for their disappearance remained unknown in 82 cases or 43.2%. Otherwise, the highest toll was due to a storm in 2005. Wind and high waves tore apiece 23 nests containing 56 eggs in the reeds and another four nests with seven eggs in the Bulrush. These 63 eggs accounted for 33.2% of all eggs lost in five years. 18 eggs (9.5%) were abandoned, ten of them after partial hatching of the clutch. At least two of the ten eggs left behind after hatching of other eggs in the clutch were fertile. The pulli were observed to hatch in the absence of the adults and did not

**Table 28:** Extent of egg loss recorded from 2003-2007.

| | Sections | Eggs lost | Nests with loss | % of nests with egg loss | Mean egg loss/ nest affected |
|---|---|---|---|---|---|
| **2003** | **Reed** | 30 | 19 | 18.4 | 1.58 |
| | **Bulrush** | 4 | 4 | 17.4 | 1.00 |
| | **Colony** | 34 | 23 | 18.3 | 1.48 |
| **2004** | **Reed** | 20 | 11 | 11.7 | 1.82 |
| | **Bulrush** | 1 | 1 | 5.3 | 1.00 |
| | **Colony** | 21 | 12 | 10.6 | 1.75 |
| **2005** | **Reed** | 74 | 32 | 34.1 | 2.31 |
| | **Bulrush** | 11 | 6 | 33.3 | 1.83 |
| | **Colony** | 91 | 40 | 35.7 | 2.27 |
| **2006** | **Reed** | 23 | 16 | 16.3 | 1.44 |
| | **Bulrush** | 1 | 1 | 5.9 | 1.00 |
| | **Colony** | 24 | 17 | 14.8 | 1.41 |
| **2007** | **Reed** | 21 | 11 | 12.9 | 1.91 |
| | **Bulrush** | 5 | 3 | 11.5 | 1.67 |
| | **Colony** | 26 | 14 | 12.6 | 1.86 |
| **All years** | **Reed** | 168 | 89 | 18.8 | 1.89 |
| | **Bulrush** | 22 | 15 | 14.6 | 1.47 |
| | **Colony** | 190 | 104 | 18.1 | 1.83 |

**Table 29:** Egg loss and its causes from 2003 to 2007.

| | Sections | Reasons of egg loss | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Predation by rails | Abandoned | Rolled out of nest | Lost in fight | Kicked out | Storm | Unknown |
| 2003 | Reed | | 2 | 4 | | 2 | | 22 |
| | Bulrush | | 1 | | | | | 3 |
| 2004 | Reed | 1 | 1 | | 1 | | | 17 |
| | Bulrush | | | | | | | 1 |
| 2005 | Reed | 3 | 3 | 1 | | | 56 | 11 |
| | Bulrush | | 3 | | | | 7 | 1 |
| 2006 | Reed | 3 | 5 | 5 | 1 | | | 9 |
| | Bulrush | | | | | | | 1 |
| 2007 | Reed | 3 | 3 | | | | | 15 |
| | Bulrush | | | 3 | | | | 2 |
| All years | Reed | 10 | 14 | 10 | 2 | 2 | 56 | 74 |
| | Bulrush | | 4 | 3 | | | 7 | 8 |
| | Colony | 10 | 18 | 13 | 2 | 2 | 63 | 82 |

survive for long. Part of the eggs might have been unfertile. Why eight eggs were abandoned shortly after laying remains unknown. 13 eggs (6.8%) landed up in the water, either as a consequence of the poor quality of the platform when the egg was laid or due to inadvertence of the incubating bird when leaving the nest. Each time two eggs or 1.0% were intentionally kicked out of a nest or were lost during fights. It is unknown whether the two eggs intentionally kicked out of a nest were so by the owner or an intruder. Ten cases of predation or destruction by rails occurred all inside the Reed sections, representing 5.3% of total egg loss. In nine cases coots and in one case a Moorhen were responsible. If coots were involved, the eggs were most often simply destroyed, at least in a first instance. The destruction was often preceded by intense aggression between both species that were nesting in close vicinity to one another. The eggs were always destroyed in the presence of generally one Great Crested Grebe. The latter seemed amazed by the action of the coot and thereafter, either remained puzzled or vigorously attacked the opponent. The rails mostly showed no interest in feeding on the content of the eggs. In all but one case, egg destruction happened after hatching of young coots. Earlier in the season, even grebe clutches started in close vicinity of coots were left unobserved for prolonged periods of time. The rails took no advantage of the inviting situation and showed no particular interest in the open to view eggs. In this respect, moorhens could have been more dangerous. In the observed case, the moorhen really fed on the egg. It also appeared that moorhens were readily chased by the grebes when approaching an uncovered clutch. This was less the case with coots. In addition to direct egg destruction, a grebe lost one egg in a fight with a neighbouring coot when in the course of the action, its egg landed in the water. Similarly, in a fight with a conspecific, one egg was pushed into the water (Table 29).

The extent of destruction of grebe eggs might have been more important than recorded and all figures must be taken as minimums. Most probably, not all losses were detected, especially during the years with a shortened monitoring program. Lost eggs were indeed often replaced quickly. Besides the rails, possible other predators were Grey Herons *Ardea cinerea*, gulls and terns that appeared regularly at the site of the colony. Even if no act of predation by the latter species was observed, the incubating grebes got always very upset when these, and especially the herons, approached their nests too close.

At Lake Neuchâtel, Renevey (1988:1) saw that a minimum of 343 clutches or 25% of all 1,373 clutches recorded between 1984 and 1986 were destroyed. Wave action was responsible for 63% of the destructions. Predation loss was negligible, accounting for only 2% of the total loss. Water level changes destroyed another 13% of the clutches and anthropogenic causes (waves caused by motor boats, penetration of the reeds by men) were responsible for 20%. Goc (1986) identified water level changes, waves, predation, accidental damage by fishermen and misuse of nests (e.g. as a resting place by Grey Herons or ducks Anatidae) as causes for egg and clutch loss at Lake Drużno. The relative importance of the different factors causing clutch destruction remained unknown. In spite of the preference of the grebes for establishing their colonies inside aggregations of Laughing Gulls, Goc observed no case of egg destruction by the gulls. On several occasions coots caused damage to the eggs of the grebes. Goc thought however that the active territory defence by the coots possibly outweighed the risks taken by the grebes when associating with them. At Lake Drużno, nest survival was highest (58%) in mixed colonies with gulls, followed by associations with coots (50%) whereas in monospecific colonies, it reached only 18%. At Lough Neagh, Perry (2000) attributed the mean nest failure rate of 43% mainly to the serious impact of the climate owing to wind and wave action. He identified the Hooded Crow and to a lesser extent the Magpie *Pica pica*, and occasionally the Black-headed Gull *Larus melanocephalus* and the coot on unguarded eggs as predators of grebe clutches. He found no higher survival rate for clutches of grebes inside gull colonies. The aggregations of the Great Crested Grebes at the Selenga River Delta experienced an egg loss of 68.5% in 1980, 32% in 1981 and 15% in 1985. The low water levels of 1980 made more favourable nesting habitat unavailable to the grebes and water level fluctuations later in the season caused high damages on early nests. With increased water levels in 1981 and especially 1985, the large majority of colonial nesters switched to solitary breeding and this reduced the loss attributable to predation by harriers *Circus sp.* and large gulls (Podkovyrov 1986). From Lake Menzelinskoe, Binov et al. (1981) reported predation by the Hooded Crow as main reason for the grebes' egg and clutch loss. Such losses were increased during periods of anthropogenic disturbances to the colonies or in the absence of protecting gulls and terns. At the Houtribsluizen, Leys et al. (1969:2) recorded 263 nests. 152 nests containing 367 eggs were destroyed, mostly at early stages of incubation. Wave action caused the large majority of the losses, a limited number of clutches was abandoned. As only a total of about 100 breeding pairs were present, re-nesting was frequent and every pair produced about 2.5 clutches on average. Stanevičius (1994) registered no case of nest destruction by waves on eutrophic lakes of south Lithuania. He argued that Great Crested Grebes were able to identify the habitat zones where their platforms could be subject to risks by waves and they avoided them.

At the end, egg and clutch loss was largely circumstantial and conditioned by local factors. Most of the causes identified would affect solitary and colonial nests alike. Atmospheric conditions provoking changes in water levels or wind and wave action would be similarly detrimental to the grebes' nests, whether isolated or grouped. Territorial pairs, just as colonial birds, could associate with other species for better protection thereby taking the same risks for their clutches. Globally, climate and predation were identified as the two major causes for egg destruction, directly followed by anthropogenic causes. Threats stemming from humans were indeed manifold and difficult to assess, especially as their effects were often more indirect. In general, anthropogenic threats cover a wide array of factors including wetland and nesting habitat destruction, introduction of predators, detrimental leisure activities (boating, egg collection, …), other disturbances, pollution. Again, a priori their effects would not differ between nesting types.

Colonial nests could nevertheless be more vulnerable because of two reasons: the aggregations are easily detected and the aggressions between the grebes themselves could lead to egg loss. If predation is an issue and without the opportunity of protection by more aggressive species, solitary nests could be better hidden and escape to the attention of the predators. The colonies are identified quickly and their sight may even attract additional predators. Depending on the predator's species and its numbers, occasionally the association by the grebes could help to discourage the enemy. Even though the risk of predation might be higher, coloniality could enhance the chances of survival of the adults and thereby contribute to the lifetime reproductive success of the grebes.

As seen previously, conspecific aggression can lead to egg loss and it could be the only prejudice of nesting aggregations that has no counterbalancing benefit. The incurred losses can be direct (egg destruction caused intentionally or inadvertently in the course of a dispute) or indirect (inattentiveness to the clutch increasing the risk of predation).

The Great Crested Grebes generally have evolved protective measures to counter different situations of egg loss. Those related to climatic conditions will be exposed in the next section. With respect to predation, the association with more aggressive species has already been enumerated. Also egg covering protects the clutches as they then can pass unnoticed by predators. The incubating grebes, when leaving their clutches in view of approaching dangers, do so in a very hidden manner; they glide into the water and dive away, reappearing only at some distance from their nest. It is expected that egg covering and inconspicuous leaving of the nest is more efficient in solitary than in colonial pairs. However, active defense of the clutches as it was observed against rails, gulls and terns might better pay off in a colony. It has also to be mentioned that, even if an egg or a clutch is lost, the physiological conditions of the grebes allow quick replacement.

To conclude the chapter, a particular case of egg loss, namely egg desertion, deserves our attention. It has often been assumed that eggs deserted after prolonged incubation times or after partial hatching of a clutch must be infertile. Renevey (1988:1) tested 280 grebe eggs in this respect. Only two (0,7%)were infertile. However the analysis of 36 eggs revealed high values of micro-pollutants. The values were expressed in relation to the total weight of the egg content. For PCB an average value of 8.89 (range 0.37- 42.26) was found and for all DDT, the value was 5.24 (range 0.29-50.69). In addition, traces of metal were found in the shells of all eight eggs analysed in this respect.

## 2.3.2 Storm damage and reaction of the Great Crested Grebes

It has often been insinuated that low fledging success in colonial Great Crested Grebes is mainly a consequence of wave and wind action that already reduce the hatching success. In particular, storms can wash away all the eggs of a colony and many pairs thereafter may not attempt replacement clutches. At Enkhuizen, field work in 2005 also included the experience of a storm and this provided a unique occasion to follow the behaviour of the grebes under such circumstances.

On 8 April, the mapping of the existing platforms, including the registration of the quality and the content of each platform, was just finished when heavy winds brought hale and rain along in late afternoon that started to destroy the nests of the birds. The storm lasted for most of the night and it calmed down in the morning of the next day. It left all but two nests either completely demolished or reduced to the state of floating heaps with the eggs well inside the water at their centre or having disappeared.

On 8 April, the colony recorded a total of 61 platforms, 53 inside the Reeds and eight inside the Bulrush. The low number of platforms inside the latter area was a consequence of the still poor condition of the habitat there; old stands offered hardly hold to the platforms and fresh stands were still absent. Nine Reed platforms and three Bulrush platforms had to be considered as rather basic. 29 platforms of the colony contained eggs, 25 nests in the Reed zones held 62 eggs and four nests in the Bulrush zone had seven eggs.

Towards late afternoon, after the storm had built up, a quick check of the situation in the colony at 8.30 p.m. recorded first damages to the platforms which had flattened and started to drift slowly apart. The grebes tried to counter the negative effects by strongly multiplying their building efforts. Their success was however limited. In some nests, as a result of the flattening of the platforms, the eggs had already sunk to the level of the water.

In the very early morning hours of 9 April, the storm had calmed down, but the wind remained strong for most of the day. The mapping inside the colony at 7 a.m. recorded only three platforms inside the reeds that had survived in good condition whereas 29 were reduced to loose heaps or basic platforms. The three solid platforms had suffered no egg loss and they still contained zero, two and four eggs. 21 platforms had completely disappeared. In the Bulrush zone, only two loose heaps remained. While some pairs had definitively abandoned their platforms, others tried to save the remains by frenetic building.

From six platforms in the reeds under special observation, four held eggs (one, two, three and four eggs respectively) on 8 April. In the morning of 9 April, all eggs were floating in the wet, surrounded and retained mostly on the surface

**Table 30:** Great Crested Grebe nests with egg recovery after the storm.

| Platform | Eggs on 8 April | Eggs on 9 April | Full clutch size | Hatching information | Time from 9 April to hatching |
|---|---|---|---|---|---|
| 55* | 3 eggs | 3 eggs | 3 eggs | 2 pulli and 1 abandoned egg on 6 May, when family left | 24 days |
| 56* | 2 eggs | 1 egg | 7 eggs | 3 pulli and 4 eggs on 6 May | 24 days |
| 8 | 2 eggs | 2 eggs | 6 eggs | 2 pulli and 3 eggs on 6 May | 25 days |
| 10 | 3 eggs | 3 eggs | 4 eggs | 2 pulli and no eggs, left on 6 May | 24 days |
| 23 | 4 eggs | 4 eggs | 5 eggs | 3 pulli and 2 eggs on 30 April | 18 days |
| 25 | 2 eggs | 2 eggs | 6 eggs | 3 pulli and 2 eggs on 6 May | 24 days |
| 41 | 4 eggs | 1 egg | 5 eggs | 1 pullus, eggs unknown on 6 May | unknown |
| 98 | 3 eggs | 2 eggs | 5 eggs | 3 pulli and 2 eggs on 6 May | 24 days |
| 106 | 1 egg | 1 egg | | abandoned | |
| 109** | 2 eggs | 1 egg | 8 eggs | 8 eggs on 6 May | > 28 days |
| 123 | 3 eggs | 3 eggs | 5 eggs | 2 pulli and 3 eggs on 30 April | 19 days |
| 127 | 4 eggs | 1 egg | 3 eggs | 2 pulli and 1 egg on 6 May | 25 days |
| 138 | 2 eggs | 2 eggs | 4 eggs | 2 pulli and 2 eggs on 6 May | 25 days |
| Total | 35 eggs | 26 eggs | 61 eggs | 25 pulli, min. 27 eggs still incubated, 1 egg abandoned, 5 eggs lost | |

* Indicates platforms closely monitored.
** Indicates platforms without hatching when monitoring was stopped.

by the disintegrating nesting material. It has to be noted that during incubation, the specific gravity of eggs decreases due to loss of water, thereby increasing its floating abilities (Goc 1986). Thus, only eggs old enough to float or younger eggs held back on the water surface by drifting nest weeds may be recovered. The owners of such floating eggs were trying to rebuild the platforms around the eggs. They fortified one side of the platform and then pulled the eggs with their beak upon the rebuilt part. They continued their building efforts around the eggs, elevating other parts slightly beyond the level of the eggs before again pulling the eggs with the beak towards the higher weed. The pair with two eggs on 8 April finally recovered one egg. It continued laying thereafter and its full clutch reached seven eggs on 17 April. The pair with three eggs saved them all and continued incubation without adding further eggs. The other two pairs were unable to recover any eggs and laid new clutches later.

The owners of eleven other nests were able to rebuild their platforms and to recover some eggs until midday on 9 April. In total, 13 pairs recovered 26 out of 35 eggs out of the water (Table 30). One additional platform holding one egg on 8 April and destroyed by the storm was rebuilt on 9 April and again contained one egg later on that day. It seemed however more plausible that this egg was freshly laid rather than recuperated out of the water. Another pair having saved one egg abandoned its nest about one week later. Eleven of the twelve remaining nests increased their clutch size after 9 April by receiving 36 additional eggs. The full clutches of the twelve nests counted 61 eggs or 5.08 eggs per nest, a rather high figure when compared to the annual averages of complete clutch size for the entire colony that were comprised between 3.75 and 4.19 eggs in the five years of the study (Table 19).

In order to assess how fast the females of the eleven nests were able to resume laying after egg loss, respectively whether they were able to sustain normal laying intervals to increase their number of eggs again after egg loss, a hypothetical average laying interval for after-storm eggs for nests with egg loss recovery was calculated. The obtained mean intervals per nest ranged from 1.2 to 8 days, including a possible laying interruption. For all pairs, the time from clutch initiation before the storm to hatching of the first pullus (Table 30) was calculated. The comparison of general incubation times for the colony (§ 2.2.8) with the after-storm times to hatching and after-storm laying patterns of nests with egg recovery in 2005 permitted then to detect whether hatched chicks could stem out of pre-storm or out of after-storm eggs. It was thereby assumed that, due to the incubation interruption caused by the storm, individual incubation should have lasted for at least 25 days which corresponds to the lowest yearly average found.

In seven nests with egg recovery a total of 14 chicks hatched before after-storm eggs added could have been incubated for more than 24 days. It must therefore be assumed that all 14 chicks stemmed from pre-storm eggs that were saved out of the water. An additional two pre-storm eggs might have hatched later in these nests. In three nests, five pulli hatched when after-storm eggs could have been incubated for exactly 25 days, so that it was still highly likely that the eggs concerned were laid before the storm. Indeed, the incubation interruption due to the storm triggered an extension of the incubation time of on average about 2.7 days to a mean of 27.25 days (n=8, Table 27). In one nest, the hatching date of the only pulli could not be determined and another nest still knew no hatching 28 days after the storm.

In summary, from 26 eggs exposed for up to 16 hours to the cold water of Lake IJssel, 14 (53.8%) surely produced pulli, five eggs (19.2%) most likely hatched and two additional (7.7%) may have hatched. This result is very interesting from several points of view:

- First, it proves that embryos must be highly resistant to direct and prolonged exposure to cold. Eggs, freshly laid or a couple of days old, having passed between approximately eight and 15 hours in the water at maximum air temperatures of 5° C still produced pulli. Grebes are known to interrupt their incubation now and then, normally covering their eggs when leaving the nest. Kalinin (1991) found that egg covering will slow the cooling of the clutch during such interruptions and at air temperatures higher than 19°, even the need to cover could be reduced. For Pied-billed Grebes *Podilymbus podiceps*, the temperature of the not incubated, but covered nest-cup did not decrease by more than five degrees to 31° C at water temperatures of 20° C and air temperatures between 11 and 23° C (Davis et al. 1984). In the Red-necked Grebe *P. grisegena*, during nocturnal egg neglect lasting up to 9 hours egg temperatures fell to below 30° C or even approached and fell below 20° C. As a consequence, incubation periods were prolonged (Nuechterlein and Buitron 2002). But an incubation interruption does generally not trigger an immediate drop and to such low values in egg temperature as it has certainly been the case in Enkhuizen. Schiermann (1927 in Melde 1995) reported of a clutch where after 40 hours of incubation interruption still one pullus hatched in the incubator. But even in this case, the decrease of the clutch temperature may have been slow without finally reaching temperatures comparable to Enkhuizen.
- Second, the eggs must be able to survive wet conditions. This is however already a more general prerequisite as clutches are incubated in moist or even wet nests. The characteristics of the eggshell provide special protection against water inlet and flooding of the pore canals that could lead to suffocation of the embryo. The eggshells are waterproof due to their chalky cover (Lack 1968) and the morphology of the inner orifice of the pore canal insures an adequate flux of respiratory gases throughout incubation. The feature protects the egg against water entry, microbal infection and the occlusion of the pores with mud (Board et al. 1984).
- Third, the grebes that had lost part or their entire clutch were in a position to resume laying quickly. Two pairs that lost their complete first clutch of four eggs in the storm were incubating again four and six eggs later. Thus, they produced a total of eight and ten eggs in a row. On one hand, such high numbers could have been laid by two or even more females. On the other, it is also true that one female grebe is able to lay 13 eggs in sequence if the eggs are removed from the nest (Fugle and Rothstein 1977 for the Pied-billed Grebe) or even more than 20 eggs if the clutch is always reduced to one after laying (Hennicke 1903 for the Great Crested Grebe). In Enkhuizen, egg loss did not directly negatively affect the final clutch size, and this is in agreement with

Lack's hypothesis that a clutch is limited by the number of eggs a female's food resources allow her to form (Fugle and Rothstein 1977). However, the laying conditions of different females seemed to diverge greatly, as not only witnessed by the differences in final clutch size, but also by the hypothetical laying intervals. The figures suggest that some females needed to recover before they were able to produce new eggs, whereas others were immediately able to resume laying. It could be that once a laying cycle is complete, it just needs more time to produce additional eggs. As analyzed earlier more in detail, parasitic egg laying by conspecifics impacted clutch sizes, too.

- Fourth and even more important, the event showed that Great Crested Grebes were able to recover eggs floating in the water by rebuilding their nest around them. Washouts by wave action during wind storms are a major cause of egg and clutch loss in grebes and they can annihilate entire colonies. When the wind calmed down, J.J. Vlug often found masses of the eggs of a Great Crested Grebe's colony on Lake Geneva to cover the ground below the lake's surface and the shore (pers. comm.). Once eggs are sunk, they cannot be recovered and such losses may explain to a large extent the often rather low reproduction in colonies. It was already known that the species does not simply abandon nests or their content in a storm. Grebes try to save their clutch by intense building that is however stopped once visibility fades, meaning at night. Replacement clutches can contribute to minimize the effects of storm damage on the seasonal breeding success. The successful recovery of floating eggs is new to our knowledge and it must be added to the means helping the Great Crested Grebes to counter the effects of a storm.

