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Author: Konter, André

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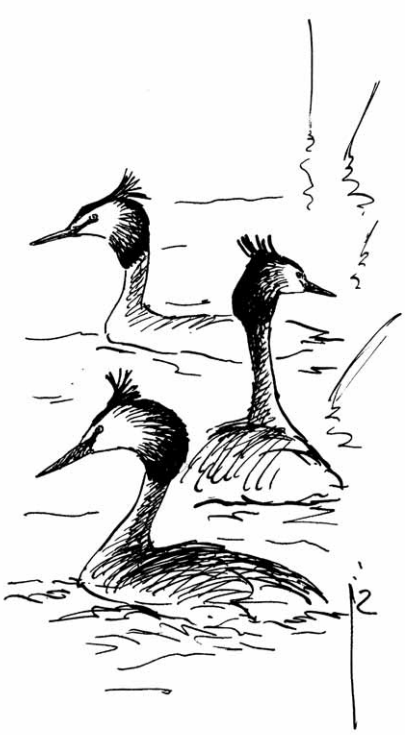
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Seasonal evolution of colonial breeding in the Great Crested Grebe *Podiceps cristatus*: a four years' study at Lake IJssel

André Konter[1]



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A field study at the Dutch IJsselmeer on colonial nesting of Great Crested Grebe *Podiceps cristatus* over four breeding seasons focused on the phenomenon of breeding aggregation. Grebes settled in two types of habitat: 'Bulrush' and 'Reed'. Pairs in Bulrush nested later in the season, and therefore produced smaller clutches, compared to pairs breeding in Reed. Breeding pairs showed high variability in the timing of arrival, nest building and egg laying ('laying date'). Pairs that started nest building early in the season took more time to produce a clutch. They also produced larger clutches, but experienced more egg loss, compared to pairs breeding later in the season. Corrected for laying date, year and habitat, there was no effect of coloniality, as measured by nearest neighbour distance, on clutch size and egg loss. I conclude that colonial breeding in the Great Crested Grebe results from suitable habitat progressively filling-up with breeding pairs, without accruing any reproductive advantages.

Key words: *Podiceps cristatus*, colonial breeding, timing, platform building, nest spacing, clutch size, cuckoldry

[1]45 rue des Romains, L-6478 Echternach; collaborator of the Museum of Natural History, Luxembourg, L-2345 Luxembourg (podiceps@pt.lu)

INTRODUCTION

Bird species vary widely in the size of their breeding territories, in a continuum between two extremes. On the one hand, we find the tightly packed nests of, for instance, Gannets *Sula basana* which have breeding territories limited to little more than the area around the nest that an individual can defend as it incubates. On the other hand, birds of prey defend huge areas that typically include food resources as well as the nest site (Alcock 2001). Colonial breeding is a widespread phenomenon and particularly common among seabirds (e.g. Laridae, Alcidae), herons, egrets (e.g. Ardeidae) and some passerine families (e.g. Plocidae, Leahy 1983, Ligon 1999, Newton 1998, Rockwood 2006). Researchers have proposed several hypotheses which may explain why birds breed in colonies, two of the most popular being the 'Information centre' hypothesis and the 'Dilution effect' hypothesis (Alcock 2001). The 'Information centre' hypothesis states that birds breed in colonies because they benefit from the usage of common feeding grounds. When food distribution varies over time, the best feeding grounds have to be detected, and individuals

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unsuccessful at feeding may follow apparently successful individuals from the colony to the currently rewarding feeding sites. The 'Dilution effect' hypothesis states that individuals benefit from colonial breeding due to an increased protection against predators, e.g. due to dilution or communal anti-predator defence. The ecological and evolutionary reasons for the extent of colonial breeding comparing different species and/or populations, and the effects of variation in colony size on reproductive success remain two highly active research fields for ornithologists.

The present paper concentrates on colonial breeding in the Great Crested Grebe *Podiceps cristatus*. Most grebe species Podicipedidae defend a territory around their nest-site, in which other grebes are not tolerated, and where also other water birds are often harassed. However, the spacing of nests is quite flexible (Fjeldså 2004). The building-up of colonies has been reported for many members of the family, with large variability in the distances between nests. In the highly gregarious Western Grebe *Aechmophorus occidentalis* most nests are in colonies, up to hundreds or even thousands on one lake, with minimum distances between two platforms rarely below 2 m (Storer & Nuechterlein 1992). In the North-American Eared Grebe *P. nigricollis californicus* colony formation starts from a nucleus composed of early grouped platforms (McAllister 1958). Also in the European nominate *P. n. nigricollis* breeding is normally colonial, from two to several hundreds of nests in a colony, with nests as close as 0.5 m (Koop 2003). From the South-American colonial Silvery Grebe *P. occipitalis*, Burger (1974) reported that nest distances were inversely correlated with the number of platforms in the colony, with mean distances of 1.8 m in the largest and 4.3 m in the smallest colonies. The very gregarious and hardly aggressive Hooded Grebe *P. gallardoi* of Argentinean Patagonia normally nests in dense colonies of 5–99 pairs with platforms placed totally open to view on extensive milfoil *Myriophyllum elatinoides* vegetation (Fjeldså 1986, Konter 2001). Semi-colonial breeding on prime nesting substrate has been reported for the territorial Red-necked Grebe *P. grisegena holboellii* for a case of 5–10 pairs building their nests within 50 m total distance (Nuechterlein *et al.* 2003).

The Great Crested Grebe is generally described as a solitary breeder that fiercely defends extended territories during the breeding season. However, examples of aggregated nesting with limited distances between nesting platforms are known from most parts of its range (Vlug 1983, Simmons 1989, Fjeldså 2004, Konter 2005). Here, I present data on reproduction of such a colony at the Dutch IJsselmeer during a four-year study. I focus on the timing of arrival of the grebes, nest initiation, laying and the spatial distribution of nests over time, and explore whether these parameters affect reproductive success. From true colonial birds, one generally expects a high degree of synchrony in dates of settlement and egg laying. The question then arises, what are the reproductive benefits or costs of close breeding in such aggressive birds? Colonial breeding may come about by individuals forced to breed close to neighbours as the season progresses, i.e. close to already occupied nests. In such a scenario, colonial breeding is not expected to benefit individuals in terms of reproductive success. However, if individuals prefer to breed colonially because it pays them in reproduction, close-by breeding of grebes can be expected from the early season onwards. In the latter scenario, the reproductive success of colonial breeding grebes is expected to be higher compared to the success of solitary breeding grebes.

STUDY AREA AND METHODS

Recording of arrival, settlement and clutch initiation of the Great Crested Grebes took place between 16 March and 8 June 2003 (18 days of field work during 10 weekends), 31 March and 19 May 2004 (11 days during 4 weekends), 12 March and 8 May 2005 (23 days during 9 weekends) and 17 March and 7 May 2006 (19 days during 6 weekends) at the Companieshaven of Enkhuizen, a yachting harbour located in the western part of the Dutch Lake IJssel or IJsselmeer. Daily fieldwork lasted on average seven hours. The harbour

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contained three colonies, in the sense of Goc (1986) who arbitrarily used an average distance criterion of 10 meter or less between nest platforms to call a Great Crested Grebe concentration a colony: 'City', 'North' and 'Footbridge'. The latter, subject of the investigations, was subdivided into three areas as follows. Reed I, a stretch of Reed *Phragmites australis* about 100 m long, 2–6 m wide and covering approximately 300 m^2, was followed by an open area of 7 m in length. Reed II, 86 m long, 2–6 m wide and covering 350 m^2, was again separated from the next emergent vegetation by an open stretch of 30 m. Then the Bulrush zone, 1–6 m wide, extended for 72 m covering 200 m^2 with *Typha latifolia*. The surface indications are limited to the vegetated areas available for nesting. Observations were performed from the elevated footbridge at a distance varying between 2 and 10 m from the nesting platforms of the grebes. Disturbance attributable to the monitoring program was judged unimportant, as the birds were accustomed to the presence of humans on the footbridge. For a more complete description of the area, see Konter (2005). Due to Reed cutting in autumn, the vegetated area did not change in aspect or surface from one breeding season to the next, except for 2006 when excavation work inside the harbour led to the dumping of silt on top of the middle part of Reed I, thereby making this part unavailable to the grebes and cutting the zone in two parts. The first part of Reed I was reduced in length to 41 m covering 80 m^2. The next 23 m where then unusable, leaving a length of 38 m and a surface of 175 m^2 available to the grebes in the second part of Reed I. As work was stopped by the end of March, it had otherwise no negative impact on the breeding of the grebes.

In each year and for each day of observation, the platforms present were recorded on a 1:100 map of the area, the chronology of each platform and the progress in nesting was noted. In addition, grebes present inside the harbour were counted (see Konter 2005). Over the four years, 437 breeding events were recorded. The nesting date was defined as the date on which a pair permanently occupied and defended a nesting platform, and started building the nest (1 = 1 January). The nearest neighbour distance was determined on this nesting date, as defined by the distance in meters to the nearest occupied platform. The laying date was defined as the date the female laid her first egg. The time delay was the interval (in days) between the nesting date and laying date. These three parameters were known for all 437 events. Additional data on clutch size and the number of eggs lost before hatching were determined for 381 out of these 437 events. A clutch was considered complete if during at least three days no new eggs were added. Egg loss was noticed either by direct observation or by a reduction in nest content between two visits. Data were analysed with ANOVAs and Generalised Linear Models GLM in SPSS 15.