## 2.4 Re-nesting and second clutches, hatching and breeding success

It has often been pretended that the breeding success of nesting aggregations in the Great Crested Grebe is very low. In order to maintain such local populations, immigration from more successful places would be needed. To some extent, this assessment is based on wash-outs that within a few hours destroy the clutches of entire colonies. The grebes however may counter the negative effects by laying replacement clutches and the pairs are not necessarily limited to one clutch per year. The aggregation with other conspecifics does not prevent individual pairs from raising more than one brood in a season. The question then arises whether the breeding success is really that low in colonial Great Crested Grebes. If it were the case, why would the birds then invest in low return rates?

### 2.4.1 Re-nesting and second clutches

In colonial grebes, the differentiation between replacement and second clutches and the re-use of the same nest by a second pair is difficult. Especially if egg laying is asynchronous, the re-occupation of a nesting platform shortly after the initial pair left with its hatched chicks may signify either that the pulli were lost quickly and the adults returned for a replacement clutch or that a different pair initiated its first or its second clutch. Whatever could be the reason for the re-use of the nesting platform, it contributes to increase the breeding success of the colony as a whole.

Until the end of May in 2003, re-nesting occurred in at least 25 nests of the Footbridge colony. Generally, it could not be determined whether these were replacement or second clutches or whether a new pair had occupied an old nest after the first occupants had left. In May, due to the growth of the new vegetation, it proved more and more impossible to follow nesting progress. Further cases of re-nesting remained possibly undetected and only for four of the 25 platforms re-occupied, the clutch size was determined. These contained 3, 4, 4 and 5 eggs and on average four eggs. A last visit to the colony on 20 August detected a total of six active nests. The dense vegetation surely hid other active platforms. In addition, nine families with a total of 19 chicks were observed inside the harbour.

In 2004, re-nesting was detected in six nests. This low figure was a consequence of the short program of that year and the real number was surely much higher. In five of these nests, previous hatching was observed. For two re-uses, the full clutch was known and contained three and four eggs.

In 2005, in two nests a lost clutch was replaced and in another 37 nests, re-nesting was observed. 34 of these second clutches were initiated in May, shortly before the research program was stopped and therefore, no information on full clutch sizes was available.

In 2006, four cases of re-nesting were recorded. One case was possibly a replacement clutch receiving four eggs and in two cases, an old platform was re-occupied after hatching.

In 2007, the harbour of Enkhuizen was visited a last time outside the program on 25 August. Seven families with a total of 15 chicks were seen close to the Footbridge, three active nests were detected and, based on adults observed to enter the vegetation, additional nests were supposed to be still active.

The observations suggested that in all years the colony remained in use until rather late in the year and possibly into September although from mid-May onwards, the number of breeding pairs was considerably reduced. Some pairs not able to gain early access to the colony might have waited until the first families left for the open lake to occupy the platforms abandoned by them. Possibly they were less experienced birds that either now encountered less resistance by the neighbours on their eggs left behind or they had become mature only later in the season. In a limited number of cases, where the first clutch was lost fast, the second clutch in the same nest might have been a replacement clutch. It seemed however more reasonable to believe that in most cases new pairs initiated their first clutch. Indeed, several times when a family left, its platform was already re-occupied before it could have reached the exit to Lake IJssel. After mid-June of each year, the chances increased that the re-use of a nesting platform meant a second clutch. From this point in time onwards, the first chicks of each season could have reached independence and their parents could have decided to re-nest. Assuming that an average of 20 nesting platforms remained active from after mid-June until into September of each year, about 40 pairs per season or 35% of the colonies inhabitants could have laid a second clutch.

In colonies, it is generally quite difficult to detect to what extent re-nesting occurs or second or even third clutches are laid. Only if a colony is devastated by a storm, it is reasonable to assume that the new clutches are replacement clutches, at least in their large majority. Van der Poel (2000) speculated that colonial Great Crested Grebes do not raise more than one brood per year, but a prematurely lost clutch could be replaced. At the Houtribsluizen, Leys et al. (1969:2) recorded the presence of roughly 100 breeding pairs that laid 263 clutches in 1967. On average, each pair laid about 2.5 clutches. Most of them were replacement clutches. Mayr (1986) speculated that second clutches were depending on the total number of breeding sites available. If these were very limited, competition would exclude surplus pairs from settling down early. These would have to wait for families to leave to occupy their abandoned platforms. Late breeders thus prevented early breeders from returning to their original platforms for a second brood and this would also explain the general absence of second clutches in Eastern Europe. This absence could also be explained by the timely limited breeding season in many regions that after successful rearing of a first brood does not leave enough time for a second brood. However, the pairs could attempt replacement clutches if their pulli were lost early so that they would be part of Mayr's late breeders. Replacement clutches occurred in Enkhuizen, too. Nevertheless, due to the start of nesting very early in the season and the long duration of the breeding season on the IJsselmeer, the impact of second clutches on the breeding success of the colony must not be disregarded. Even if it remains generally unclear to what extent replacement or second broods increase the fitness of colonial grebes, their contribution to the annual production of pulli is possibly important, at least at location with an extended breeding season. When depending on the association with other species for successful breeding, second broods could be largely excluded, except if this brood happens in a more solitary way. Without extreme limitations in breeding habitat, there seem to be no other obvious reasons why colonial breeders should be less inclined towards second broods than territorial pairs.

### 2.4.2 Hatching success

An important step to successful breeding is successful hatching. The hatching success is limited by the clutch size and thereafter by the number of eggs that survived incubation. Similarly to solitary breeding pairs, colonial Great Crested Grebes raise their chicks away from the nesting platform and from other families. Thus, if we assume aggregated nesting to be less successful, we could expect that this is mainly a consequence of a reduced hatching success.

**Table 31:** Number of nests with hatching, pulli hatched and eggs yet not hatched.

| Year | Section | Number of nests with hatching | Number of pulli hatched | Eggs still incubated | Hatching success/pair | | Mean clutch size |
|---|---|---|---|---|---|---|---|
| | | | | | Minimum | Maximum | |
| 2003 | Reed | 28 | 47 | 21 | 1.68 | 2.43 | 3.76 |
| | Bulrush | 4 | 7 | 6 | 1.75 | 3.25 | 3.73 |
| | Colony | 32 | 54 | 27 | 1.69 | 2.53 | 3.75 |
| 2004 | Reed | 13 | 19 | 34 | 1.46 | 4.08 | 4.00 |
| | Bulrush | / | / | / | / | / | 3.75 |
| | Colony | 13 | 19 | 34 | 1.46 | 4.08 | 3.96 |
| 2005 | Reed | 19 | 38 | 47 | 2.00 | 4.47 | 4.20 |
| | Bulrush | 2 | 3 | 2 | 1.50 | 2.50 | 3.53 |
| | Colony | 21 | 41 | 49 | 1.95 | 4.29 | 4.19 |
| 2006 | Reed | 21 | 47 | 39 | 2.24 | 4.10 | 3.73 |
| | Bulrush | 2 | 4 | 2 | 2.00 | 3.00 | 3.30 |
| | Colony | 23 | 51 | 41 | 2.22 | 4.00 | 3.67 |
| All years | Reed | 81 | 151 | 141 | 1.86 | 3.60 | 4.06 |
| | Bulrush | 8 | 14 | 10 | 1.75 | 3.00 | 3.64 |
| | Colony | 89 | 165 | 151 | 1.85 | 3.55 | 3.99 |

Only few data dealing with hatching success were available at the Footbridge colony, due to the fact that most families left the colony directly after hatching, but also because in most years the research program ended before the major hatching period started. For most nests, complete hatching data were not obtained and besides pulli hatched, eggs continued to be incubated in many nests. Therefore, a minimum hatching success including all pulli hatched was calculated. Supposing that in nests with hatchlings all eggs still incubated hatched later, a maximum hatching success was obtained. The calculations were limited exclusively to successful nests. Excluding the few cases where a complete clutch was predated, it was in most cases impossible to decide whether in a nest that had contained eggs and that was found empty during a next visit, hatching failed or the adults had left with their brood. The percentage of successful nests in the colony remained unknown.

All years combined and for the colony as a whole, a minimum hatching success for successful pairs of 1.85 pulli was recorded (Table 31). In comparison to the mean clutch size, 46.4% of all eggs would have hatched in successful nests. Including eggs still incubated, the maximum success rate would be 3.55 pulli or 89% of nest content. Differences between vegetation types were limited and reflected differences in mean clutch size. In between years, differences were more important and they could not be entirely explained by differences in mean clutch size. In some years, the maximum hatching success exceeded the mean clutch size. This was primarily a consequence of an imbalance in hatching records between lower and higher clutch sizes as a result of the timely limitations of the research program. Indeed, pairs incubating two or three eggs where first pulli hatched on a Monday most probably had already left the site of the colony for the next observation round in the afternoon of the following Friday. On the contrary, clutches of four eggs and more were very likely to be included in the hatching records as at least one of the pulli should have hatched on an observation day. In conclusion, the hatching results must be considered with due care.

At Yverdon, Berthoud (1963) found 125 nests out of 132 to produce hatchlings. 116 nests containing 472 eggs produced 360 hatchlings or 3.1 pulli per nest. 94.7% of the nests were thus successful and their hatching success was 76.3%. From colonies established inside ponds of Lake Neuchâtel, Renevey (1988:1) reported 70% of totally successful nests in 1984 (n=232), 87% in 1985 (n=203), 81% in 1986 (n=254) and on average 79% from 1984-1986 (n=689). In addition 14% of the nests were partially successful in 1984, 7% in 1985, 12% in 1986 and 11% on average. Only a mean of 10% of the nests failed completely during the three years. Colonies along the shoreline of the lake itself were much more vulnerable and had only respectively 38% (n=223), 53% (n=229), 41% (n=232) or on average 43% of totally successful nests. In addition, 16%, 19% and 15% or a mean of 17% (n=684) were partially successful. On average, 40% of the lake nests failed completely each year. The mean numbers of hatchlings produced per breeding pair were 2.96 pulli, 3.04 pulli and 2.97 pulli respectively or on average 2.99 pulli inside the ponds. Directly on the lake, it were 1.73 pulli, 2.42 pulli and 1.68 pulli respectively or on average 1.94 pulli.

At Lough Neagh, Perry (2000) calculated a five-year mean of 0.45 young hatched per breeding pair inside reeds. Inside Spike Rush *Eleocharis palustris*, it were 0.41 young and inside bulrush 0.65 young.

At Lake Żarnowieckie, inside reeds and including egg loss in successful nests, 45% of all eggs or 2.09 pulli hatched per breeding pair in 1980 and 88% or 3.85 pulli in 1981. Inside bulrush in 1981, it were 78% or 3.34 pulli. The differences inside reeds between 1980 and 1981 were attributable to flooding of nests by a fast rise of water levels in July 1980, a phenomenon that occurred not in 1981(Moskal and Marszałek 1986).

At the Houtribsluizen, the number of hatchlings produced per nest before 15 July of each year was 2.14 to 2.94 pulli. Thereafter, the average varied between 2.0 and 2.83 pulli. The hatching success in successful nests was 76% (Leys et al. 1969:1).

It has to be said that in many studies the hatching success was not directly measured. Due to the difficulties of access to colonies, it was hardly manageable to survey the hatching process in each individual nest. In addition, frequent visits to a colony by the survey team could have reduced clutch sizes due to predation following the temporary abandonment of the nesting platforms by the grebes. In order to nevertheless obtain data, the families with very small chicks and the number of pulli were often counted. This method led however already more to defining brood size rather than hatching success. Moreover, due to the dispersal of the families, counting them accurately on a bigger body of water encounters many difficulties. Also, the number of pulli back-brooded is difficult to assess as these remain largely hidden inside the adults' back feathers.

Theoretically, changing water levels, wind and wave action should affect solitary and colonial nests in the same way and, a priori, egg loss due to wash-outs should not affect aggregated nesting more than dispersed nests on a same lake. Even if it holds true that for an aggregation, those nests more at the edges might be more vulnerable, it is also the case that not all territories of solitary pairs offer the same degree of protection. More over, why should birds aggregate at totally unfavourable locations? Even if we admit that the choice offered to a pair could be different from choosing between good and poor habitat, and often deals more with establishing a breeding territory in less suited habitat or becoming a non-breeding floater (Kristan et al. 2007), why should the big numbers be generally pushed to the comparably lower quality sites? It seems more reasonable to predict that the grebes concentrate inside the best habitat available and that a solitary pair cannot defend such a place unless it is not suited for receiving a colony. To remain territorial, the breeders would have to occupy either poorer habitat or prime habitat where aggregated nesting would be more difficult. Although the benefits of coloniality could be very changing between different locations, globally we would expect its advantages to at least annihilate its disadvantages and, therefore, the hatching success of colonial Great Crested Grebes should generally not be inferior to that of territorial breeders.

Factual evidence in this field is difficult to obtain. Independently from the mode of breeding, the hatching success is highly variable in time and in space. A proper assessment in colonial Great Crested Grebes needs a comparison with solitary breeders at locations where both occur simultaneously within the same season. Moskal and Marszałek (1986) compared both types of nesting at Lake Żarnowieckie. For colonies inside reeds, they recorded 50% of successful nests in 1980 (n=156) and their hatching success was 45% whereas 34% of dispersed nests were successful and had a hatching success of 47%. In 1981, the aggregations inside reeds experienced 93% of successful nests (n=81) with 88% of the eggs hatching whereas 85% of solitary breeders experienced hatching for on average 71% of their eggs. Inside bulrush, 64% of colonial nests (n=76) were successful and hatched 78% of their eggs in 1981. Territorial pairs had 82% of successful nests where a mean 74% of the eggs hatched. The mostly better hatching success of colonial grebes was not biased by lower average clutch sizes. On the contrary, for all locations and in all years, mean clutches were

0.14-0.84 eggs bigger inside aggregations than for dispersed nests. Goc (1986) found 57% and 58% of the colonial clutches associated with gulls to survive incubation on Lake Drużno. Pairs in mixed colonies had the on average biggest clutches. In mono-specific colonies, clutches were smallest and only 18% of the clutches survived to hatching while 28% of dispersed nests survived. The low hatching success in mono-specific colonies was explained by the absence of protection by the gulls and the simultaneous easy detection of the aggregations by predators. The high breeding failures generally led to the disappearance of the aggregations in successive years.

Sachs (1998), studying Red-necked Grebes on a Minnesota lake where both dispersed and colonial nesters co-occurred sympatrically, found that fitness, measured as a hatching success, was significantly higher for colonial pairs than territorial pairs. Rates of nest failure (mostly due to wave destruction) were lower at the colony sites, and predation was lower, too. The marginal differences in predation rates between colonial and dispersed nests, according to Sachs, may have represented a near balance between the former's protection from land predators (by open water) and its putative attraction of aerial predators. Microsatellite data detected no genetic structure in the population of the colony so that kin selection could a priori be excluded. Sachs concluded that colonial individuals gained fitness benefits from rare high quality habitat, with no benefits being attributed solely to the aggregation of conspecifics.

In conclusion, both comparative studies on Great Crested Grebes and the one on Red-necked Grebes suggested that aggregation with conspecifics rather provided advantages to the grebes. Contrary to the common believe, the hatching success of colonial grebes could be superior to the one of solitary pairs. Even though in some cases the latter hatching success was better, it could nevertheless have been beneficial for the adult grebes to concentrate. According to Vlug (2007), the K-selected Great Crested Grebes concentrate more on their lifetime reproduction. Within a season, the survival of the adults has therefore priority over the breeding success. Also Moskal and Marszałek (1986) concluded that most pairs at Lake Żarnowieckie preferred colonial nesting because it might have increased the survival chances of adult birds. At the end, coloniality could not only lead to an increased seasonal fitness, but also to a better lifetime reproduction as the survival chances of the adults seem to be enhanced.

### 2.4.3 Breeding success

The breeding success is ideally expressed by dividing the number of pulli reaching fledging or independence from their parents within one season by the number of pairs having bred (breeding or fledging success per pair or per breeding pair). Already determining the approximate number of pairs having bred might be difficult. Simple counts of grebes risk including a difficult to assess proportion of non-breeders. The detection of all breeding platforms over a whole breeding season may encounter logistic constraints and leaves the problem of identification of second clutches unsolved. On bigger lakes, correct knowledge about the nesting population of one colony might not be enough as for raising the chicks, the families will melt with others from neighbouring colonies where clutch sizes could have differed. Accurately counting the number of fledglings encounters even more obstacles. Due to the asynchronous breeding, the replacement and second clutches, not all chicks reach independence around the same point in time. Once independent and no longer fed by their parents, the juveniles get very mobile and disperse. According to own observations, they readily take wings and explore the surroundings, possibly also flying to neighbouring bodies of water. Very often, late fledglings are not considered because research programs end prior to their independence or even their hatching. An additional difficulty when dealing with coloniality stems from territorial pairs using the same lake. It is about impossible to differentiate "solitary" fledglings from "colonial" fledglings.

To partially circumvent these problems, many authors simply determine brood or family size. This is an intermediate measure between hatching and fledging success, but limited to pairs with at least partially successful hatching where the brood survived until the day of the count. This method is based on a picture of the situation at a particular moment of the season that is chosen so as to have a high likelihood of being representative. It is nevertheless limited by the fact that very often after an initial period of common brooding, the mates separate, each then continuing to care for half of the surviving chicks. The difficulty then is to correctly fix the number of families. If one partner looses its part of a divided brood, it most often deserts the region to integrate a moulting group. Occasionally even without division, one adult deserts the family. In addition, early and late broods could not be adequately included.

Due to the fact that in Enkhuizen the families left after hatching for the open lake where they melted with families of other colonies existing on Lake IJssel, very limited data about the breeding success of the Footbridge colony were available. Few adults stayed between the boats with their pulli, at least for a short period of time. The average brood size over three years (no records from 2005 and 2007 existed) of these pairs was 2.77 pulli (n=13). The visits of August 2003 and 2007 yielded a family size of 2.13 pulli (n=16). Possibly, August figures concerned at least partially second clutches that contributed to an increase of the breeding success stemming from first clutches. The findings provided no accurate idea about the breeding success at the Footbridge colony.

Other studies at different locations around the IJsselmeer calculated a low fledging success. In the 1970s, the colonies at Hoorn and De Ven brought up a yearly maximum average of 0.9 young per breeding pair and both colonies continued to grow (Vlug 1980). At the Houtribsluizen a maximum of 0.4 to one pulli per breeding pair reached independence in the years 1966 to 1968. The mortality rate of chicks remained high not only directly after hatching, but also during rearing. This appeared to be mainly a consequence of poor feeding conditions inside the body of water chosen by the grebes. The adults' food flights to the nearby IJsselmeer guaranteed their own survival while their contribution to the nutritional needs of the chicks remained very limited. A similar situation was known from Binnenbraak close to Monikendam: in 1968, 13 pairs of Great Crested Grebes reared 8-9 pulli to independence (Leys et al. 1969:1).

Studies at different locations surveyed the brood size of families. This measure includes all pulli that are registered at a particular date, whether just a few days old or close to independence. Counts of the entire Lake Sempach population in summer 1976 (n=138 pairs) and 1977 (n=126 pairs) resulted in 0.18 and 0.74 juveniles per pair present. Per successful pair, 1.8 and 2.1 juveniles were obtained respectively. Other big Swiss Lakes showed a similarly low and even worse breeding success (Fuchs 1978). For colonial grebes at Lake Żarnowieckie, Moskal and Marszałek (1986) indicated an overall brood size of 1.88 chicks (n=159) in 1980 and of 2.92 chicks (n=157) in 1981. The respective brood sizes of only successful pairs were 3.83 chicks (n=78) and 3.82 chicks (n=120). On Lake Menzelinskoe, the average number of pulli brooded per one adult was 1.3 (n=148) in 1974, 1.5 (n=8) in 1976 and 1.8 (n=74) in 1977 (Blinov et al 1981).

Fuchs (1978) measured the fledging success of successful pairs only on Lake Sempach and calculated 1.8 fledglings (n=13 successful pairs) in 1976, 2.1 fledglings (n=89) in 1977, 1.5 fledglings (n=19) in 1980 and 1.8 fledglings (n=42) in 1981. Renevey (1988) recorded 1.10 young over six weeks old per successful pair on Lake Neuchâtel itself whereas on related ponds, it were 1.15 young.

A limited number of studies provided data about the breeding success of an entire breeding population. In Saxony in 1981, the colony of Glauchau only had 13 fledglings out of 98 eggs (Tuchscherer et al. 1998). Assuming that the 98 eggs were laid by 25 pairs, the fledging success of the colony was 0.52 young per breeding pair. On Lake Sempach, Fuchs (1982) assessed the fledging success with respect to the May population of adult Great Crested Grebes. He found 0.8 independent young (n=160) in 1978 and 0.35 young (n=156) in 1979. On Lake Neuchâtel itself, populated by at least 1,600 pairs of Great Crested Grebes (Vlug 1979), Renevey (1988:2) estimated that 50% of the pulli disappeared in the first week of their life. About 35% of the hatchlings reached the age of six weeks. The total production of young reaching independence for the entire south-eastern shoreline of Lake Neuchâtel was 360 in 1984 and 580 in 1985 and 1986. Compared to a breeding population of about 1,600 pairs, this meant a rearing success of 0.3 –0.4 young per pair. Vlug (1979) aggregated data found in literature and concerning to major parts colonies. He calculated productivity rates based on all breeding pairs. For the Netherlands, he indicated 1.22 fledglings, for Mazury 1.28 fledglings and for the Netherlands, Mazury and Macedonia together 1.27 fledglings (n=4,684). He also registered a rather high productivity on lakes covering over 200 ha and having a wide coastal vegetation belt. Such lakes produced 1.66-2.14 fledglings per pair in Mazury and 1.61 fledglings in the Netherlands. Breeding colonies in narrow coastal vegetation succeeded in raising 0.78-0.96 chicks per pair only.

While all these figures have to be considered with care, they nevertheless insinuate a high probability of low breeding successes for many colonies. As it is highly plausible that aggregated nesting leads to increased hatching success, the brood reductions would then occur during the rearing phase when in principle territorial and colonial pairs do a priori not differ. Even though their nesting is aggregated, the colonial pairs raise their young in isolation, away from the colony. Cold temperatures and rainy weather, limitations in food resources, predation and anthropogenic disturbances should affect "solitary" and "colonial" pulli alike. In consequence, under the same conditions the reductions of brood sizes until fledging should be equal. Directly comparable data in support of the assumption were unfortunately not available, so that only a more general comparison with fledging rates in literature was attempted. Many indications mixed up the data of solitary and colonial breeders and it was not always clear to what extent the fledging rates were more representative of one or the other type of breeding. At Leiden, van der Poel (2000) recorded about 3 fledged young per territorial pair in a territorial population that he had previously colour-ringed. In Saxony, Litzbarski and Litzbarski (1983) recorded 1.6-2.7 juveniles per breeding pair (n=532) spread over eight locations. At least 82 of the pairs had bred in colonies. At the Luxembourgish ponds of Remerschen, all territorial pairs were successful in 1984 and they raised on average 1.5 chicks to independence (Konter 2004). Fiala (1974) indicated 0.8 fledglings per pair at Namest, Arratíbel et al. (1999) 1.25 fledglings for Spanish Navarra, Ulfvens (1988) 1.37 fledglings for a Finnish lake population and 1.55-1.60 fledglings for Finnish archipelago grebes.

Although the fledging success rates of solitary and colonial pairs listed here were not directly comparable, they indicated however that aggregated nesting could often result in rearing on average less than one chick per breeding pair while dispersed nesting away from sites with colonies would mostly lead to a mean fledging success of above one pullus per breeding pair. How could such a contradictory difference be explained? Five factors might theoretically lead to a greater vulnerability of chick rearing in a colonial situation. First, the predation pressure on chicks could be higher than on lakes with only solitary breeders. The increased abundance of pulli in the first case could induce some predators to a greater specialization on such prey. Second, the adults could have more difficulties to correctly assess the food resources in cases of aggregation where the feeding territory is communal. Third, in spite of correct food predictions, the strategy of individual pairs consists in trying to maximize their own fitness. As a consequence, the high hatching rates would necessarily need a global correction when confronted to a global food limitation. This correction affects then different pairs to varying degrees. Fourth, assuming a high site fidelity, an initially good colonial breeding success would in time cause fast population increases leading to overcrowding of the place, thereby reducing the relative production of young. Even though emigration might then follow, population levels could remain high as new generations would always first return to their place of hatching. Fifth, the competition for food could lead to a relative depletion of prey in direct vicinity of the colonies and thereby force the adults to travel longer distances for feeding. Food delivery rates and its distribution to the chicks during the hatching process could be affected thereby and the families would at the end leave with descendants in sub-optimal body conditions.

### 2.4.4 Coloniality and reduced fitness

Spatial and temporal variation in habitat conditions generates strong selective pressure for habitat selection (Cody 1985 in Johnson 2007) which in turn influences reproduction and survival of individual birds (Brown 1969 in Johnson 2007). As other species, the Great Crested Grebes select habitats to maximize their individual fitness. Those occupying habitats that maximize their lifetime reproduction will contribute most to future gene pools (Newton 1998). Colonial Great Crested Grebes could however globally experience a lower breeding success than solitary breeders. The question then arises why the grebes should accept a reduced fledging success.

At minimum, the annual reproduction rate of a population should secure its survival. Fuchs (1978) estimated that a yearly fledging success of 1.2 young per breeding pair was needed to stabilize a population in the species. The equilibrium rate of Fuchs was possibly too high. His calculations were based on a maximum age for the Great Crested Grebe of 14.5 years and in his study, only two birds out of 148 (1.35%) reached the age of ten years. Meanwhile, data available from ringing proved that the species can reach the age of at least 23 years and ten birds out of 529 analysed (1.90%) were older than ten years (Konter & Konter 2004), suggesting that even a fledging success of about one pullus per pair could be sufficient. Notwithstanding, many colonial sites would already struggle with self-sufficiency and their survival would only be guaranteed through immigration from sites with a better rearing success. Astonishingly, most experienced either stable or even increasing population numbers. The Great Crested Grebes there appeared to accept lower fledging rates and, on top, apparently others immigrated to such unfavourable sites. How could such a behaviour be explained?

Bearing in mind that individuals try to maximize their fitness, they choose from the best habitat available. However, there will often be time lags between the moment when a choice is made and the time when the consequences of the choice are realized (Orians & Wittenberger 1991 in Kristan et al. 2007). On the individual level, the assessments could still be correct. The quality of a habitat in the absence of competition or fundamental habitat quality may nevertheless differ from the quality actually experienced by competing occupants or realized quality (Johnson 2007). The colonial grebes would remain trapped within their initial choice and the seasonally increasing intra-specific competition would decrease the rearing success on a global scale. A limited number of dominant pairs could still achieve a good individual rearing success and their return to the colony for a next season would be justified. For the majority of the pairs, emigration to better sites would be a logical consequence. If site fidelity is strongly developed, such a decision could need some time and this could explain why many colonial populations do not simply collapse.

So far, our view was largely limited to what happens within one season. Fitness is however a matter of lifetime, so that even colonial pairs realizing a poor reproductive success in one year could still reap benefits. The safety of the colony could increase their chances of survival and thereby, their chances for a better rearing success in future years, the more as their breeding experience would be enhanced.

Also, emigration is not always an option. It presupposes that additional unoccupied habitat is available. Could it then be that a more general scarcity of nesting sites leads the pairs to try unfavourable sites or to occupy a prime habitat in important numbers rather than to decide not to breed at all? It holds true that following protection from persecution, eutrophication and, later, site protection measures, possibly also profiting from climatic changes, the Great Crested Grebes were subject to substantial increases in total numbers in the 20th century. Population increases may have played a part in the northward expansion of the species into Fenno-Scandia (Cramp & Simmons 1977). Most European populations experienced still considerable growth between 1970 and 1990. They remained stable or increased across much of Europe during 1990-2000 and the overall total population for Europe only moderately decreased at the beginning of the 21th century (BirdLife International 2004). Excluding Russia, the total European population was estimated at 320,000 breeding pairs in 2000 (Heath et al. 2000). In parallel to the total population growth, aggregated breeding became more and more common and individual colonies experienced partially substantial rises in nesting numbers. Here just a few examples in support of this evolution. On the Swiss Lake Geneva, the Great Crested Grebe was first registered as a breeding bird in 1905 with two pairs near Les Grangettes (Poncy in Knopfli 1956). In 1927, Richard (in Knopfli 1956) stated that the species was about to settle all over the lake and in the 1970s Vlug (1979) counted a breeding population of 1,600 pairs. The site of the Footbridge colony held only two pairs in 1972 and ten pairs in 1979. In 1982, it were already about 30 pairs, in 1985 about 50 pairs (Vlug pers. comm.) and during recent years about 120 pairs. On Lake IJssel, only one colony holding nine pairs was registered by Vlug in the part he explored in 1968. In the same part in 1983, nine aggregations held a total of 498 breeding pairs (Vlug 1983).

Following the population increases, we could effectively have reached in the course of the late 20th century a situation where, according to Vlug

(2007), Great Crested Grebes have a surplus of stable survival habitats at their disposal, but where their breeding habitat is fairly limited and unpredictable. It is therefore likely that the adults have long life expectations and rather confined prospects for successful breeding in each season. In such situations, natural selection generally leads to allocating much energy to survival adaptations (K-selection). In each season, the choice would be between becoming a non-breeding floater or taking the limited chance of successful breeding under sub-optimal conditions. This could explain why Great Crested Grebes breeding in colonies on large lakes subsist in spite of an often comparably poor reproductive success. The adult grebes' contribution to the future gene pool of the species is then a matter of long life and of total life production rather than of annual productivity. The grebes breeding under these conditions would not invest in their broods to an extent endangering their proper survival. Even though their breeding success is low, they could gain experience contributing to better results in later years of their long life. At the end, for each individual grebe, two or three successful breeding seasons would be enough to ensure the long term survival of its genes. This would also mean that though the breeding success of aggregations might be comparably low, it would still be at a minimum self-sufficient. In support of this hypothesis comes that at least since the 1980s, a major percentage of the European Great Crested Grebe population breeds in colonies. If their breeding success needed compensation from dispersed nesters to maintain colonial numbers, how could the global growth in grebe numbers have continued for so long?

The methodological limitations for a correct assessment of the breeding success in colonial Great Crested Grebes certainly underestimated the fledging rates while our still imperfect knowledge about life expectations in the species possibly set the equilibrium rearing success too high. It remains that aggregated nesting tends to produce sub-optimal numbers of independent young. This is however less a consequence of coloniality per se, but more of a generalized scarcity of nesting habitat. Indeed, different comparative studies of territorial and colonial nesting on the same body of water either suggested that aggregated nesting could produce more off-spring than dispersed nesting (Koshelev 1977, Moskal & Marszałek 1986) or found no evidence for a reduced breeding success of colonial pairs in comparison to solitary breeders (Bukacińska et al. 1993, Goc 1986). It is therefore likely that on a given body of water, colonies occupy the better sites and push solitary breeders to habitat of secondary quality. As a consequence, logically colonies should not perform worse and could even perform better than dispersed pairs on the same lake. The lake's population as a whole would be trapped in a kind of prisoner's dilemma forcing possibly all pairs, whether colonial or territorial, into suboptimal pay-offs. Its breeding success could be lower than the one realized by solitary breeders at other locations where the formation of colonies cannot be realized due to habitat constraints. Under the given circumstances aggregated nesting would nevertheless prove to be beneficial at the end.

# 3 Ethology of colonial Great Crested Grebes

In the preceding chapter, it was agreed that albeit under some circumstances or in some aggregations a more social behaviour might be exhibited by the Great Crested Grebes, the common pattern of colony formation consists of territory defence and intrusion. In such a situation, the colonial grebes have to accept sooner or later a more confined definition of breeding territory where the access restrictions to other grebes concern at the end the immediate vicinity of the nesting platform. The meaning of "immediate vicinity" remains rather flexible and dependent on circumstances

The present chapter focuses on how coloniality may impact the behaviour of the grebes. It describes and analyses how the process of settlement and acceptance of close neighbours could work within a colony, here the Footbridge colony.

## 3.1 Arrival at the breeding grounds

Previously, it was already established that the grebes arrived not all in one shot at the Compagnieshaven. Different birds could have differing behaviours in this respect. It was generally not known whether late arrivals were of birds having migrated for longer distances for wintering or whether they could have been waiting for some time closer to the breeding grounds and mainly on Lake IJssel. From the observations at Enkhuizen, it appeared that upon arrival, especially earlier in the season, the motivation for a quick settlement inside the area of the colony was not given in all grebes. On all observation days in March and early April single and paired grebes were observed on the water surface inside the harbour. Apparently, they were just lingering around there while others had already started their platform construction. These grebes were not all part of the settled population as was proven for example by a count in the evening of 25 March 2003: inside the Footbridge colony, 87 grebes were counted for 50 platforms started while another 41 grebes hang around in front of it. The large majority of the grebes, whether inside or outside the colony, were clearly in pairs. The few single Great Crested Grebes could still have been waiting for a partner before trying to settle. But why did the pairs refrain from settling? Different explanations are possible:

- The pair could have just arrived from further away and needed to refuel energy after a long travel.
- The pair bond was still young and it needed confirmation before a settlement attempt could be risked.
- Both partners were young birds that physiologically were not yet completely ready for breeding.
- The pair wanted to avoid a long lasting territory defence ahead of egg laying, taking however other risks associated with later settlement.
- The pair waited for the new vegetation growth that permitted safer nesting, especially in periods of bad weather.
- Due to the aggressive defence of settled pairs, unsettled grebes were unable to establish themselves right away.

These birds often left for Lake IJssel, paired grebes guarding their mate, and it is assumed that it were the same birds that returned some hours later to the open water surface in front of the Footbridge colony.

In a study in the south of the Netherlands, Ulenaers and Dhondt (1991) showed that in each year the local territorial population arrived in two well separated periods. About half of the breeding pairs arrived before the end of March and a second group later in April and in May. This pattern was suggested to reflect differences in migratory behaviour, whereby late birds were migrants.

## 3.2 Extent of water courtship

In the Great Crested Grebe, it is not clear to what extent pair bonding happens already at the wintering sites. If a pair was formed over winter, we would expect the mates to migrate together. In solitary breeders, there are however cases where the partners reach the nesting sites with a few days difference in their arrival dates and others where they arrive at the same moment in time. Similarly, it is not known to what extent mate fidelity occurs from one season to the next. According to van der Poel (1984), the phenomenon of two same grebes nesting together in two consecutive years is more a consequence of site fidelity than of attachment to a specific partner. A renewal of a previous pair bond could then be rather common in solitary breeders whereas in aggregations, it could be more exceptional.

Except for head-shaking, water courtship can often only be observed for a comparatively short period in territorial pairs. In the colony of Enkhuizen, the ritual displays of the grebes seemed to last for long. This is of course a matter of perception and maybe only a consequence of the high numbers of grebes present and of their dispersal in arrival dates. Quite often the displays of two grebes were interrupted by a third or even fourth bird showing up. The reasons for such interventions appeared to be of two kinds: either an already settled individual or pair tried to disrupt the establishment of a firm bond by the other pair and, thereby, to delay or even prevent them from settling, or a grebe without a partner attempted to get himself in the bond that was about to form. Similar disturbances are more occasional on the breeding grounds of solitary pairs. They could be more a rule in aggregations and lead to a greater number of display repetitions, all the more as changes in partnership should not be seldom. At the Footbridge colony, such switches could be witnessed once in a while. To what extent mate or site fidelity were involved in the competitions for partners remained unknown. The later arriving mate of the previous year could insist to breed again with the same partner and site fidelity, if not simply limited to the colony itself, but to a particular spot within it, could provoke the same result.

Within established pairs, competition often occurred while one mate was away for feeding. Although generally the guard left behind threatened immediately at approaching foreigners, the latter could then counter by head-shaking, thereby appeasing and courting the opponent. The guarding grebe generally joined into the head-shaking with some hesitations. It could then suddenly attack the intruder, so as if it remembered its duties. Occasionally, other courtship followed and both grebes took actively part in it. As the process took time, there was always a good chance that the previous partner returned and immediately chased the intruder. Often, the latter escaped quickly and the reunified pair, after vigorously shaking the heads, engaged in additional displays.

While in some pairs a quick transition from water courtship to platform activities was observed, an important percentage of the population spent a long time with initial pair bonding activities. For yet unsettled grebes, it appeared to be of prime importance to courtship intensively to tighten the pair bond before trying to enter the colony. Many cases were observed where the way into the vegetation was preceded by endless displays including weed tricks, retreat and discovery ceremonies.

Water courtship preceding nest site establishment may be prolonged basically because of the following reasons:

- The frequent interruption of ritual displays makes that quite a number of them remain incomplete and may need repetition.
- First time breeders that anyhow need more time for pair bonding, may need even longer if frequently interrupted in their efforts or if forced to change the candidates for pair bonding.
- If experienced colonial birds were more attached to the site of the colony itself than to a particular mate, a quick renewal of a previous pair bond would be excluded.
- Before getting hold of a precise spot for platform building, the need for trust into the partner could be increased. Indeed, a colonial pair has to impose its presence to the already settled grebes. Without a confirmed bond, the intruding mates are too easily separated and driven away.
- If the pair is unable to settle quickly, it remains exposed for longer to mate rivalry and the risks for changes in partnership are increased.
- Travelling to the feeding grounds located well outside the harbour and leaving the partner to guard the platform provide additional opportunities for switches in partnership.
- A limited number of grebes may have to wait until first breeders already leave with their chicks to take over their nesting sites. These may need to extend their courtship while waiting.
- The highly competitive situation stimulates the grebes.

Van der Poel (2000) also recorded intensive and long lasting courtshipping at a colony located at the Dutch Gooimer near Huizen. He observed a number of ceremonies that were interrupted by a third bird chasing away one of the original partners. The new pair immediately resumed the displays. Van der Poel called the phenomenon "flirting". The displays of the Great Crested Grebe are supposed to lower the mutual aggressiveness of the future partners against one another. Presumably, courting surrounded by so many conspecifics and at the same time having to threaten and to fight against so many rivals, van der Poel continued, keeps the level of aggression against possible mates elevated and it takes much longer and much more courtship to decrease it.

## 3.3 Access to the colony and getting established

It was assumed that the first settlers chose a place balancing against one another several aspects: their previous nesting experience, the quality of the vegetation and the competition with other early settlers. As a result, the entire vegetated area was occupied by pairs with still extended territories. Their owners occasionally threatened at one another, some times for longer, but intense aggression remained generally absent. Newcomers had to gain access to the colony and to settle in between the existing platforms. Early in the season when a majority of grebes remained unsettled, the few settlers might not have been in a position to counter all the settlement attempts that were undertaken by numerous pairs yet in search of an own "territory". With more grebes having started a platform and less space remaining available inside the colony, the number of settled neighbours that could oppose the settlement of new pairs rose in time. New settlers had to built ever closer to existing platforms. Possibly the resistance of established grebes was not equal everywhere and dominant pairs were able either to delay close settlement to their platform or to maintain a greater distance to neighbouring pairs. The observations at the Footbridge colony provided evidence that only by insisting, the newcomers could gain access. The following sequences illustrate the process. They are based on episodes recorded at the Footbridge colony.

**Active territory defence:** Especially early in the season, settled grebes were often observed to swim in front of the reeds and from there, to threaten in forward display for several minutes at unsettled grebes that were still at some distance and not yet trying to enter the habitat. The threatening could be preceded or interrupted by aggressive calls.

**Exploring the habitat:** Unsettled grebes explored the colony by stealing along the border of the vegetation, one partner leading. They prudently entered the vegetation here and there and seemed to check the resistance of settled pairs. In the beginning, they were easily chased by the latter. If more undisturbed, the intruders could occasionally stay for a longer inspection inside the vegetation.

**Successful defence:** Above all the first intrusions of a pair failed when encountering the resistance of settlers. Either the newcomers retired quickly or after a short period of mutual threatening. In some cases, after the successful defence of their territory by both mates, the winners either reared and invited or quickly copulated on their platform so as to emphasize ownership of the site. More often, they engaged in a vigorous bout of head shaking.

**Intruder displacement attack:** On 16 March 2003, twice a different pair was attacked when attempting to enter the vegetation and fled. Again on the open water, both were observed to attack and chase another unsettled pair that was hanging around in the vicinity.

**Insisting:** While early pairs could be prompt in gaining access to the colony, later settlers encountering more defenders had to insist for longer and to repeat their intrusions, even engaging in fights. Thus, on 16 March 2003, two intruders intensively threatened at two settlers close to the latter's platform. In both pairs, one partner, probably the male, was a bit advanced. At times, the intruding female appeared undecided of whether to insist or to draw back and she made occasional short moves away from the others. The threatening was regularly interrupted by short ritualized preening or a quick and nervous head shake. After about six minutes, the males started token diving that lasted for 40 seconds. Again half a minute of threatening followed before the intruders draw back. They were back again only five seconds later, resuming the threats at short distance and getting closer to the settled pair. The aggression lasted for another 50 seconds before the intruders this time retired for longer. On 23 March, a new basic platform existed at approximately 9 m distance from the platform of the settled pair.

On 24 April 2004, two newcomers were refrained from platform building by both neighbouring pairs threatening at them. The intense threats lasted for several minutes before the intruders draw back. On the same day, they returned several times to the place and one day later, a loose heap had built up in between the two established pairs. Similarly, on 2 April 2004, two pairs owning platforms were both engaged in low threatening at a third pair trying to settle. The three pairs were arranged in a kind of triangle with, as usual, one partner each time a bit advanced and maybe distant from the opponent for less than one meter for most of the time. Slight movements back and fro while maintaining the threatening postures altered the distances not markedly. Now and then one partner in each pair performed token diving. The scene lasted for about 30 minutes before the intruders left. Possibly the same pair was back about two hours later and the six grebes engaged in a new prolonged round of mutual and intense threatening. A few days later, a new pair had established itself in close vicinity of the two settled pairs.

**Gaining a foothold:** With platform initiation, intruders were more difficult to chase. On 29 March 2003, a new platform was started at about 5 m from an existing platform. In late afternoon, the earlier settlers moved in the direction of the new heap where they threatened at the builders. Both pairs remained at opposite sides of the platform, most of the time in forward display that was occasionally interrupted by token diving. The scene lasted for about 20 minutes before the earlier settlers retired.

On 5 April 2003, a single grebe was observed to prudently enter the vegetation three times at the same place with weed in its beak. Twice, it was chased. The third time, it succeeded in depositing the load at an unoccupied spot. Similarly on 2 and 3 April 2004, two different pairs entered the Reeds and deposited some weeds on the water surface. The weeds sank to the ground. Settled grebes threatened at the newcomers that nevertheless stayed for a while. In one intruding pair, one partner invited on the open water surface so as to proclaim ownership. Both pairs were observed later to repeat the intrusion. The next check of the colony recorded two new platforms at the locations of the actions.

In late March 2005, the platform courtship of the settled pairs was frequently interrupted by new birds in search of a nesting space at two places. While one settled grebe was inviting on the platform, the intruders initiated their platform in the vicinity. The partner was divided between mounting its mate and dashing at the newcomers. Two or three times, it chose to attack and the intruders draw back hesitantly. Eventually, the continued disturbances paid off and both new platforms grew in size.