RESULTS

Timing of arrival and egg laying

In all years, the numbers of Great Crested Grebes present at the Footbridge colony increased from early March until mid-April or early May (Fig. 1). This increase was in line with the total numbers present inside the Companieshaven (Fig. 1). When comparing the total number of adult Great Crested Grebes present in the Footbridge colony to the number of nesting birds based on platform counts (Fig. 1), it appeared that in March a considerable population of yet unsettled grebes was present. In the course of April, more and more pairs settled so that by early May most, if not all grebes had found a place in the colony.

The timing of breeding and reproduction varied across years and habitats (Fig. 2). In general, pairs nesting in the Reed were significantly earlier and produced more eggs compared to pairs nesting in the Bulrush (Table 1). For the subsequent analyses, results were corrected for year and habitat effects (note that the interaction was not significant). Moreover, to correct for differences in the timing of breeding between years, I calculated the adjusted laying date by subtracting the mean of the year from the laying date.

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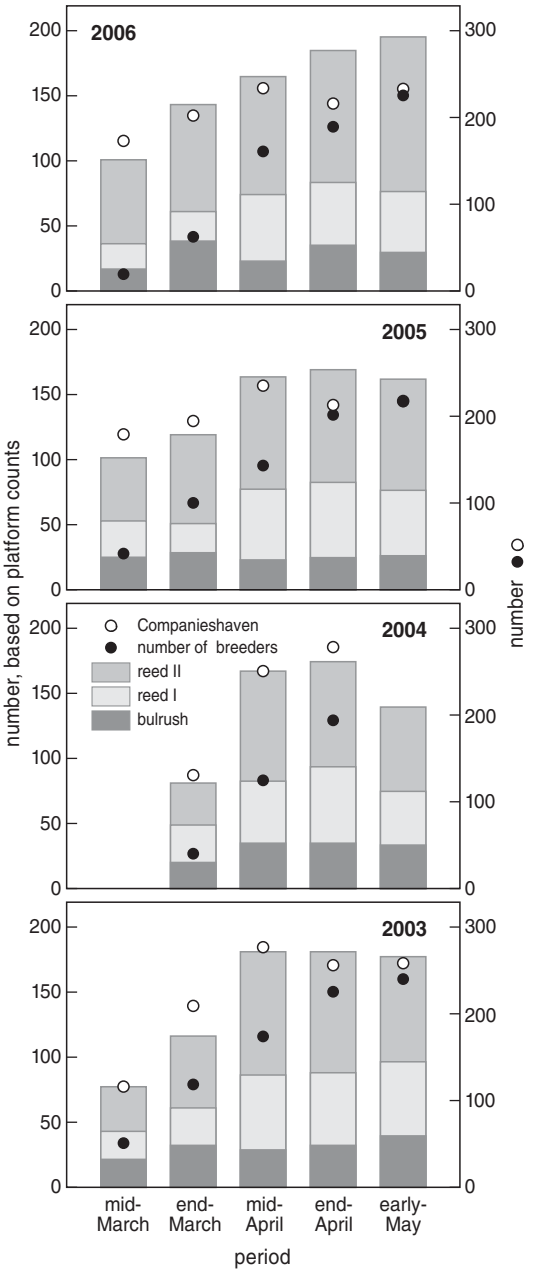


Figure 1. Number of all grebes present at the Footbridge colony (breeders and nonbreeders) and birds at the study area (Companieshaven). The number of breeders present at the three different parts of the main study area (Bulrush, Reed I and Reed II) is based on platform counts.

Early spring distribution of nests

The average nearest neighbour distance NND between platforms of nesting grebes decreased significantly in the course of the season (Fig. 3A, three-way ANOVA effect of nesting date covariate $F_{1,437} = 106.3$, $P < 0.001$). NND did not differ between years ($F_{3,437} = 0.9$, $P = 0.45$), instead was significantly larger in the Bulrush habitat compared to the Reed habitat ($F_{1,437} = 77.3$, $P < 0.001$). Accordingly, nesting densities were higher inside the Reed habitat (data 2004–2006: 14.3, 14.5 and 16.2 platforms per 100 m^2) compared to the Bulrush habitat (9.5, 8.5 and 8.5 platforms per 100 m^2).