**Imposing the presence:** Even once a pair had gained a foothold inside the colony, its presence was not yet accepted and it continued to face aggression, mostly threatening, but occasionally also fights, from its neighbours. Neighbours with older and stronger platforms could disturb copulas on more basic platforms in their direct neighbourhood, possibly a last attempt to discourage the newcomers from staying. On 29 March 2003, a pair owning an already solid platform threatened for about three minutes without interruption at another pair having a basic platform at only 3 m distance. Then all four grebes relaxed, swam to the opposite sides of their platforms where they either started preening or building.

On 1st April 2004, three times in a row, the same neighbouring pairs engaged in fierce up-right fights. One of their platforms was already very solid, the other was still basic. On 18 April, threatening and chasing involving neighbouring pairs was witnessed at several occasions. Always, one of the pairs had only recently succeeded in establishing itself while the platform of the other existed for some time.

**Partner change:** Very seldom, an unsettled grebe was observed when trying to get into an established pair. On 22 March 2003 however, at a newly started platform, a third Great Crested Grebe appeared several times and started head shaking with one of the partners. While the latter was inclined to engage in mutual courtship, its mate, who was not yet in full breeding plumage, each time attacked the disturbing bird and pursued it under water. The third grebe returned again and again. After some 30 minutes, the courted grebe prevented its mate from attacking the intruder by intervening in the latter favour and chasing its previous mate away. The first partner returned several times, but it kept being driven away. The extent of changes in partnership of established pairs was probably limited. It was hard to detect as the different grebes could generally not be distinguished.

**Settling near incubating pairs:** Newcomers settling in the vicinity of established grebes that were already incubating were supposed to have an easier access to the colony. While the birds on their eggs should be reluctant to get off their platform, their reactions could sometimes be harsh. On 23 April 2005, at three places three unsettled pairs were observed to profit from the presence of only the incubating partner of an established pair to intimidate this one by threatening intensively. In the Bulrush, two of the intruders even pecked several times at the beak of an incubating grebe and they stayed close with high threatening for quite some time. The grebes on their eggs were not inclined to leave them and all three new pairs initiated their own platform not far away.

On 30 March 2003, two intruders started building in 1 m distance of a nest that had already received a first egg. The incubating grebe threatened intensively from the nesting platform. The intruders kept building until 30 minutes later when the mate of the neighbour returned and chased them. Five days later, supposedly the same newcomers were still insisting and the new platform had grown. Two upright fights between the two pairs were observed. On 12 April, the platform of the intruders had been moved to a distance of two metres where it appeared to be better tolerated. An additional pair now started platform building directly in front of the incubating grebes. Both partners being present, probably the male of the earlier settlers engaged in a vigorous fight with the newcomers. Its mate jumped off the eggs and assaulted the second intruder. While all four grebes were fighting, the eggs remained unobserved for about one minute. Already towards the end of that weekend, the first grebes seemed to have accepted both new pairs and later, apart of threatening, no more intense hostility was observed between them.

On 7 May 2005, a pair had started to build a platform inside the Bulrush. On the next day, both partners of one neighbouring pair attacked the new settlers, leaving their eggs unattended. After two fierce fights, the male of the established pair was successfully grasping the head of the intruder male and pushing it below water, holding it there for close to two minutes. The intruder remained motionless, then, short of oxygen, it suddenly attempted to free itself. The second attempt was successful and it escaped, pursued by the territory owner. In parallel, the established female first returned to its eggs, jumped onto the platform, but left it again immediately without settling down. The intruding female saved itself onto the new platform. It did not try to help its mate that was in trouble behind the platform, but barred the way to an intervention of the established female.

**Adjustment of location:** Sometimes, the resistance of settled pairs forced the newcomers to adjust the location of their platform. On 2 April 2005, a pair moved its basic platform for a bit more than one meter to gain more distance to its quarrelsome neighbours. While moving always with a mouthful of weed from one site to the other, surrounding settlers profited from the occasion and stole nesting material.

**From intruder to settler:** Once settled, the newly established grebes quickly became territory defenders themselves. On 25 March 2005, two pairs gained access to the colony that at this moment of the season still held few platforms. Already on the next day, both pairs were threatening at and actively pursuing unsettled pairs.

**Late aggression:** Even late during incubation, the grebes could occasionally strongly oppose newcomers. On 7 May 2003, three different grebes left their nests for chasing each time conspecifics trying to establish themselves in the vicinity. Two times they left their clutch and once even a newly hatched pullus behind on the platform.

**Strange behaviour:** During the weekends of 17 and 24 April, a particular grebe, easily recognized by the interruption of the usually dark nape stripe by washy white feathers, exhibited a strange behaviour. It slowly and prudently approached at least three different incubating grebes with its head held rather high. The birds on their nests threatened. The intruder did not retaliate; on the contrary, it started head-shaking and the incubating conspecifics hesitantly interrupted their threats and slowly joined into the display, apparently unable to withstand. The intentions of the "head-shaker" remained unclear and its sex was unknown. It could have looked for extra-pair copulation although this might not have served its cause with birds already incubating. It might have attempted dumping of parasitic eggs or it just might have tried to prepare the grounds for a later settlement.

The above examples and other observations allowed drawing a more general picture of the settlement process from the point of view of individual pairs. Getting established starts with a pair passing in front of the water vegetation, one bird leading, probably most often the male. Both grebes procede prudently, holding their necks bent forward with all nuptial and other feathers sleeked. In search of a nesting site, they furtively try to enter here and there. The threatening of settlers, occasionally accompanied by a short dash in their direction, may initially be enough to discourage the pair from further entering into the vegetation. The first excursions alongside the colony help to detect potential places possibly with less resistance. Again and again, the unsettled pair creeps along the vegetation. When relatively unmolested, either because the nesting density is still low or because most settlers are out on the IJsselmeer for feeding or because the partners left behind are incubating, the intruders deposit some water weeds at a selected site or invite there on the open water. When aggressed, first they still may save themselves quickly. But they come back soon, they gain confidence to affront the settlers and thereby get more and more difficult to be chased. Slowly, but surely they assemble their nesting material. Depending on circumstances and possibly on character traits of individual grebes, the mutual aggressions can now continue for more or less time. They can simply peak in token diving or lead to intense fighting. Eventually, the intruders succeed in establishing themselves even though sometimes they have to slightly adjust the location of their platform. Occasionally, the opposition of settled grebes may be too strong. The intruders give up and repeat the process at another place. Once established, the aggression against neighbours is lowered in time and the new settlers quickly exhibit the same behaviour against intruders as other settlers to defend the place. It is indeed in the interest of all settlers to exclude additional pairs from settling as every increase in density may reduce the suitability of the site by increasing the costs related to coloniality.

## 3.4 Site fidelity of colonial Great Crested Grebes

According to ringing data, Dutch Great Crested Grebes showed a high fidelity to their breeding places and they exhibited site tenacity to their place of birth (van der Poel 1984). No Dutch grebes ringed during the breeding season were found at a distance of more than 25 km from their ringing site in a later breeding season, and the species thereby displayed a high fidelity to its previous breeding area (Adriaensen et al. 1993). Similarly, adult grebes ringed at the Swiss Lake Sempach and their young seemed to return preferably to that same lake for breeding in later years (Fuchs 1982). Even on the European level, Great Crested Grebes were generally highly faithful to their previous nesting areas and juveniles often returned to their hatching places for later breeding (Konter & Konter 2006). Although none of the studies was able to differentiate between solitary and colonial grebes, it must a priori be assumed that in this respect both behaved in the same way. In adult territorial grebes, site tenacity would even explain mate fidelity from one breeding season to the next. Colour ringing of grebes at Leiden proved indeed that later arriving females chased the new partner of their previous year's mate to renew their pairbond. Van der Poel (pers. comm.) concluded that it was rather attachment to exactly the same site than keeping faith with the previous partner that brought both together again. In the context of colonies, this reasoning would lead to high annual return rates of previous year breeders and their off-spring to the same aggregation. Would the adults also try to again occupy exactly the same spots inside the colony and would they then thereby achieve a high degree of mate fidelity?

In order not to disturb the natural behaviour of the colonial Great Crested Grebes at the Footbridge colony, it was not attempted to catch some of them for colour ringing. Assuming that experienced birds were early settlers occupying the better sites and that, independently from atmospheric and habitat conditions, they showed site fidelity, not only with respect to a particular colony, but also with respect to a particular spot inside this colony, the early space patterns of settlement could have exhibited a high degree of accordance in between years. Based on this idea, the platforms started in March of all years were aggregated on one map. Thereafter, the accordance of those platforms recorded towards the end of March in the year holding the lowest number of platforms (2006, n=36) with early platforms of other years was analyzed. For a particular end-of-March platform, a high degree of accordance with a March-platform of another year existed if the locations of both were within one meter distance. Otherwise the accordance was judged to be low or not existing. The year 2007 was not considered for this analysis.

**Table 32:** Concordance of 2006 March-platforms with March-platforms in 2003, 2004 and 2005 expressed as numbers of 2006-platforms agreeing to a given succession (H=high concordance, L=low concordance).

| | H-H-H | L-H-H | L-L-H | H-L-H | L-H-L | H-H-L | H-L-L | L-L-L |
|---|---|---|---|---|---|---|---|---|
| Reed I | 3 | 0 | 2 | 1 | 1 | 2 | 0 | 1 |
| Reed II | 5 | 2 | 4 | 3 | 0 | 0 | 5 | 0 |
| Bulrush | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 4 |
| Total | 8 | 3 | 7 | 4 | 1 | 2 | 6 | 5 |

Table 32 displays the numbers of March platforms built in the years 2003-2005 that were concordant with the platforms existing at the end of March in 2006. A high degree of concordance (a concordant platform for all three preceding years) could only be found for three out of ten platforms in Reed I (30%) and for five out of 19 platforms in Reed II (26.3%). No Bulrush platform had another platform within one meter of its location in all three preceding years (n=7). Concordant platforms in two previous years existed for an additional three platforms in Reed I (30%), five platforms in Reed II (26.3%) and for one platform in the Bulrush (14.3%, n=7). Concordance in none of the three preceding years was found for a total of five platforms (13.9%), one in Reed I (10%) and four in the Bulrush (57.1%).

An overall degree of concordance was calculated by comparing the number of concordant location to the total number of possible cases of concordance for the three years of comparison. In the two Reed sections, the percentage of concordance obtained was rather elevated with 60%, in the Bulrush, it was only 19%. However, the eight platforms in the reeds that had concordant platforms in all three preceding years experienced very different fates from 2003 to 2006. Only one platform received each year a stable clutch of four eggs. All seven other concordant platforms either disappeared in some years or received full clutches of variable size or their owners were chased by coots. Experienced grebes should have been better able to avoid these fates. Therefore, although close site fidelity may have contributed to concordance, it seemed more reasonable to attribute similarities, and possibly also dissimilarities, in early spatial distribution of nests to other factors such as habitat.

Without colour ringed birds, it was impossible to accurately test mate fidelity. As adults might preferably return to their previous breeding sites, they have a good chance of encountering there their previous mates, too. If the grebes were only loyal to the site in its broader sense, the same pair bonds would not necessarily be renewed. However, a preceding positive breeding experience could be a strong argument for a renewal of the bond. A limited number of observations where an apparently later arriving bird insisted and finally succeeded in getting into an established pair pointed at the possibility that at least some grebes could be attached not only to their previous nesting site, but also to their previous mate.

Concerning first-time-breeders, if indifferently all grebes returned to exactly their hatching place for later breeding, depending on size, colonial populations would be exposed to a high risk of in-breeding. In particular, the increase in numbers of an aggregation over the years would have been triggered by the addition of birds stemming from the initial lineages. Due to the difficulties of sexing grebes, the studies based on ringing recoveries were not able to differentiate between male and female birds. It remained therefore unknown whether differences in return rates between the sexes would have lowered the risk.

## 3.5 Records of fights between grebes

A first assessment of the aggressive behaviour displayed by the colonial Great Crested Grebes at Enkhuizen could be obtained through the records of fights occurring between them. These were noted down from 2003 to 2006. Theoretically, few fights should be expected very early in the season as few grebes have arrived. With more and more grebes establishing themselves, the number of fights could grow in parallel to the density of the colony. In parallel, a process of habituation should have largely contributed to reduce intra-specific fights between settled grebes.

Fights between the grebes were more or less common throughout the nesting season (Fig. 17). Early in the period of colony establishment of each year, up to mid-March, the number of fights per hour remained comparatively low. Later in the second half of March and with the intensification of the settlement process, fighting became more common and the number of physical disputes rose quickly. It remained important, but fluctuating, at least until late in April of each year (Table 33, Fig. 15). The number of nesting platforms steadily increased from March until early May in all four years. Generally, the number of fights per hour did not increase in line with the number of existing nesting platforms. When linking the number of fights per day directly to the number of platforms (Fig. 16), fighting was rather important from after mid-March onwards. A downward trend appeared already during the first half of April and a noticeable decline in the number of fights

**Table 33:** Average number of fights per hour between grebes observed by chance.

| Date | 2003 | | 2004 | | 2005 | | 2006 | |
|---|---|---|---|---|---|---|---|---|
| | Fights | Number of platforms | Fights | Number of platforms | Fights | Number of platforms | Fights | Number of platforms |
| 9-Mar | 0.14 | 19 | | | | | | |
| 16-Mar | 1.26 | 29 | | | | | | |
| 18-Mar | | | | | | | 0.16 | 11 |
| 20-Mar | | | | | 2.63 | 25 | | |
| 23-Mar | 2.59 | 44 | | | | | | |
| 26-Mar | | | | | 3.76 | 51 | 2.50 | 32 |
| 30-Mar | 1.68 | 61 | | | | | | |
| 2-Apr | | | 2.24 | 40 | 4.73 | 52 | | |
| 5-Apr | 1.74 | 60 | | | | | | |
| 8-Apr | | | | | | | 1.69 | 55 |
| 9-Apr | | | | | 2.68 | 61 | | |
| 13-Apr | 3.31 | 75 | | | | | | |
| 16-Apr | | | | | 3.56 | 77 | 1.82 | 82 |
| 18-Apr | 2.40 | 88 | | | | | | |
| 23-Apr | | | | | 1.03 | 96 | | |
| 25-Apr | | | 2.73 | 98 | | | | |
| 29-Apr | | | | | | | 1.74 | 96 |
| 30-Apr | | | | | 1.17 | 102 | | |
| 1-May | 3.03 | 114 | | | | | | |
| 6-May | | | | | | | 0.97 | 115 |
| 7-May | | | | | 0.98 | 111 | | |
| 8-May | 2.49 | 122 | | | | | | |
| 9-May | | | 0.34 | 112 | | | | |
| 17-May | 0.20 | 92 | | | | | | |
| 18-May | | | 0.59 | 82 | | | | |

occurred at the latest towards mid-April, long before the colony reached its maximum number of platforms in the course of the first decade of May. Differences in between years in the pattern of average daily fights per platform, especially in late March and early April, depended to a large extent on weather and habitat condition that also triggered differences in the timing of settlement from one year to the next.

Indications on parties involved in physical disputes were available for the following dates:

- 18 April 2003: from 15 upright fights recorded, eleven involved one partner of an incubating pair and one grebe with a freshly started platform. No fight concerned neighbouring pairs which both had eggs.
- 30 April 2003: well established pairs fought against intruders in all twelve fights. Even incubating grebes left their nests for getting involved.
- 31 March and 1st April 2004: from 19 fights, seven opposed settled pairs and newcomers. In twelve cases settled pairs fought against each other. Most neighbourhoods were still very young judging from the quality of the platforms and when comparing the mapping of the platforms with the one of the previous weekend.
- 24 April 2004: almost all 27 fights opposed settled pairs and intruders. Especially in already more densely settled parts of the vegetation, the fights were often long and repeatedly engaged the same opponents.

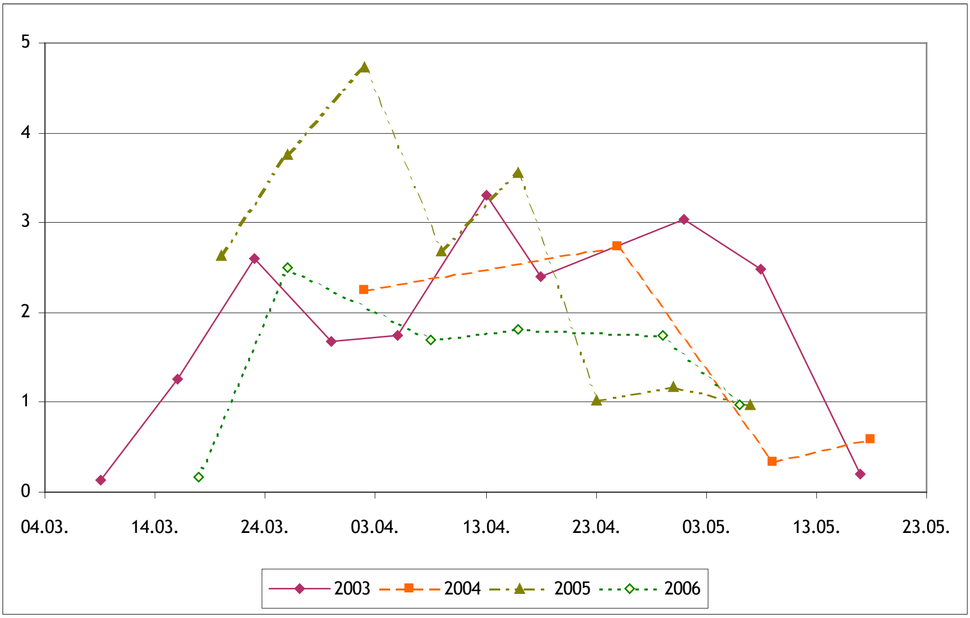

**Fig. 15:** Evolution of the number of fights per hour observed by chance in the Footbridge colony (2003-2006).

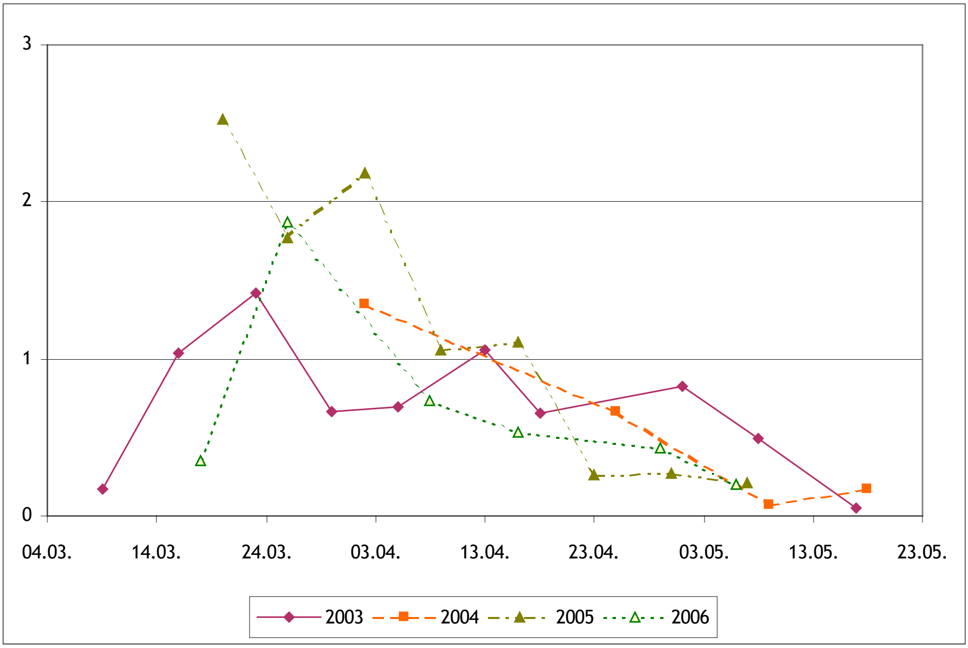

**Fig. 16:** Evolution of the number of fights per day (24 hours) and per existing platform observed by chance in the Footbridge colony (2003-206).

- 20 March 2005: from 13 fights, ten were surely engaged between settlers and intruders.
- 25 and 26 March 2005: high pressure from intruders on already established pairs provoked at least 40 out of 50 fights recorded.
- 25 March 2006: from 24 fights recorded, most occurred in late afternoon upon the return from feeding on the IJsselmeer of established pairs. Newcomers that had meanwhile started platform building were fiercely aggressed.

The above episodes provide enough evidence for postulating that physical disputes opposed mostly settled grebes and intruders. Directly after new pairs had initiated their platforms, fights with neighbours remained however possible. No occurrence of fighting between longer established neighbours, particularly after clutch initiation, was however witnessed. A process of habituation must have provoked a gradual lowering of aggression levels between established pairs. This also explains why the relative number of fights decreased in time in spit of an increase in population numbers.

## 3.6 Evolution of aggressions in a nesting zone

Aggression consists not simply of physical disputes, but includes also more ritualized forms of threatening of varying degrees of intensity (Fig. 18). To get a more overall idea about the evolution of the aggressive behaviour in the colony, all aggressions (intense threatening, pursuit, under water pursuit, and fight) were counted in zone Reed IIA during each weekend of observation in 2003 and 2004. The level of aggression was then calculated once by simply adding up the counts in the different categories and once by weighing the different categories taking into account the differences in the intensity and in the costs of the behaviours involved (see chapter 1.5).

In 2003 (Table 34, Fig. 19), the simple measures of total aggression over time displayed a peak in the beginning of the second decade of April following a sharp rise that started earlier in the month. From then on, the level of aggression dropped steadily, in spite of the fact that the number of established pairs measured by the number of platforms continued to increase for another three to four weeks. Weighed aggression followed the same pattern as total aggression. The amplitude of variation was however increased, especially during the first three weeks of April. During this period, more intense aggression predominated. Later, the differences between both measures declined, pointing at a reduction of above all more costly aggressions. The intensification of hatching in May contributed to a quick decline in the number of occupied platforms in the section under observation. Although on 17 May about the double number of established pairs in comparison to March figures were still present, both levels of aggression were far below those of March. Thus, on 29 March the weighed level of aggression was 27.7 for 15 platforms and on 17 May, it was 13.5 for 28 platforms. The figures testified an in time reduced aggressive behaviour between neighbouring pairs as otherwise, the steady increase in the number of platforms should have contributed to a steady rise in the number of aggressions. It is also noteworthy that, after the April peak, weighed aggressions were reduced faster than total aggressions so that especially more costly aggressive behaviour tended to disappear earlier. This evolution is even more apparent when looking at aggression levels per platform. Except for the April peak, the figures displayed a steady decrease of aggressiveness.

In 2004, the levels of aggression were only controlled during three observation weekends (Table 35). The levels of aggression seemed globally higher than in 2003 and they also appeared to come down only in May. When relating aggressive behaviour to the number of platforms for each day of observation, the picture changed. The early April levels remained increased, but in the third decade of April they were drastically reduced and in May, hardly any aggression was left.

In both years, a gradual habituation to the close presence of neighbouring pairs must have occurred. Once an initially high level of hostility was overcome, the aggressions recorded between neighbours, were limited to occasional intense threats that only served to protect the immediate vicinity of the nesting platforms from intrusion.

At the colony of Gooimeer, mutual aggressions on the open water surface in front of the colony, including chasing, attack flights and fights, were frequent during egg laying. After the end of May, grebes limited the expression of their

**Fig. 17:** Fighting grebes at the Footbridge colony in late March 2005.

**Fig. 18:** Intense threatening by a Great Crested Grebe.

aggressiveness mostly to ritualized forms of threatening and their intensity faded away (van der Poel 2000). The example did not analyze in detail the evolution of hostility, but it confirmed in principle the gradual habituation to close neighbours leading to the nearly disappearance of aggression in colonial Great Crested Grebes.

## 3.7 Seasonal changes in the behaviour of individual pairs

While in 2003 and 2004 the aggressive behaviour within a particular zone of the colony was assessed, irrespective of the parties involved, in 2005 and 2006, the attention was focussed on individual pairs

**Table 34:** Mean aggressions per observation weekend and number of platforms in Reed IIA in 2003.

| Date | 23.03. | 29.03. | 05.04. | 12.04. | 19.04. | 01.05. | 07.05. | 17.05. |
|---|---|---|---|---|---|---|---|---|
| Intensive threatening | 7.5 | 6.67 | 12.67 | 12.50 | 13.00 | 7.33 | 4.80 | 2.50 |
| Pursuit | 10.00 | 3.33 | 4.00 | 11.00 | 8.00 | 5.67 | 3.80 | 3.00 |
| Under water pursuit | 1.50 | 6.67 | 4.33 | 4.50 | 3.67 | 2.00 | 2.40 | 2.50 |
| Fight | 1.00 | 0.33 | 0.33 | 3.00 | 2.33 | 0.33 | 0.60 | 0 |
| Total aggression | 20.0 | 17.0 | 21.3 | 31.0 | 27.0 | 14.3 | 11.6 | 8.0 |
| Weighed total | 33.5 | 27.7 | 30.3 | 52.5 | 43.3 | 23.7 | 19.0 | 13.5 |
| Number of platforms | 14 | 15 | 21 | 25 | 30 | 38 | 40 | 28 |
| Total aggression per platform | 1.43 | 1.13 | 1.01 | 1.24 | 0.90 | 0.38 | 0.29 | 0.29 |
| Weighed total per platform | 2.39 | 1.85 | 1.44 | 2.10 | 1.44 | 0.62 | 0.48 | 0.48 |

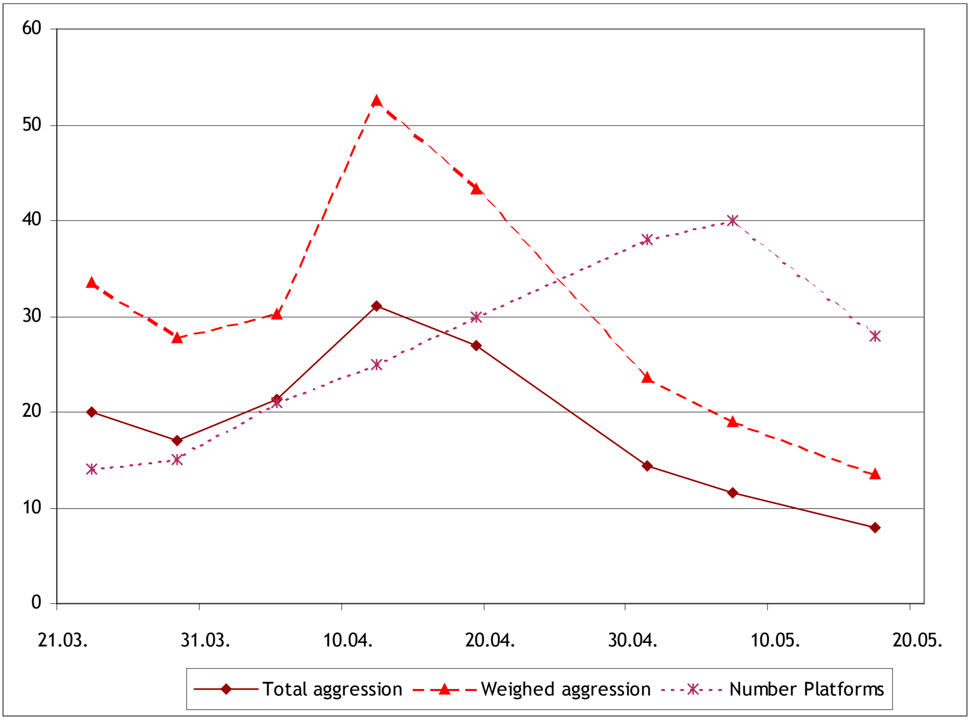

**Fig. 19:** Evolution of the number of aggressions per 30 minutes of observation in Reed IIA in 2003.

and changes in their behaviour in the course of the nesting season. For pairs selected, their platform attendance, their breeding progress and their aggressiveness were recorded. The values of total, weighed and high level aggression for the different pairs were calculated as described under 1.5.

Theoretically, the evolution of the aggressiveness in the different pairs could be related to a number of factors such as simply the progress of time, the percentage of presence of both partners, the degree of clumping with neighbouring platforms, its progress in time, nest contents and incubation progress. Where sufficient and meaningful data were available, the correlations to weighed and high energy aggression were calculated. It was expected to detect in time an overall reduction of the levels of aggression and in particular of more costly aggressive behaviour, such as fight and active pursuit. Moreover, hostility towards new close settlers, after an initially possibly high aggressiveness, should later be limited to actions requiring low energetic demands, mainly ritualized low intensity threatening. In densely packed colonies, regular threats may remain necessary throughout the season to keep the constantly passing neighbours at a minimum distance from the edge of the own platform, but more intense aggression should be avoided at the latest once incubation has started.

It was not believed that the behavioural patterns of individual pairs within a nesting season would be completely identical. Differences between experienced and less experienced pairs were expected in addition to those stemming from circumstantial conditions like the location of the platforms or character traits of individual grebes. For better comparability of individual behaviours, the analyses differentiated experienced grebes from those lacking experience. According to Konter (2008), experienced birds are expected to settle early, to readily initiate their clutches and to lay normally sized clutches of three to five eggs. By applying these criteria to the twelve pairs followed individually (seven in 2005 and five in 2006), pairs B, D1 (2005), BB, B2 and D2 (2006) were classified as experienced and pairs A1, C, D (2005), AA and CC (2006) as inexperienced. Pairs A and B1 of 2005 exhibited no clear pattern: both settled early, but initiated their clutches neither readily nor late. While nest A received a normal clutch of four eggs, nest B1 finally held seven eggs.

**Table 35:** Mean aggressions per observation weekend, number of grebes present and number of platforms in Reed IIA in 2004.

| Date | 01.04. | 25.04. | 08.05. |
|---|---|---|---|
| Intensive threatening | 10.44 | 13.50 | 2.50 |
| Pursuit | 9.11 | 9.83 | 2.00 |
| Under water pursuit | 3.00 | 4.17 | 0.25 |
| Fight | 1.22 | 1.61 | 0 |
| Total | 23.8 | 29.1 | 4.8 |
| Weighed total | 38.3 | 60.3 | 7.0 |
| Number of platforms | 11 | 37 | 40 |
| Total aggression per platform | 2.16 | 0.79 | 0.12 |
| Weighed total per platform | 3.48 | 1.63 | 0.18 |

Pair A initiated its clutch just two days before a storm that destroyed close to all nests. Pair B1 did so on the day of the storm. This may have biased the related data and therefore, the two pairs were considered separately.

**Behavioural patterns of experienced pairs:** Pair B (Table 36, Fig. 20), an early settler, raised its aggression tremendously shortly after settling, in line with the increase in numbers of neighbouring platforms. With clutch initiation, the level of aggression dwindled. At the same time, the number of neighbours within 3 m stayed stable. In the storm night of 2005, the pair lost its four eggs. The day after, while rebuilding its platform, pair B again strongly increased its territorial defence activity. In parallel, most other neighbours fixed their storm damages and two new pairs tried several times to settle in close vicinity. On the next weekend, the replacement clutch was initiated and the aggression level of pair B had again come down. It continued to shrink, in spite of the fact that since the replacement clutch was started, seven other platforms were clumped with it. Twice, the sharp increases in aggression levels were almost entirely triggered by high energy cost hostility (Fig. 21), and twice, after clutch initiation high cost aggression practically disappeared.

Concerning the attendance to the nesting platform (Table 36), directly after settlement both partners were seldom present and the platform remained

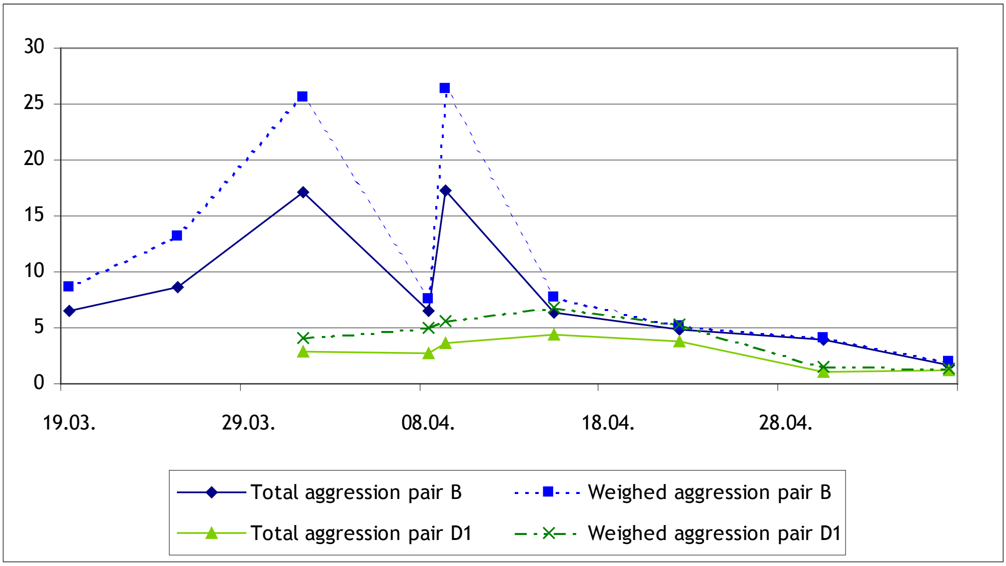

**Fig. 20:** Evolution of total and weighed aggression in pairs B and D1 in 2005.

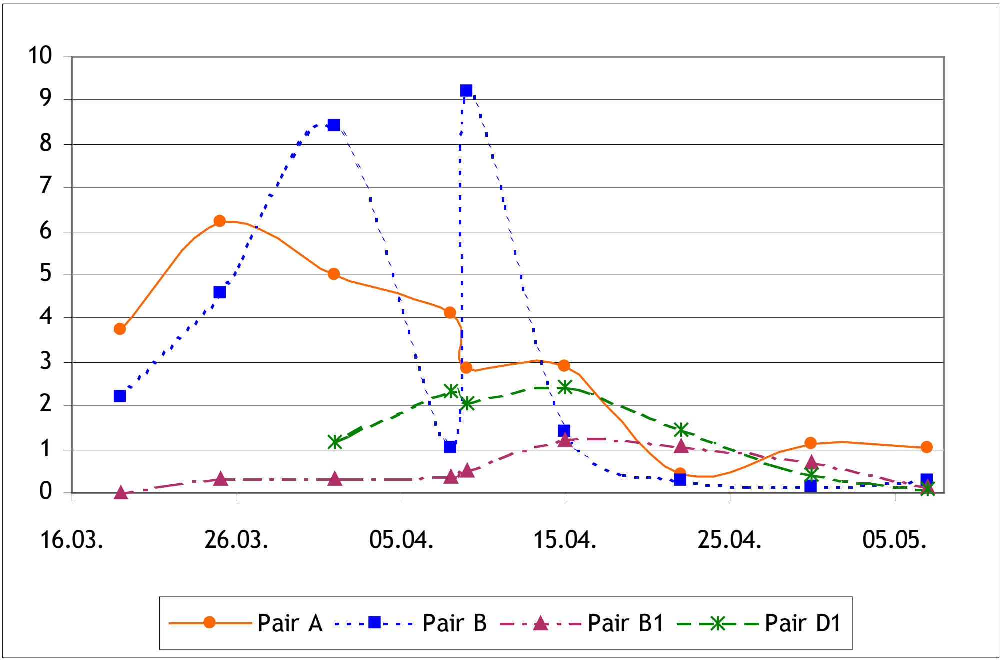

**Fig. 21:** Evolution of high cost aggression in pairs A, B, B1 and D1 in 2005.

**Table 36:** Summarized nesting data of pair B in 2005 (LH: loose heap, BP: basic platform, PF: platform without eggs, R: platform rebuilt during the day, x e: nest containing x eggs; x p: nest still hosting x pulli, (a): abandoned, (d): destroyed).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 19.03. | 34.7% | 41.4% | 23.9% | 6.49 | 8.70 | PF | 1 | 2.0 m |
| 25.03. | 64.8% | 35.0% | 0.2% | 8.67 | 13.24 | PF | 2 | 2.0 m |
| 01.04. | 41.3% | 58.3% | 0.4% | 17.19 | 25.61 | PF | 4 | 1.5 m |
| 08.04. | 21.8% | 78.2% | / | 6.51 | 7.54 | 4 e | 4 | 1.5 m |
| 09.04. | 45.5% | 54.5% | / | 17.22 | 26.41 | LH, 0 e | 3 | 1.5 m |
| 15.04. | 50.2% | 49.8% | / | 6.34 | 7.72 | 2 e | 7 | 1.5 m |
| 22.04. | 13.0% | 87.0% | / | 4.86 | 5.14 | 4 e | 6 | 1.5 m |
| 30.04. | 17.2% | 82.8% | / | 4.00 | 4.14 | 5 e | 7 | 1.5 m |
| 07.05. | 32.7% | 67.3% | / | 1.63 | 1.90 | 5 e | 7 | 1.5 m |

**Table 37:** Summarized nesting data of pair D1 in 2005, platform first registered on 25 March (clumped then with one other platform) and observed from 1st April onwards (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 01.04. | 63.2% | 36.8% | / | 2.86 | 4.04 | PF | 1 | 3.0 m |
| 08.04. | 100 % | / | / | 2.71 | 5.03 | 3 e | 1 | 3.0 m |
| 09.04. | 100% | / | / | 3.59 | 5.64 | R, 3 e | 1 | 3.0 m |
| 15.04. | 87.3% | 12.7% | / | 4.41 | 6.86 | 3 e | 2 | 3.0 m |
| 22.04. | 78.3% | 21.7% | / | 3.85 | 5.31 | 3 e | 2 | 3.0 m |
| 30.04. | 76.4% | 23.6% | / | 1.13 | 1.56 | 3 e | 2 | 3.0 m |
| 07.05. | 41.4% | 58.6% | / | 1.21 | 1.32 | 2 p, 1 e (a) | 2 | 3.0 m |

even entirely unattended for 24% of the time. Thereafter, always at least one partner was present. While completing their construction, the presence of both partners first increased to 65%, then it dropped to 41% just before the first clutch initiation. It was further reduced to 22% after clutch completion. The destruction of the nest by the storm triggered again an increased simultaneous presence of both partners that remained at about 50% while the platform was rebuilt and the replacement clutch was initiated. During incubation, both partners were present for only about 15% of the time, but close to hatching, both adults were present more often (32.7%).

Pair D1 (Table 37, Fig. 20) established itself only in late March. Throughout its nesting, the pair maintained comparably low levels of aggression, possibly triggered by the increased nearest neighbour distance, a consequence of the structure of the habitat at their nesting location. The levels slightly rose after the storm night, while rebuilding the platform and recuperating all three floating eggs out of the water, and immediately thereafter, while two additional pairs tried to gain a stronghold in its close vicinity. After habituation to one new neighbour, the aggressiveness of pair D1 came down. In comparison to pair B where high cost aggression was twice elevated in the pre-laying phase, pair D1 maintained a relatively much lower level. For the first about two weeks of incubation that followed directly the storm, high level aggression was however comparably higher (Fig. 21).

**Table 38:** Summarized nesting data of pair BB in 2006 (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 24.03. | 85.2% | 12.0% | 2.8% | 20.43 | 22.45 | BP | 2 | 2.1 m |
| 08.04. | 70.8% | 21.2% | / | 8.52 | 10.91 | 3 e | 3 | 0.8 m |
| 16.04. | 38.3% | 61.7% | / | 3.14 | 3.55 | 5 e | 4 | 0.8 m |
| 29.04. | 19.0% | 81.0% | / | 2.85 | 2.85 | 5 e | 4 | 0.8 m |
| 06.05. | 14.8% | 85.2% | / | 2.05 | 2.56 | 4 p, 1 e | 4 | 0.8 m |

**Table 39:** Summarized nesting data of pair B2 in 2006 (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 18.03. | | | | | | BP | 0 | 4.5 m |
| 24.03. | 84.4% | 11.4% | 4.4% | 8.48 | 10.30 | PF | 1 | 2.5 m |
| 08.04. | 35.5% | 74.5% | / | 4.28 | 5.12 | 3 e | 3 | 1.5 m |
| 16.04. | 40.0% | 60.0% | / | 1.68 | 1.79 | 4 e | 4 | 1.5 m |
| 29.04. | 56.0% | 44.0% | / | 1.81 | 2.23 | 4 e | 4 | 1.5 m |
| 06.05. | 46.7% | 53.3% | / | 0.94 | 0.94 | 3 p, 1 e | 4 | 0.6 m |

**Table 40:** Summarized nesting data of pair D2 in 2006, platform first registered on 8 April (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 08.04. | 76.3% | 23.7% | / | 3.35 | 5.02 | 2 e | 4 | 1.5 m |
| 16.04. | 95.1% | 4.9% | / | 3.26 | 4.53 | 4 e | 4 | 1.5 m |
| 29.04. | 76.0% | 24.0% | / | 4.74 | 5.93 | 4 e | 4 | 1.5 m |
| 06.05. | 76.5% | 23.5% | / | 0.94 | 1.18 | 3 p, 1 e | 5 | 1.5 m |

Platform D1 was always attended, initially by both partners for 63% of the time. During early incubation and over the storm weekend, both adults were always present most of the time. This certainly contributed to recuperating all three eggs out of the water. Throughout incubation, the double presence of the mates remained superior to 75%. This fact and the increased aggressiveness during this period explained why no parasitic eggs were added to this clutch while pressure for brood parasitism was high. During hatching, the presence of both partners was reduced to 41% of the time, most probably caused by one adult fetching food for the first hatchlings.

The experienced pair BB (Table 38, Fig. 22) established itself in late March, at the begin displaying high aggression levels that continuously shrank. From mid-April onwards, hostility remained low. Directly after clutch initiation, aggressiveness was still comparably high, most certainly a consequence of the important pressure stemming from attempts for parasitic egg laying and from new settlers that led to an increase in direct neighbours and a decrease of the distance to the nearest platform. The initially high levels of total and weighed aggression resulted to a major extent from low cost threatening. Expensive aggression was relatively low from the start of settlement on,

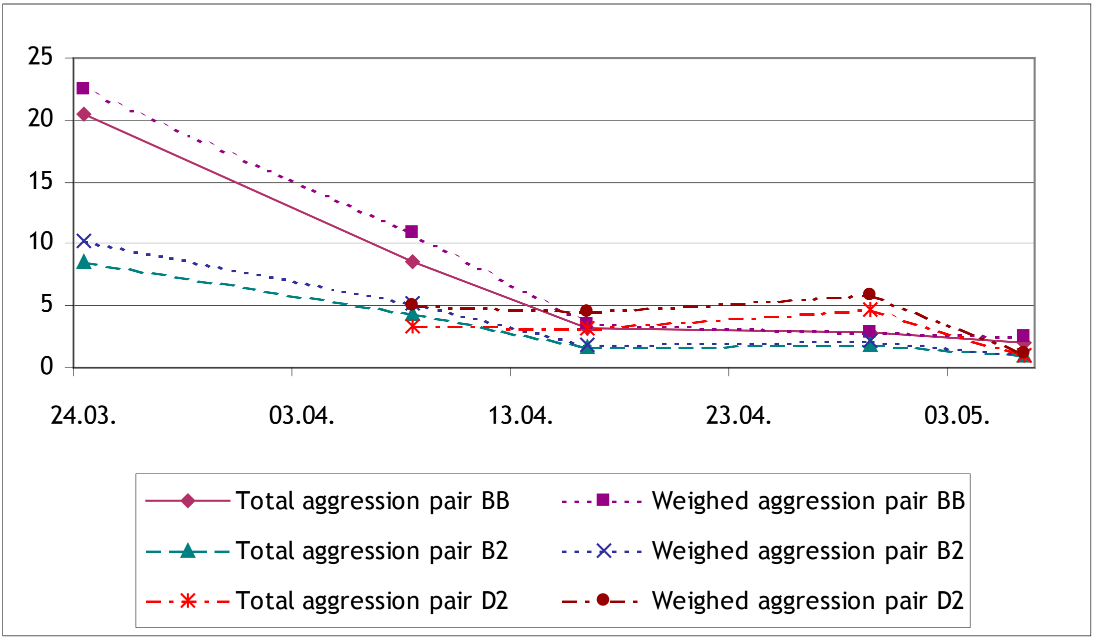

**Fig. 22:** Evolution of total and weighed aggression in pairs BB, B2 and D2 in 2006.

and it remained at a stable level throughout egg laying. It was even markedly lowered thereafter, possibly due to habituation to existing neighbours (Fig. 23). It is noteworthy that high energy aggression was limited at all times to periods where both partners were present (Table 48).