The time delay between nest initiation and egg laying was on average 11.9 days (± 9.7 SD, n = 437) and was negatively related to the nesting date (four-way GLM log-link, $\chi^2 = 302.3$, $df = 1$, $P < 0.001$, Fig. 3B). This shows that grebes occupying platforms in the early season delayed egg laying, which enhanced synchronizing of egg laying between grebes. The delay did not depend on NND ($P = 0.15$) or habitat ($P = 0.16$), but did vary significantly among years ($P < 0.001$; see also Fig. 2).

Clutch size and egg loss

Clutch size significantly decreased with adjusted laying date (Fig. 4A, Table 2). Corrected for this effect and yearly differences, clutch size did not differ between pairs breeding in Bulrush and Reed (Table 2), showing that the lower productivity of Bulrush-pairs (Table 1) was due to these pairs laying later in the season. Similarly, the NND did not influence clutch size (Fig. 4B, Table 2).

Egg loss varied among years (2003–2006), with eggs recorded as lost being 7.4%, 4.7%, 14.3% and 5.1%, respectively. The percentages of nests affected in successive years were 28%, 11%, 35% and 15%, respectively. These figures must be considered as minima as losses might have been missed when lost eggs were replaced before a next nest scan. From the total of 144 eggs lost in the four breeding seasons, the highest toll was due to a storm in 2005 (Konter 2007a). As the storm occurred early in the season when most pairs had

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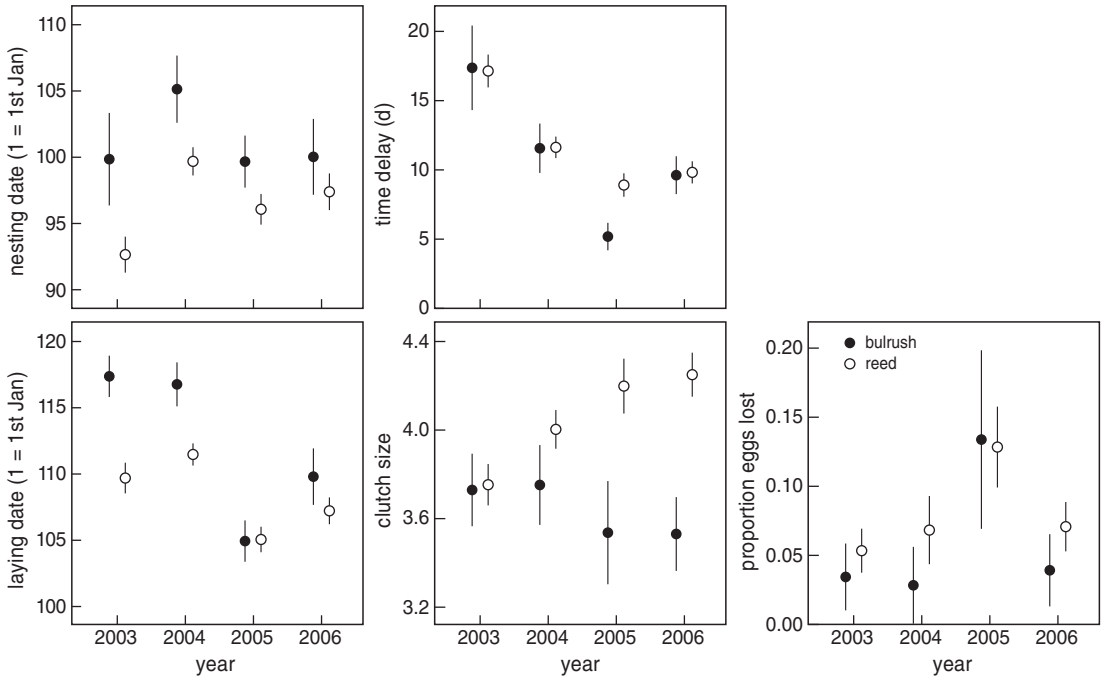


Figure 2. The timing of breeding, clutch size and the proportion of eggs lost varied across years and habitats. Depicted are means with SE. See Table 1 for ANOVAs.

Table 1. The timing of breeding, clutch size and proportion of eggs lost depending on differences between years (2003–2006, *df* = 3), habitats (Bulrush or Reed, *df* = 1) and their interaction (*df* = 3), using separate ANOVAs.

	n	Year		Habitat		Year x Habitat	
		F	*P*	*F*	*P*	*F*	*P*
Nesting date	437	3.0	0.029	9.6	0.002	0.5	0.69
Laying date	437	13.6	<0.001	10.8	0.001	2.3	0.076
Time delay[a]	437	15.6	<0.001	0.6	0.42	0.7	0.56
Clutch size	381	0.4	0.76	11.1	0.001	2.1	0.11
Egg loss[b]	381	1.8	0.14	0.9	0.34	0.1	0.98

[a]Time delay: days between nesting and laying of first egg.
[b]Proportion of eggs lost, arcsine-transformed before analysis.

not yet initiated their clutches, the egg loss was limited and the grebes were able to replace their losses. When corrected for effects of year and laying date (Fig. 4C), egg loss was not related to NND (Fig. 4D) or habitat (Table 2).