The initially high time of presence of both partners was only slightly reduced during egg laying. During incubation, it fell continuously and remained low during hatching (15%). Weighed aggression appeared to be related to the progress of time (corr. -0.91), the percentage of presence of both partners (corr. 0.92), nest content (corr. -0.97), the number of clumped platforms (corr. -0.99) and the variation in the number of clumped platforms (corr. 0.89). High cost aggression was best correlated with the percentage of simultaneous presence of both partners (corr. 0.91).

Pair B2 (Table 39, Fig. 22) followed about the same pattern as pair BB. Having only one closer neighbour in March, its initial levels of aggression were however only about half of those of pair BB. During egg laying, new pairs settled within 3 m, nevertheless aggression was continuously reduced. It remained almost absent from mid-April onwards. High cost interventions were noticeable at the utmost during the settlement weekend and thereafter disappeared very quickly (Fig. 23). Curiously, during egg laying, the few such aggressions nearly all occurred while one grebe was absent. An explanation therefore could be that the new settlers preferably tried to get into the colony when only one partner was guarding. Once the clutch was complete, the rare expensive aggressions were limited to periods with simultaneous presence of both partners (Table 48).

The percentage of simultaneous presence of both partners dwindled from initially 84% to only 35% during egg laying. It remained at around 50% thereafter until hatching. Weighed aggression seemed correlated to time (corr. -0.92), and clumping (corr. -0.99), high cost aggression only to clumping (corr. -0.98).

Pair D2 (Table 40, Fig. 22) settled a bit later in the season, towards late March, but it immediately initiated its clutch, so that it was incubating when first observed. The levels of aggression, though never high, displayed a negligible peak in late April, mainly supported by threats, to come completely down in May during hatching. The late increase in hostile behaviour could be explained by settlement attempts of new pairs in this already relatively densely populated part of the colony. High cost aggression were limited at all times and exhibited a slight downward trend until the end of April before quasi disappearing (Fig. 23). During laying, more than half of the expensive aggressions happened while one partner was absent. Thereafter, all such aggressions occurred with two grebes present. At all times, both partners were present for more than 75% of the time.

The fast settlement and clutch initiation by pair D2 and its low aggressiveness throughout its nesting at a dense part of the colony provided a good example of a pair that imposed itself quickly without excessive expenditure of energy for territory defence.

**Behavioural patterns of a priori inexperienced pairs:** Pair A1 (Table 41, Fig. 24) settled early. Its initially low hostility was due to the absence of intruder pressure and close neighbours. It rose seriously without becoming really high until early April due to hostile interactions with probably always the same pair that was trying to establish itself close. Platform courtship of pair A1 was frequently interrupted. The aggressions culminated over the weekend of 1st April when pair A1 had finally to move its platform to a greater distance. As a consequence, the levels of aggression in pair A1 dropped markedly just prior to the storm of 8 April. They increased slightly the day after. They started a continued downward trend when the pair initiated its clutch in the week after the storm. The nest received two late parasitic eggs without provoking a visible reaction with respect to hostility. The periods of elevated aggression were almost entirely triggered by high cost aggression (Fig. 25) that however dwindled after mid-April.

In March, directly after its initiation, the platform of pair A1 remained partially unguarded and both partners were seldom present prior to the storm. Thereafter and during clutch initiation, the simultaneous presence of both mates increased. It declined to only 6% of the time thereafter and remained low while their nest received parasitic eggs.

The behaviour of the pair deviated from that of experienced grebes by its initially low attendance to the platform that was possibly already responsible for the early moving of the platform. Clutch initiation was delayed, maybe a consequence of the early increases in aggressiveness that deviated energy reserves from egg production. The later low simultaneous attendance to the nest by both partners offered the opportunities for the dumping of the two parasitic eggs. These facts rather pointed at an inexperienced pair.

Pair C (Table 42, Fig. 24) settled early. It maintained two platforms throughout the observations that it both protected actively. As a result, the partners maintained a high aggressiveness, total and weighed, for three weeks after settlement. Hostility included a good deal of high cost aggression (Fig. 25). Other grebes were discouraged from constructing their platforms in close vicinity. On the day prior to the storm, aggressions were noticeably reduced. In the storm, one platform was lost, the other reduced to a loose heap. The day after, the pair's aggressiveness increased again while defending the emptied space. As it then started a new platform out of sight for the observer, a further continuation of behavioural recording became impossible. The new platform received a first egg on 15 April. Pair C exhibited a high double presence at all times.

Both grebes invested much energy in the defence of an increased area around two platforms that may have caused their late clutch initiation.

Pair D (Table 43, Fig. 24) established itself towards the end of March, but it was only included in the observation program over the storm weekend when pair C moved out of sight. At this time, its aggression levels were rather high. In spite of the dense nesting in the area, the aggressiveness of pair D was steadily reduced during egg laying and during the early stages of incubation. It rose again in late April when an additional pair started building in a distance of only 2 m from the nest D. As soon as the newcomers were convinced to abandon their plan, aggression levels fell again. The peaks of aggression in the pair were always triggered by high cost interventions (Fig. 25) that globally however remained limited.

Over the two days of the storm, pair D left its platform unguarded for some time. Both partners were present for 80% of the time directly after the storm when rebuilding the platform. During laying and incubation, the simultaneous presence

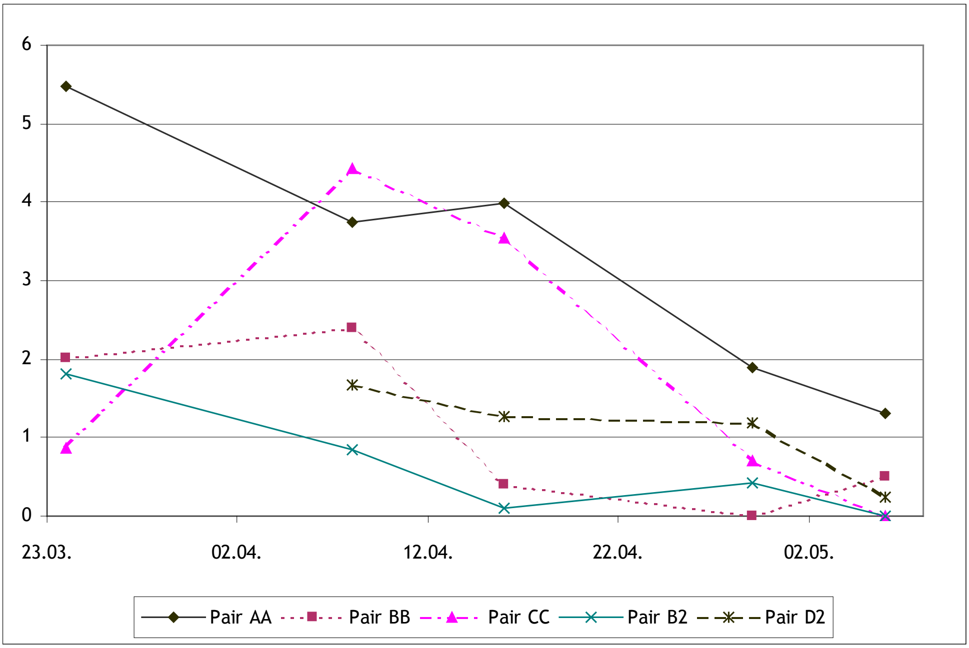

**Fig. 23:** Evolution of high cost aggression in pairs AA, BB, CC, B2 and D2 in 2006.

of both grebes was reduced until hatching when it rose to 65%.

With pre-egg laying hostility high followed by a constant reduction while on the eggs, except for a short period in order to prevent another pair from settling, the pattern exhibited by pair D could still classify as that of an experienced pair. Only the delayed clutch initiation did not fit into the picture.

The inexperienced pair AA (Table 44, Fig. 26) owned a loose heap on 18 March that it left mostly unguarded at that time. One week later, it exhibited a really high readiness for aggression, total, weighed and high level, that was tenacious to be reduced. Even though it continuously shrank over the season, the pace of reduction was slow. Until late April and early May, the pair retained comparably high levels of aggression. Especially high energy aggression took time to come down and remained above the levels exposed by other pairs until the end of the monitoring program (Fig. 23). Even after its really late clutch initiation, the pair's speed of aggression reduction changed not and the sole pair that had settled close was still continuously chased. However, with the appearance of the first egg, all expensive aggressions occurred while both grebes were present (Table 48). The comparably important hostile behaviour certainly contributed to having at the end only two closer neighbours while in the directly adjacent part of the colony, nesting was much denser.

After the initial careless period, both partners of pair AA were simultaneously present for always more than half of the time during the long guarding of the platform. Only during incubation, the percentage fell for a short time during that a new pair was able to settle close. The levels of weighed and high cost aggression appeared to be correlated to time (corr. -0.99 and -0.97) and nest contents (corr. -0.95 and -0.92). In total, the territorial defence of the pair needed high investments in time and energy that may have provoked the late clutch initiation. The behaviour seemed to lack experience.

Similarly to pair AA, pair CC (Table 45, Fig. 26) settled early, but both partners were mostly absent from their platform on 18 March. The aggressiveness in pair CC was not low in March and it

**Table 41:** Summarized nesting data of pair A1 in 2005 (abbreviations: see Table 36 - *: on 1st April, the pair moved its platform for 2.2 m).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 19.03. | 40.5% | 45.8% | 13.7% | 0.76 | 0.91 | PF | 1 | 3.0 m |
| 25.03. | 41.1% | 54.1% | 4.8% | 1.95 | 2.71 | PF | 2 | 2.3 m |
| 01.04. | 21.8% | 71.3% | 6.9% | 6.74 | 9.60 | PF | 2* | 4.5 m |
| 08.04. | 12.2% | 86.9% | 0.6% | 3.87 | 5.42 | PF | 0 | 4.5 m |
| 09.04. | 77.4% | 22.6% | / | 4.62 | 8.21 | LH | 0 | 4.5 m |
| 15.04. | 57.3% | 42.7% | / | 2.94 | 4.78 | 2 e | 0 | 4.5 m |
| 22.04. | 6.0% | 94.0% | / | 2.92 | 3.05 | 4 e | 0 | 4.5 m |
| 30.04. | 27.8% | 72.2% | / | 1.42 | 1.99 | 5 e | 0 | 4.5 m |
| 07.05. | 19.2% | 80.8% | / | 1.88 | 1.96 | 6 e | 0 | 4.5 m |

**Table 42:** Summarized nesting data of pair C in 2005 until the site was abandoned in the night of the storm (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 19.03. | 81.2% | 15.4% | 3.4% | 7.87 | 10.49 | BP | 0 | 5.0 m |
| 25.03. | 53.1% | 42.5% | 4.4.% | 10.78 | 14.41 | PF+BP | 1 | 3.0 m |
| 01.04. | 81.2% | 13.5% | 5.3% | 11.64 | 15.22 | PF+BP | 0 | 3.5 m |
| 08.04. | 64.9% | 35,1% | / | 2.06 | 3.77 | BP | 0 | 3.5 m |
| 09.04. | 70.3% | 29.7% | / | 6.89 | 10.91 | LH | 1 | 2.8 m |

**Table 43:** Summarized nesting data of pair D in 2005, platform first registered on 2 April (clumped then with 4 other nests) and observed from 8 April onwards (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 08.04. | 30.8% | 50.3% | 18.9% | 9.26 | 10.97 | PF | 4 | 0.5 m |
| 09.04. | 80.1% | 6.1% | 13.8% | 10.33 | 12.63 | LH | 4 | 0.5 m |
| 15.04. | 35.8% | 64.2% | / | 6.89 | 8.41 | 3e | 5 | 0.5 m |
| 22.04. | 15.6% | 84.4% | / | 4.86 | 5.00 | 4e | 4 | 0.5 m |
| 30.04. | 32.8% | 67.2% | / | 8.29 | 10.29 | 4e | 4 | 0.5 m |
| 07.05. | 64.5% | 35.5% | / | 3.93 | 4.75 | 1 p, 2e | 4 | 0.5 m |

increased further in April, during clutch initiation and early incubation. The bulk of the hostile behaviour triggered high cost (Fig. 23). During egg laying, the pressure stemming from new settlers remained high and the pair's full clutch size of six eggs gave a strong indication for brood parasitism. The fierce territorial defence over clutch completion was nevertheless unable to keep intruders off and possibly left other females with opportunities for parasitic egg dumping in nest CC. Such

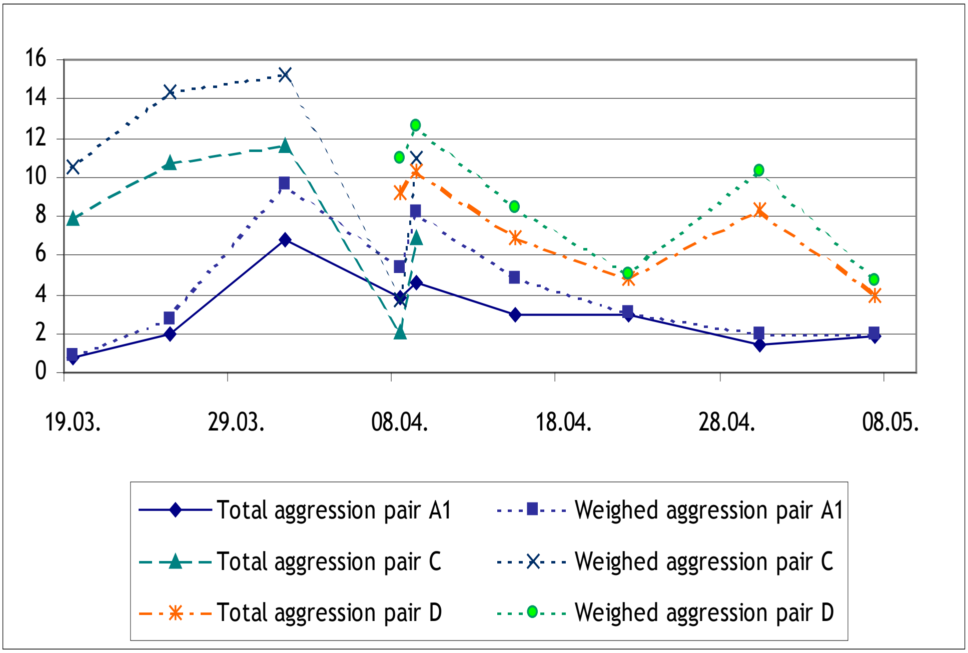

**Fig. 24:** Evolution of total and weighed aggression in pairs A1, C and D in 2005.

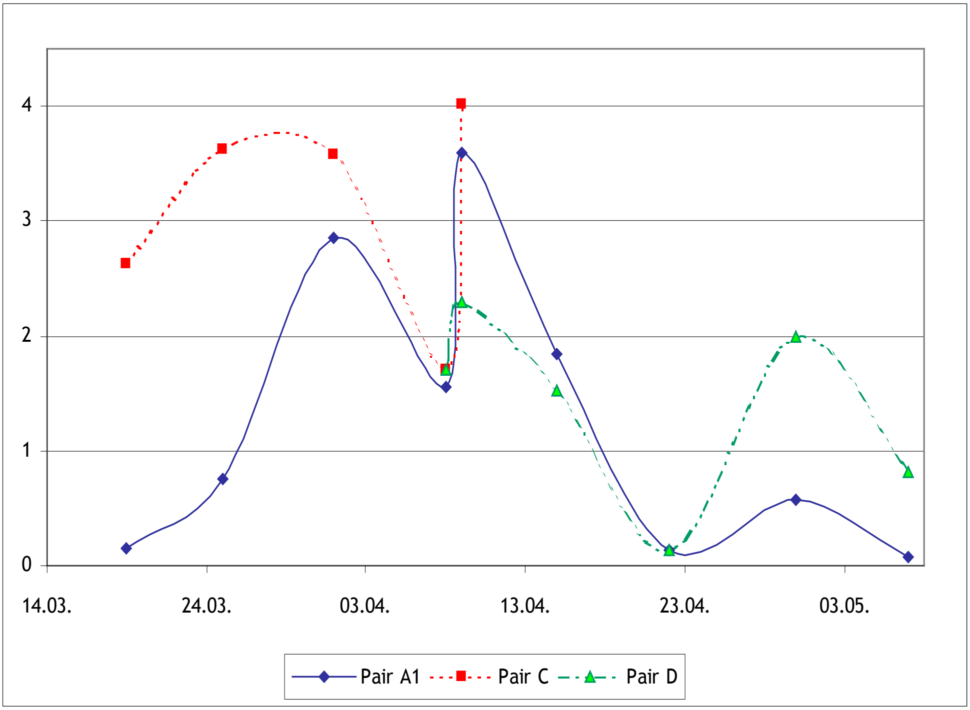

**Fig. 25:** Evolution of high cost aggression in pairs A1, C and D in 2005.

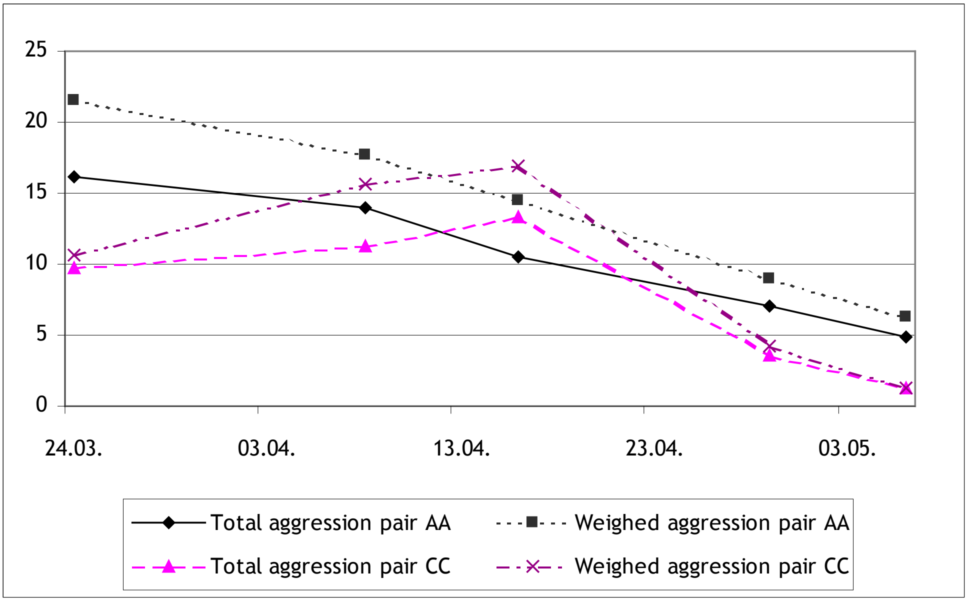

**Fig. 26:** Evolution of total and weighed aggression in pairs AA and CC in 2006.

**Table 44:** Summarized nesting data of pair AA in 2006 (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 18.03. | | | | | | LH | 0 | 3.7 m |
| 24.03. | 75.2% | 15.9% | 8.9% | 16.11 | 21.58 | BP | 0 | 3.7 m |
| 08.04. | 57.8% | 42.2% | / | 13.98 | 17.73 | PF | 1 | 2.5 m |
| 16.04. | 61.2% | 38.8% | / | 10.45 | 14.43 | 1 e (d) | 1 | 2.5 m |
| 29.04. | 35.5% | 64.5% | / | 7.11 | 9.01 | 4 e | 2 | 2.5 m |
| 06.05. | 60.2% | 39.8% | / | 4.92 | 6.23 | 4 e | 2 | 2.5 m |

**Table 45:** Summarized nesting data of pair CC in 2006 (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 18.03. | | | | | | LH | 0 | 4.8 m |
| 24.03. | 32.3% | 47.1% | 20.6% | 9.78 | 10.65 | BP | 1 | 2.6 m |
| 08.04. | 71.0% | 29.0% | / | 11.25 | 15.68 | 1 e | 1 | 2.6 m |
| 16.04. | 34.6% | 65.4% | / | 13.38 | 16.93 | 5 e | 4 | 2.6 m |
| 29.04. | 36.2% | 63.8% | / | 3.56 | 4.27 | 6 e | 4 | 1.7 m |
| 06.05. | 37.7% | 62.3% | / | 1.31 | 1.31 | 2 p, 4 e | 5 | 1.5 m |

occasions were even more given as over 60% of the expensive aggressions occurred with only one partner present (Table 48). Only by the end of April, aggression levels in pair CC were finally low.

Pair CC had a simultaneous presence for about one third of the time throughout its nesting that was increased only during clutch initiation. The high investment in territory defence, especially late in the program, and performed with only one partner present that had to abandon its care for the clutch, could only be expected by a relatively inexperienced pair.

**Behavioural patterns of pairs A and B1:** Pair A (Table 46, Fig. 27) settled early and exhibited initially a rather high aggressiveness. The levels were reduced comparably slowly. After replacement clutch initiation, directly after the night of the storm, territorial defence activities, possibly as a consequence of pressure stemming from new settlers or for parasitic egg laying, were still important: the number of neighbouring pairs increased from two to four and two additional pairs tried to force their entry into this sector of the colony. Most hostility now only involved low cost threatening. In the beginning, a major part of the aggression caused high energetic costs that were progressively reduced in time and these quasi disappeared after clutch completion (Fig. 21).

A gradual decrease from 67% to 39% in the simultaneous presence of both birds of pair A was observed until first clutch initiation on the day of the storm. Directly after the storm, both grebes were again present more often. After the new clutch was started, the simultaneous presence of both declined, but it increased again close to hatching. Total aggressiveness appeared to be related to the progress of time (corr. -0.90).

The long pre-egg laying phase and the initially high levels of aggression qualified pair A as inexperienced. Being given the high settlement pressure in the area of its nesting, hostile behaviour might have been unavoidable. As could be expected from experienced pairs, the energetic demand on hostile behaviour was kept low to the extent possible.

Pair B1 (Table 47, Fig. 27), settling early, maintained low aggression levels for most of the time. In the storm, the pair lost one egg, but recuperated the second. Thereafter, as a protective reaction against nest parasitism, the partners became a bit more aggressive for about two weeks. Using mostly low cost threatening, brood parasitism could not be avoided and nest B1 received an abnormally high number of eggs. It was only during this period that high cost aggression could occasionally be witnessed at all (Fig. 21).

The attendance of their platform by pair B1 varied greatly in time without that this appeared to be related to any events.

The pair's low degree of reactivity to settlement pressure and parasitic egg dumping could be interpreted as a consequence of experience. If the avoidance of energy expenditure could be justified with respect to clumping, it cannot with respect to brood parasitism and the pair might best be classified as inexperienced.

In summary, the initial aggressive behaviour of experienced pairs seemed to be largely depending on circumstances, meaning structural features of the habitat and settlement pressure by other grebes. With clutch initiation, all five pairs exhibited a tendency for lowering their aggressiveness and especially for limiting more costly interventions. Occasionally, the tendency could be countered by new pairs insisting to settle in close vicinity while the birds under special observation were already incubating. Generally, they reacted by increasing low cost threatening. Rarely, they then displayed more expensive aggression, but only when both partners were present. After clutch initiation, high nesting density in itself provoked hardly high cost aggression and threats could be more frequent.

Mainly in situations where intruder pressure was high and new pairs established themselves close, aggression rose. In time, the pairs got habituated to new settlers and changed their mutual behaviour from threat chases or even fight to short ritualized threats. The attendance to the nesting platform appeared to be more circumstantial. Although well adapted to the particular situations, no overall rule or tendency could be detected.

Inexperienced pairs behaved differently. They were less able to control the situations in which they got involved throughout the season. More particularly, they had difficulties to keep aggression levels under control, even while incubating. Their high energetic expenses contributed to prolong the pre-egg phase and they were unable to prevent other grebes from settling close or from dumping parasitic eggs in their nests. In addition, the attendance to their nesting platform was not always in line with the requirements of the different situations.

**Table 46:** Summarized nesting data of pair A in 2005 (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 19.03. | 67.3% | 29.1% | 3.6% | 10.90 | 14.63 | PF | 0 | 3.5 m |
| 25.03. | 63.0% | 23.2% | 13.8% | 12.66 | 18.87 | PF | 1 | 3.5 m |
| 01.04. | 47.6% | 52.4% | / | 9.67 | 14.69 | PF | 2 | 3.2 m |
| 08.04. | 38.8% | 61.2% | / | 8.23 | 12.34 | 1 e | 3 | 3.0 m |
| 09.04. | 68.0% | 13.3% | 18.7% | 6.89 | 9.76 | LH, 0 e | 3 | 3.0 m |
| 15.04. | 31.8% | 68.2% | / | 8.69 | 11.58 | 3 e | 4 | 2.0 m |
| 22.04. | 13.1% | 86.9% | / | 2.50 | 2.92 | 4 e | 2 | 2.0 m |
| 30.04. | 31.2% | 68.8% | / | 3.86 | 5.00 | 4 e | 2 | 2.0 m |
| 07.05. | 55.1% | 44.9% | / | 2.85 | 3.89 | 2 p, 2 e | 3 | 1.5 m |

**Table 47:** Summarized nesting data of pair B1 in 2005 (abbreviations: see Table 36).

| Date | % of time with x grebes present | | | Level of aggression | | Condition of platform | Number of platforms within 3 m | Nearest distance to neighbour |
|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 0 | Total | Weighed | | | |
| 19.03. | 77.0% | 19.7% | 3.3% | 3.49 | 3.49 | PF | 1 | 3.0 m |
| 25.03. | 32.3% | 29.8% | 37.9% | 1.52 | 1.84 | PF | 3 | 1.5 m |
| 01.04. | 70.6% | 24.7% | 4.7% | 1.85 | 2.19 | PF | 3 | 1.5 m |
| 08.04. | 57.0% | 43.0% | / | 3.87 | 4.26 | 2 e | 2 | 1.5 m |
| 09.04. | 43.9% | 56.1% | / | 2.05 | 2.56 | R, 1 e | 2 | 1.5 m |
| 15.04. | 53.1% | 46.9% | / | 3.80 | 5.02 | 7 e | 3 | 1.5 m |
| 22.04. | 13.3% | 86.7% | / | 6.37 | 7.43 | 7 e | 4 | 1.0 m |
| 30.04. | 67.5% | 32.5% | / | 3.12 | 3.83 | 7 e | 3 | 1.0 m |
| 07.05. | 59.0% | 41.0% | / | 1.66 | 1.81 | 3 p, 4 e | 3 | 1.0 m |

## 3.8 Control of aggression levels

The previous section showed that especially experienced pairs were able to control their levels of aggression and to adapt them according to the needs of the circumstances. A gradual process of habituation to neighbouring pairs helped to overcome possibly high initial mutual hostility. The questions then arise: what triggers such a process and how does it proceed? Have the grebes evolved behavioural features that help to gradually overcome their predispositions for territory defence? Could a population evolve over time ethological adaptations contributing to more sociability?

In spite of the fact that on several occasions incubating grebes left their clutches for chasing intruders, in the majority of intrusion cases, the grebe on its eggs seemed very reluctant to leave the nest and limited its defence to intense threatening and upset calling from the nesting platform. Therefore, with clutch initiation, the predisposition for care of the eggs is expected to get more and more prevailing.

Once incubating, aggression against established neighbours faded away, also due to behavioural adaptations as witnessed in Enkhuizen. Indeed, incubating grebes were never seen to be facing their close neighbours. They were always sitting on their eggs either with their view obstructed by the

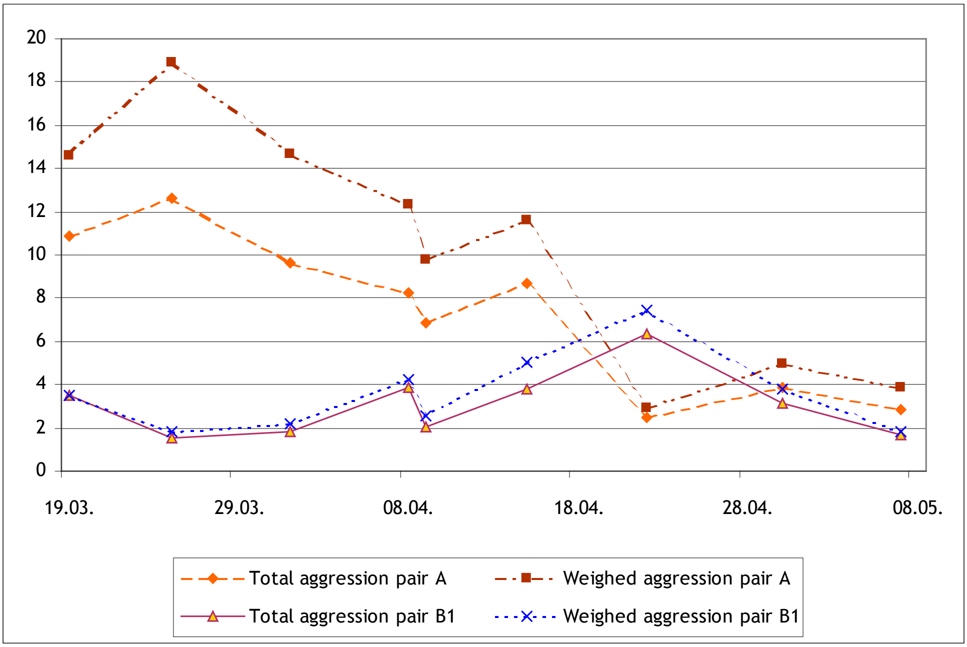

**Fig. 27:** Evolution of total and weighed aggression in pairs A and B1 in 2005.

vegetation or facing in a different direction of other near platforms. As reported before, some platforms were only at distances of 30 to 50 cm from one another. Especially under these circumstances, the incubating neighbours were always turning their backs to one another.

Generally when not feeding, the partners of incubating grebes remain often close to the nest where they rest in the pork pie posture. If this principle was applied inside the densest parts of the Footbridge colony, the entire water surface between the platforms would have been occupied by floating birds. Such close contact would probably have led to a constant renewal of aggression. At the Footbridge colony, only few resting partners were observed at the same moment in time to stay in direct vicinity of their nests. These were normally positioned so as to be at maximum distance from other platforms and they did not face the closest neighbours. Many partners also remained in front of the vegetation where they rested at a greater distance from their own nest, often in company of other grebes.

The particular behaviour of the incubating and resting grebes aimed at avoiding visual contact with close neighbours, especially within the limits of their nesting "territory". Without visual trigger, aggressiveness could be overcome. When resting further away from the nesting platform, a kind of flocking behaviour, similar to that observed by

**Table 48:** Expensive aggressions in 2006 in relation to the number of partners present.

| Date | Pair AA | | Pair BB | | Pair CC | | Pair B2 | | Pair C2 | | Pair D2 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 |
| 24.03. | 18 | 1 | 9 | 0 | 1 | 2 | 7 | 2 | 7 | 6 | | |
| 08.04. | 6 | 5 | 5 | 0 | 11 | 0 | 1 | 7 | 12 | 26 | 8 | 10 |
| 16.04. | 14 | 1 | 2 | 0 | 6 | 10 | 1 | 0 | | | 12 | 0 |
| 29.04. | 8 | 0 | 0 | 0 | 5 | 0 | 3 | 0 | | | 5 | 0 |
| 06.05. | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | | | 1 | 0 |

Creutz (1970) for solitary breeding Great Crested Grebes, was occasionally witnessed. It is indeed common that territorial pairs inhabiting the same body of water come together at a neutral part of the site at a particular time of the day. They all actively swim towards this zone where they then loaf for a while before separating again. Similarly, the colonial pairs of the Footbridge colony could rest and preen together on the open water surface in front of the nesting habitat. In these loose gatherings, social attraction could have played a role.

In Enkhuizen, the nesting density was extremely high in all five years of the study. Unfortunately, no data about the nesting density at the Footbridge colony prior to this program existed so that it is difficult to assess whether the degree of aggregation was a recent fact or not. In 1983, the colony consisted of 41 pairs (Vlug 1983), but no information on the size of the vegetated area at that time was available. According to the owner of a boat, in 2002 only about 80 nests should have been part of the colony. It was not known to what extent his count was accurate. Maybe that the present program was started during a year when population pressure triggered an increase of the breeding population and thereby a further reduction in the distances between nesting platforms. Such a step could explain more vigorous and long lasting aggression during settlement than would be expected normally. Indeed, solitary breeders nesting at distances of 100 m and more from one another will not switch from one year to the next to aggregations where neighbouring platforms come close to touching without reacting vigorously for a prolonged time to counter the evolution. One can reasonably assume that first aggregations in a population still cater for greater distances between neighbours, even though some variability may exist. In a gradual process over years, the distances between platforms might shrink if the prevailing conditions favour such an evolution. Expressed more generally, the evolution from a territorial breeder to a member of a densely packed colony is a step by step process provoking at each stage a new process of habituation. Only after successful completion of one step, meaning behavioural adaptation to the associated circumstances, the next step becomes possible. It is thereby expected that the behaviour of the grebes is also based on past experience and that, in time, the birds learn to optimize their reaction to closer neighbours.

Except for some more general remarks, I was unable to find any other study with detailed behavioural records of colonial Great Crested Grebes. Supposedly this fact is related to the difficulties encountered at most sites to establish a convenient hide from where ethological observations become possible without disturbing the grebes. Most colonies exist at more remote locations where human presence is rather exceptional. If such a colony is approached by boat, the attention of the population will be diverted from their normal activities and it is then very difficult to correctly assess the level of aggression and its evolution in time. A correct assessment is at the end only possible if a continued observation is carried out with no or minimal disturbance.

Goc (1986) postulated that the territorial reaction by a settled pair of Great Crested Grebes is evoked by a visual or auditory contact with another individual. In a dense, mobile and noisy gull colony the sight of another individual is, in spite of the small absolute distances between grebe nests, only one of many strong stimuli reaching a bird. The grebe being overwhelmed with stimuli, it would be kind of overcharged with reacting to each of them and therefore, it would only exceptionally reply to one of them.

Blinov et al. (1981) found that conflicts occurred most often during the settlement of the grebes and the establishment of "borders". These could then escalate into fights. Once incubating, little aggressive behaviour was witnessed. Koshelev (1977) confirmed that each pair had a clearly delimited territory from which it kept other individuals off. Trespassing was mostly avoided by warning and threatening acts and postures. Harsh territorial conflicts leading to fighting were seldom. While admitting that incubating grebes were extremely unwilling to leave the nest and rather permitted other grebes to settle in between, Koshelev (1985) stated also that under high nesting density intra-species aggression increased sharply. Under such conditions, incubating birds could leave their clutches unobserved in territorial defence.

The general picture described by these authors suites quite well the observations at Enkhuizen. One can therefore conclude that, though depending on nesting density, aggression is more or less important during colony establishment. It weakens the more the borders between neighbours are recognized. With clutch initiation, the aggressiveness displayed is normally very ritualized and of low intensity. Curiously, Goc's (1986) deductions were not necessarily in agreement. He found no indication for stress in colonial grebes due to overcrowding. He argued that a colony does not form by a gradual decrease in the size of territories, but by a rapid switch in their sizes accompanied by a step-like change in the behaviour of the birds. As a result, sharp conflicts between neighbouring pairs would not be frequent. Nevertheless, he admitted a function of territorialism aiming at maintaining a suitable distance to other pairs. A shortening of this distance would cause disturbances in the activities connected with breeding. The only disturbance Goc then cited was intra-specific nest parasitism.

It cannot be excluded that grebes nesting for years in colonies with unchanged densities have over time gained experience that helps them to overcome their aggressiveness rather quickly, so that their stress during colony establishment would be minimized. They would have learned to save their energy for more rewarding investments, being reproduction. With additional pressure on density however, their reactivity could again increase and it could need them a few years to get accustomed to the new situation. Over longer time periods, a population used to denser nesting could even evolve genetic adaptations that favour a less aggressive behaviour in aggregated nesting. We could indeed imagine that birds able to best avoid intra-specific disputes increase their fitness and contribute most to future generations. Their qualities would in time spread out in the population and a quick building up of a dense colony without triggering abnormal stress for individual birds could be favoured.

## 4 Concluding discussion: the Great Crested Grebe, a species in transition from solitary to colonial breeding?

Siegel-Causey and Kharitonov (1990) examined the features of coloniality in birds in general within an evolutionary context. According to them, the consensus of recent studies is that coloniality is evolutionary advanced compared with less complex population structures such as solitary nesting and loose aggregations of territorial nesters. They also postulated that coloniality must have evolved more than once, possibly more than ten times, and different adaptive forces may operate in different lineages of colonial breeding. Rolland et al. (1998) detected that coloniality even evolved independently at least 21 times in the 320 bird species included in their sample study. As a consequence, coloniality may serve different functions in unrelated groups of birds. Siegel-Causey and Kharitonov admitted that the change from being essentially independent individuals to members of a breeding colony can represent in some species a significant change in sociality. We therefore might expect other manifestations of grouping to show up previously to aggregated nesting and that these would function to facilitate the transition from strict territorialism to coloniality. Various factors have been proposed as adaptively significant for colonial breeding and Zubakin (1983 in Siegel-Causey & Kharitonov 1990) suggested to distinguish between causal factors or those facilitating the transition from solitary to colonial nesting in a lineage, formation factors or those likely to promote a particular type of colonial breeding within a lineage and maintenance factors or those promoting the retention of the behaviour. In addition, he classified the birds into obligate and facultative colonial species. Fisher (1958 in Alexander 1974) posed that the progressive modification of structure or function occurs only in so far as the variations are of advantage to the individual. Therefore, any theory of social behaviour describing the selective forces causing and maintaining group-living must consider that groups form and persist because all of the individuals involved somehow gain genetically (Alexander 1974) or at least limit the losses they would incur otherwise.

According to Siegel-Causey and Kharitonov, a chief causal factor in the evolution of coloniality is the presence of unpredictable or abundant food resources located outside the limits of the nesting habitat. Factors promoting the formation of particular forms of coloniality are the influence of terrestrial and avian predators, the supply of suitable nesting sites and the stability of the colony habitat. Maintenance factors are generally consequential and include such features as breeding synchronisation and social facilitation.

Siegel-Causey and Kharitonov built a transitional pathway leading from single territorial pairs to one of the three types of colonies identified in relation to their degree of social interaction: the "nominal" colonies presenting minimal group adherence, the "anonymous group connections" having a more developed flocking behaviour and the "obligate-colonial" where the degree and the nature of group adherence define nesting densities.

Where do we have to position the Great Crested Grebe within this overall framework? As we do not expect the grebes to pass from a stage lacking even outside the breeding season any manifestation of sociality worth to be mentioned to a situation of gregarious coloniality, predispositions should show up in solitary breeders before causal factors can gain ground. Thereafter, causal factors could facilitate or trigger the passage from territorial to aggregated breeding by helping to evacuate remaining hurdles. What formation factors would then have promoted the appearance of Great Crested Grebe colonies, and what consequential maintenance factors could be identified in today's aggregations? In the following, these different aspects are investigated, keeping always in mind the interest of the individual grebe.

**Predispositions for coloniality observed in solitary breeding Great Crested Grebes:** An important part of the Great Crested Grebes performs the activities directly related to reproduction in isolation from conspecifics and maintains large individual all purpose territories when nesting. Even though, outside the breeding season or outside their territory, these birds are not completely insensitive to social interactions.

Throughout their breeding range, Great Crested Grebes assemble prior to breeding on the open surface of bigger bodies of water from where solitary nesters disperse later. While the prime aim of the aggregations is to promote mate selection, they will initially, during advertising, force the grebes to reduced aggressiveness as otherwise approaching a potential partner is excluded. Once a choice is made however, showing again increased aggression could be favoured, above all by males, on one hand, to prevent rivals from entering into displays with the mate and, on the other, to convince the partner of one's qualities.

On the breeding grounds, prior to and during incubation, the territorial breeders of various bodies of water have been noticed to come regularly together in a neutral zone for a common round of loafing (Creutz 1970, pers. observations). The groupings disperse again after a short while without that aggressions are observed. Except for mutual bouts of head-shaking, courtship displays are absent, too. The implications of these social interactions remain however unclear. They could simply be an expression of mutual attraction that could prevail again once the distribution of territories realized satisfies all parties present. In the context of the individual's fitness, it could also be beneficial to gain information on the survival of neighbouring pairs and thereby obtain indirect information about possible predation risks.

As previously mentioned, large moulting aggregations occur for instance on Lake IJssel, on Swiss lakes and on bigger lakes in Schleswig-Holstein. During this period of autumnal renewal of flight feathers, the grebes are flightless and can only escape predators by swimming or diving. While such an aggregation is easily detectable by predators, it confers to each of its individual members the advantages of early warning and predator disorientation. It thereby enhances the individual survival chances to the next breeding season.

Outside the breeding season, loose flocks of Great Crested Grebes roosting together are a common picture on many bodies of water. During comfort activities, the vigilance of the individual bird is reduced. The combined attentiveness of all members of such a group is expected to more than compensate for the lower individual attentiveness.

Also when not breeding, grebes can often be seen feeding not far from each other. The benefits from not defending a winter feeding territory would stem from the reductions in energy expenditure and injury risks related to aggression, in a situation where the individual mobility and the huge feeding areas at the disposal of the species would not justify territoriality. The improved sociability could in addition serve mate selection and, depending on circumstances, lead to cooperative feeding. In the African Crested Grebe, feeding groups exceeding occasionally 50 birds chase fish on South-African lakes (pers. observation). These seem to improve the hunting success of group members. In addition, larger groups of grebes clumped outside the breeding season could discourage other species feeding on similar prey from using the same site.

Though the manifestations of gregariousness observed might be weak, they could help in an aggressive territorial breeder to pass the barrier to more aggregated nesting types if favoured by circumstances.

**The abundance of food and the scarcity of nesting sites as causal factors of coloniality:** The quantity of food available to the individual depends on the population that will feed on it. In the breeding season, the size of this population is basically limited by the breeding habitat at disposal. If food is scarce, rather evenly distributed and highly competed, it should be more advantageous for a pair to build the nest directly within the feeding territory and breed solitarily. This implies that the place is defendable and is worth to be defended. On the contrary, in a situation of relative food abundance with respect to nesting, or at least prime nesting habitat, denser nesting could occur. According to Rolland et al. (1998), coloniality in general terms is highly correlated with the absence of feeding territoriality. In the context of the Great Crested Grebe, the hurdle of exclusive feeding area would need to be evacuated.

The data obtained at the Footbridge colony permitted the conclusion that the aggregated breeding of the Great Crested Grebes there was imposed on the species by a general scarcity of nesting sites, not only of prime nesting sites, coupled with a plentiful of food. Given these circumstances, it was not worth and not practical to defend a feeding territory. Similarly, Koshelev (1985) estimated that colonial nesting was typical for the species on large bodies of water rich in fish, but with limitations in nesting habitat.

Fjeldså (1988, 2004) noticed that colony formation in the normally territorial grebes has sometimes to be explained by a limitation of highly protected nesting-sites, in spite of the existence of plenty of alternative sites, provided the birds can use very large communal feeding areas offshore. At the German Lake Gothen, the origin of the colonies was apparently unrelated to a general scarcity of nesting sites and large fields of bulrush remained either unoccupied or occupied to a very limited extent. The abundance of food had not led to a more generalized occupation of all vegetated areas, but to a concentration at places judged to be of prime quality due to their structural features (Meyer 1992). Also on Lake Żarnowieckie, no lack of habitat was registered and in some reed beds, colonies arose almost simultaneously, whereas neighbouring reed beds remained unoccupied (Moskal & Marszałek 1986). The enhanced protection provided by prime habitat would then attract more grebes than usual to such a site. Due to intruder pressure, the initial occupants would not be in a position to defend their exclusive feeding territories. Due to the abundance of food within reach, the situation of individual grebes becomes comparable to that outside the breeding season when the need to defend an own feeding reservoir is limited. Renouncing gradually to its defence will not put at stake the individual's feeding conditions while preventing it from unprofitable activities. Indeed, territorial defence triggers costs: threatening and fighting intruders is time consuming, energetically expensive and involves the risk of injury or even death. Therefore, it is expected that birds defend territories only when the benefits of doing so exceed the costs, that is when it is worthwhile either in terms of survival or reproduction (Perrins & Birkhead 1983). If food is abundant, territory defence is not profitable.

The abundance of food resources alone might not be enough for aggregations to arise. Coupled with a general limitation of breeding habitat, it should serve as the prime cause for the development of grouped breeding in grebes. The choice offered to individual pairs would be between not breeding at all and investing all energy and time in territory defence or accepting close neighbours. The role played by a lack of prime nesting habitat remains more blurred, not only as its identification is often difficult. As long as alternative sites exist, the pairs can choose. Then, the costs associated with coloniality must at least outweigh the benefits provided by the prime location.

The whole process could work as follows. The initial limitations in prey trigger competition for this scarce resource and this is a crucial factor in the evolution of territoriality (Perrins & Birkhead 1983). While still solitary breeder on a given lake, huge all purpose territories are defended by individual pairs. The increase of the food basis in relation to the size of the nesting habitat causes a change in nesting densities. In some cases, also habitat destruction, for instance by reed harvesting or embankments, could cause the shift in the relationship between nesting habitat surface and food. Most commonly, the abundance of food resources for Great Crested Grebes would have been triggered by eutrophication leading to an increase of fish mass per volume unity of water. This process was observed in the 20th century and especially during the 1950s and 1960s: many lakes in urban or agricultural areas became increasingly eutrophic as a consequence of their use as recipients for untreated sewage and of phosphorous fertilizer run-off from agriculture. In parallel to the initial increase of biomass, the amount of cyprinid fishes generally increased considerably (Brönmark & Hansson 2005). As a consequence, the size requirements of the solitary pairs on habitat could decrease. Before this occurred at a larger scale, the solitary breeders first experienced enhanced feeding conditions for raising their broods. Therefore, in the course of the twentieth century when waters became increasingly eutrophic, partially important increases in Great Crested Grebe numbers in almost all parts of the nominate's range were recorded (O'Donnel & Fjeldså 1997). Under the previously prevailing conditions of greater scarcity of food, territoriality was advantageous. With the increase of the feeding basis, the need for an own all purpose territory decreased. In parallel, the higher population numbers naturally built up intruder pressure that would at the end have forced aggregated nesting.

In short, the increase in the food basis was key. It led to increases in population numbers that provoked shortages in breeding habitat. In agreement with Zubakin and Siegel-Causey and Kharitonov (1990), colonies were primarily formed in dependence of nearby food concentrations and the Great Crested Grebes had reached the stage of the "nominal colonies".

**Unstable ecological conditions:** In many parts of the grebes' breeding range, the habitat conditions are not stable from one year to the next or they may fluctuate drastically over years, so that the motivation for the establishment of nests in close vicinity can be changing in between seasons or over time. In the Selenga River Delta, aggregated nesting of the Great Crested Grebes occurred only if the water levels were low and prohibited access to a large part of the vegetation. In 1980, under such conditions 96% of all breeding Great Crested Grebes concentrated in eight colonies. In 1985, higher water levels again increased the surface of the habitat within reach and only one small colony subsisted (Podkovyrov 1986). For Saxony, Tuchscherer et al. (1998) noted that colonies were subject to high annual fluctuations of their breeding population and very often they survived not for long years. Koshelev (1985) declared that depending on ecological conditions, the species switched easily from colonial back to solitary breeding. This would mean that the grebes' inclination to territoriality remains high even though aggregated nesting was achieved previously.

Colonial nesting being imposed upon the grebes, the extent of their aggregation continues in principle to be dictated by their territorial behaviour in conjunction with habitat conditions. Instable ecological conditions would not promote a weakening of this probably at least to some extent genetic barrier and a further evolution in the type of nesting aggregation of the grebes. On the contrary, ecological stability of the habitat could act as a maintenance factor for coloniality by promoting learning or habituation in this long-lived species.

**Aggression and colony formation:** Even though the conditions for aggregation build up, some biological constraints against the natural tendency to grouping might persist and might need to be lifted by evolutionary changes (Rolland et al. 1998). In the Great Crested Grebe, feeding territoriality would be such a serious obstacle to colony formation. While the need for territory defence could be lifted by relative food abundance, the grebes have to overcome their inherent aggressive behaviour, too, if coloniality is to evolve beyond a mere forced clustering with a maximum of costs. This implies that establishment of a population in this new environment is aided by plastic responses, as first suggested by Baldwin (1896 in Yeh & Price 2004)

Fjeldså (2004), while admitting that a small colony can form within a few days, thought the process to start with one or a few pairs first defending a territory vigorously. As additional pairs try to gain a foothold, open fights become frequent and can sometimes last for several minutes. With increasing and persisting intruder pressure, the initial territory holders suddenly give up and more pairs can settle within a remarkably short time, defending only the immediate vicinity of their chosen nest-sites. Similarly at the Footbridge colony, from the start of settlement, the entire habitat available was used by the grebes and later settlers had to threaten or fight their way into the habitat. This process provoked a seasonal decrease in distances between nesting platforms and contributed to a rather unrelated arrival and breeding process in neighbouring pairs and for the colony as a whole. Also Koshelev (1985) observed the formation of colonies at Tiligul'liman Estuary to start with the simultaneous appearance of several pairs occupying each a territory of 5-15 m in diameter. The grebes actively protected the borders of their territories, but with egg-laying, their aggression decreased and thus, new pairs were able to settle in between. As a result, the size of "territories" and distances between the nests decreased.

In spite of the abundance of food and the intrusion pressure by unsettled grebes, both making territory defence unnecessary and ineffective, the grebes' natural inclinations are not easily overcome in the early stages of aggregation. If maintenance factors contribute to a constant renewal of grouped breeding, we could imagine that those pairs investing less in aggressions that at the end would prove useless, could perform best. As they then contribute most to the future gene pools, the inclination to territorial behaviour could be reduced in the population. This would allow consequential features in favour of a more social or gregarious way of breeding to express themselves.

**Predation: a formation or a maintenance factor?** As the Great Crested Grebes have mainly evolved passive defence against predation, hidden solitary nesting should be favoured if the risk is real. Territorial pairs of Great Crested Grebes have their nests generally well camouflaged and predation should then be minimized by spacing nests out (Perrins & Birkhead 1983). Denser nesting makes unnoticed breeding impossible. If other circumstantial conditions have already led to denser breeding, colonies act to concentrate the nesting birds (Siegel-Causey & Kharitonov 1990) and their clutches as prey. Predation could therefore be a secondary cost of coloniality (Rolland et al. 1998) that should favour correcting measures.

Simmons (1974) found some pairs forming loose colonies for example at Burghfield and Blagdon. He thought that although such arrangements could sometimes be correlated with a shortage of sites, in general, it would seem to be favoured because of the increased safety from predators it imparts. Effectively, more nests were successful in the loose colonies than elsewhere. Koshelev (1985) and Goc (1986) found an increased hatching success in mixed colonies of grebes in comparison to solitary breeders on the same lake. The grebes profited from the association with other birds that defended their sites actively, mainly breeding colonies of gulls and terns.

Unfortunately none of the studies under review mentioned whether aggregated nesting in the population observed appeared prior to its association with a more aggressive nesting species. Accepting however that individual pairs are better off if their nests are well hidden in isolation, it appears unlikely that predation pressure could act as a formation factor for Great Crested Grebe colonies. Once aggregations have evolved, the increased breeding density could attract additional predators or lead those present to a greater specialization on prey. As a return to strict territoriality would be excluded by the situation, the increased costs could only be countered by enhanced protection provided by even denser nesting or the association with more aggressive species. At the individual level, better protection of the clutches and increased survival chances for the adults would result. Moreover, whereas highly conspicuous, but otherwise well suited habitat could remain inaccessible to solitary breeders in a situation of low predation pressure, its colonization by bigger numbers of grebes could occasionally be beneficial. Higher predation pressure should however deter the grebes from nesting there and it might even limit the grebes' nesting to sites where the association with other species provides protection.

In total, predation seems to be primarily a cost of grebe aggregations. Once coloniality established, it could help to maintain aggregated nesting by reducing the fitness of solitary nesting attempts and thereby promote a further development in the type of colonial nesting.

**The role of extra-pair copulations (EPC):** Wagner (1993) suggested that the mechanisms which have produced leks also operate when monogamous females pursue extra-pair copulations. Whereas most males should suffer net costs from EPC, the fitness of most or all females can potentially be increased (Wittenberger & Hunt 1985). Males are indeed more likely to be cuckolded while the females gain genetic diversity of their offspring, insurance against male infertility and the insurance that, due to sperm competition, the most viable sperm will achieve fertilization. Wagner's hypothesis requires that a substantial proportion of females within a population demonstrate receptivity to EPC and that EPC has become part of their mating strategy. Males would then congregate in response to females pursuing EPC and preferring to select among males in groups in which phenotypic comparison may be enhanced (Alexander 1975 in Wagner 1993).

In the absence of relative food abundance, feeding territory defence could persist as an insurmountable obstacle to platform clustering. Indeed, the benefits provided from EPC to the grebes would be annihilated by the absence of secured food delivery to the off-spring while the females would run all the risks enumerated by Wagner: physical injury during intra-sexual aggressions, reduced paternal effort and venereal infections. Also, the large majority of the males would be unable to secure an adequate part in total EPC and therefore, they should oppose the formation of the clustering.

The intense observations at Enkhuizen found little support for the existence of EPC there. Especially in the eight pairs closely followed in 2005 and 2006, not even one case of EPC could be detected. Hostile behaviour in the species is not limited to males either and intense water courtship normally precedes all platform courtship. Mating itself is technically restricted by the need for a platform. These features act as additional hurdles to EPC being an effective promoting factor for grebe colonies. In an aggregation of the closely related Red-necked Grebe, EPC was relatively uncommon, too, and it was not retained as a formation factor, either (Sachs et al. 2007).

Finally, EPC must be regarded as an incidental by-product of high nesting density that could spread once the levels of aggression in the species are lowered. But that would be a cost to the large majority of males and, in time, possibly also to the females if it ended up in a reduction of chick-care provided by their partners.

**Individual preferences for solitary or colonial nesting?** Even though there is quite a lot of variability in the features associated with aggregated breeding in the different populations of Great Crested Grebes, the phenomenon, today, could still remain more or less imposed on the birds. Either, there is global or prime nesting scarcity with respect to feeding conditions. For Koshelev (1985), the nesting density of the grebe aggregations is not a measure of their sociality, but it depends entirely on ecological conditions. The breeding strategy adopted by the species remains very flexible. Together with Goc (1986), we can agree that the breeding density of the species is primarily controlled by territorialism, an inherited feature of the grebes' character. Thereafter, local conditions seem to dictate whether and how aggregated nesting occurs and to where it develops. Goc concluded however that there is no evidence to indicate that pairs nesting in colonies could not gain a territory of their own and that the grebes show an individual tendency to nest in colonies or solitary. Great Crested Grebes nesting in colonies would not necessarily experience a kind of stress due to overcrowding.

Bukacińska et al. (1993) found that there were differences between colonial and territorial birds suggesting that they were grebes of different characteristics choosing different nest sites and differing in the dynamics of clutch size throughout the season. Obviously, the transition from territorial to aggregated breeding provokes changes in the behaviour of the birds that are not evolved simultaneously in all individual grebes. Single grebes might maintain character traits of aggressive outsiders longer than others, depending on their phenotypic traits.

During the initial stages of breeding aggregations, we could expect learning processes to be important. The fact that coloniality is more prevalent in long-lived than in short-lived species (Rolland et al. 1998) is in support of this statement. Long-lived species like the Great Crested Grebe have more time at their disposal to take full advantage of their learning and to evolve a flexible adaptation to local conditions. However, the predispositions to learning are not equal on the individual level. While some pairs could adapt better to close nesting and thereby reduce its negative effects quickly, others would have more difficulties. These could preserve a greater inclination towards solitary breeding. Although they could be able to maintain slightly increased distances to neighbouring pairs, as members of a cluster their clutch initiation might be delayed and their clutch size reduced. It could be that their individual fitness is better served by territorial breeding in a degraded habitat where they would be able to reserve the energy needed for successful breeding. Similarly, pairs unable to mobilize enough energy or aggressiveness to gain access to early aggregations could be pushed to less suitable breeding sites where at least they could breed. In comparison, the latter should nevertheless perform worse than their colonial counterparts so that in time the proportion of their offspring in the total population is reduced.

The move from a solitary to a social colonial breeder is not a simple move from one equilibrium to another. It implies intermediary steps of apparently unbalanced situations that are more difficult to explain and where both, territorial and clumped nesting co-occur within one population.

**Consequential features of nesting aggregations:** Whenever individuals derive benefits from group functions, they may be expected to carry out activities that maintain the group and thereby serve their own interest as well (Alexander 1974), or, to put it differently, other selective advantages might accrue (Coulson 1985). These could serve as indicators for the degree of coloniality achieved by a species.

In the "nominal colonies", egg laying and breeding of the Great Crested Grebes would extent over a more or less long period and be generally rather asynchronous, as was the case at the Footbridge colony and at most other locations surveyed. With predation pressure promoting the retention of coloniality, the settlement and the breeding by the grebes needs to be more in accordance, especially when the protection is depending on the presence of other species. The initially long and unrelated settlement and clutch initiation by the grebes would gradually change over long time periods and the yearly process of habituation to close neighbours would happen ever quicker. At the end, the yearly reduction of territory sizes would pass hardly noticed. All members of the population could profit from the reduced levels of aggression by concentrating their activities on reproduction. Finally, the greater synchrony could become more independent from its initial cause and it might be perceived more and more as an inherent feature of the species.

Some studies concluded that clutch initiation was rather synchronous in the Great Crested Grebes. For Goc (1986), differences in breeding strategies lead to differences in egg laying dates while at the same time, social stimulation could cause synchrony of egg laying in colonies. Koshelev (1977) noted however that the adult birds waited for the vegetation to grow, and, at the appropriate time, they all started nesting rather simultaneously. The start of breeding would thus be more depending on the presence of safe nesting sites and, at the end, synchrony would be an indirect consequence of habitat constraints. Blinov et al. (1981) noted that synchrony in breeding is highest in small dense colonies and more extended in more spaced and big colonies, so that a social or at least visual stimulus cannot be excluded and might develop over time. The aggregations would later develop into more organized structures that enhance the degree of social stimulation, primarily as an adaptation against predation (Kruuk 1964 in Siegel-Causey & Kharitonov 1990).

**Behavioural adaptations:** Aggregated nesting seems only possible if this a priori territorial species also has behavioural flexibility in its nesting strategy. Tinbergen (1936) stated that a colonial bird may be just as territorial as a solitary bird. The territory is by no means of the same importance and significance in different species. This statement holds true also for different populations in the same species. Thus, Newton (1998) found that the social system shown by any one species at a particular time depends partly on features of the species itself and partly on local conditions.

In the short run, plastic responses to an evolving new situation aid the Great Crested Grebes to cope with it while limitations in their behavioural flexibility prevent them from taking full benefit from their obtruded aggregations. Within a generation, their adaptation to the local conditions is limited by their capacity of learning or of habituation, their phenotypic plasticity. A more flexible response is supported by features like the "dear-enemy-effect" predicting that disputes between neighbours are less intense than those between foreigners (Kappeler 2006) or the need for clutch protection once incubation has started and the associated reluctance to leave the eggs as they then remain unprotected. With respect to behaviour, the ritualized displays existing with the Great Crested Grebes in a context of confrontation should help to alleviate territorial conflicts, particularly between neighbours, too. Especially if a situation has been triggered by ecological constraints, it could be expected that social mechanisms to overcome conflicts and that reduce the costs of competition are evolved (Kappeler 2006). Habitat choice and phenotypic plasticity would over evolutionary time periods influence the structure of the community in this sense (Agrawal 2001 in Kappeler 2006). Generations in the far future could go beyond, profiting from genetically profitable changes. Baldwin (1896 in Yeh & Price 2004) suggested that plasticity was essential for population persistence in the new environment. But once the population is established, heritable differences accumulate by natural selection, so that the adaptive phenotype initially achieved by plasticity becomes genetic. However Price et al. (2003 in Yeh & Price 2004) doubt that a trait that is highly plastic is likely to be subject to much divergent selection pressure and it may not become genetically differentiated from the source.

The ultimate aim of reproduction is an increase of fitness by passing on one's genes to as many surviving off-spring as possible. If the maximisation of fitness requires a colonial kind of nesting, the Great Crested Grebes should be inclined towards aggregation, even if this is in contradiction to their territorial wishes and this is aided by phenotypic plasticity. On traditional "colonial" lakes where for generations the nesting of the grebes each year is aggregated, in time, behavioural adaptations in the individuals composing the population would lead to the "anonymous group connections" of Siegel-Causey and Kharitonov displaying an evolved flocking behaviour, and this situation might be reached or be within reach for some locations of Great Crested Grebe colonies. Their spacing would result from evolutions in two opposing factors, namely mutual attraction promoting the clumping and mutual repulsion expressed through aggression and spacing the platforms out (Perrins & Birkhead 1983). The greater habituation to close neighbours would already have contributed to a rather smooth and simultaneous settlement and breeding process by incorporation of first consequential features. Only in habitats where colonies are rather recent or where population pressure is about to trigger a further reduction in the size of the "territories", aggressive behaviour could remain temporarily high. As the density of a population increases, territory size gets smaller, but there is a minimum size beyond which a territory would be too small to support a bird. At the latest at this stage, additional pairs are excluded from the colony and either have to look for alternative sites or become non-breeding floaters (Perrins & Birkhead 1983). The latter could occupy the colonial platforms of early successful breeders later in the season.

The common use of highly protective sites allows a maximisation of the grebes' total fitness, but only under the condition that the possible surplus in fitness is not wasted by persisting aggression. A more territorial approach would only be beneficial in circumstances of food shortage, but it could be annihilated by a more generalized population pressure. In particular, individuals can defend territories only when it is practical for them to do so. Any social system is probably a compromise between the costs and benefits prevailing and can change with the needs of the birds and environmental circumstances (Newton 1998). The differences in the findings and interpretations on colonial breeding in Great Crested Grebes between different authors having studied at different locations would finally have to be explained by differing local conditions. As a consequence, the populations involved could have been at different stages in their move from an entirely territorial nesting scheme to a more colonial type of breeding. Such evolutionary shifts however take time. Moreover, they are not performed simultaneously in all composing populations of a species and they can also be subject to temporary trend reversals.

Biological evolution implies neither a simultaneous coordinated move by all sub-populations of a species nor the persistence of beneficial equilibriums at all stages. It is rather a phenomenon characterized by a tendency for the realized diversity of "character" variation to lag behind the theoretical maximum (Brooks & Wiley 1988 in Siegel-Causey & Kharitonov 1990). For the establishment of colonial breeding, the action of a formation factor alone is not sufficient. Maintenance factors are a higher, more constrained class and may be consequential or independent of colonial behaviour (Siegel-Causey & Kharitonov 1990). The increases in colony densities provoked by the arrival of additional pairs establishing themselves in between early settlers, the still important existence of successful solitary breeding and the absence of unambiguously social interactions in their aggregations clearly demonstrate that the Great Crested Grebe is still far from being an obligate colonial species as defined by Zubakin. The species is today engaged in the development of a more advanced flocking behaviour and an increased group adherence, so that it agrees well with the definition of a nominal colonial breeder. Only in the advanced stage three of coloniality, the minimisation of costs and the maximisation of benefits of social living (Siegel-Causey & Kharitonov 1990) would be achieved by the grebes. To reach this stage, phenotypic plasticity could not be enough, albeit the new selection pressures related to coloniality certainly provoke a move into the right direction. Nevertheless, genetic constraints could limit the potential for adaptation and changing them needs more than a handful of generations.

One question that this survey did not touch upon is how the coloniality of the Great Crested Grebe compares to that of other species inside the family. Over the different grebe species, the breeding strategies vary from fiercely territorial to rather gregarious and even within the same genus, grebe species can differ fundamentally. Generally, we could expect to find in a given lineage the least complex colonial structure in the most primitive taxa and the most complex in the most derived taxa (Siegel-Causey & Kharitonov 1990). However, sociability might be more influenced by habitat constraints than by lineage. A complete analysis of nesting schemes in a phylogenetic context would certainly warrant a more comprehensive and complete picture of the phenomenon of coloniality in grebes.

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