Predation was directly recorded for only seven eggs. Coots *Fulica atra* predated six eggs and a Moorhen *Gallinula chloropus* one egg (Konter 2007b). The extent of predation by these two nesting species within the colony might have been

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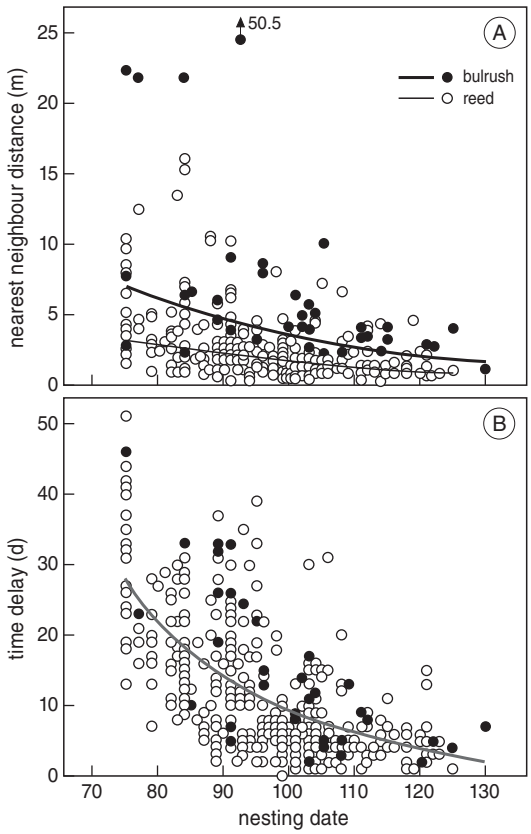


Figure 3. (A) Nearest neighbour distances NND and (B) the time delay (interval between dates of nesting and egg laying) depending on the nesting date and habitat. Both significantly decreased with nesting date (see regression lines), but NND also differed between habitats.

more important as another 65 eggs disappeared for unknown causes. Other potential predators in the colony were Grey Herons *Ardea cinerea*, gulls Laridae and terns Sternidae but no evidence of predation by these species was collected. Two eggs were lost when breeding grebes defended their platform against the intrusion efforts of Coots. At least two eggs were intentionally kicked out of a nest by a grebe, whether by the owner of the platform or an intruder remained unknown. Another ten eggs rolled out of the nest by various reasons. On four occasions, the platform receiving the egg was still so rudimentary that it was unable to withhold its content for long. At least five eggs were abandoned shortly after laying and another ten eggs after hatching of other eggs in the clutch. Some of these eggs may have been infertile but on two occasions a chick was observed to hatch from an abandoned egg. Without care, both chicks died rapidly.

DISCUSSION

Previous studies of colonial nesting in the Great Crested Grebe suggested that colonial and non-colonial birds were birds of different characteristics (Goc 1986, Bukacińska *et al.* 1993), that grouped nesting was related to changing water levels (Podkovyrov 1986), or that the distribution of colonies was depending on suitable microhabitat for nesting and the neighbourhood of Laridae for protection (Blinov *et al.* 1981). Moskal and Marszałek (1986) concluded that colonial nesting was not due to a deficit of breeding habitat, which suggested that birds nested together for a reproductive benefit.

However, Koshelev (1977), Koshelev & Chernichko (1985) and Konter (2005) believed that aggregated nesting was forced upon the grebes by a shortage of nesting sites in relation to food supply. The data presented in this paper support the latter interpretation. Corrected for laying date and habitat differences, clutch size and egg loss did not change with the nearest neighbour distance. Moreover, pairs breeding in Bulrush produced smaller clutches compared to pairs breeding in Reed, and this was due to pairs in Bulrush breeding later in the season, not due to differences in nearest neighbour distances. This suggests that the consistent decrease in nearest neighbour distances through the season, and thus the building-up of small colonies and aggregations, must be due to other reasons than reproductive benefits. After the chicks hatched, the nesting platforms were abandoned, and pairs with chicks showed no interest to stay close to other breeding pairs any longer. On the contrary, pairs with chicks were highly aggressive against other pairs with chicks.

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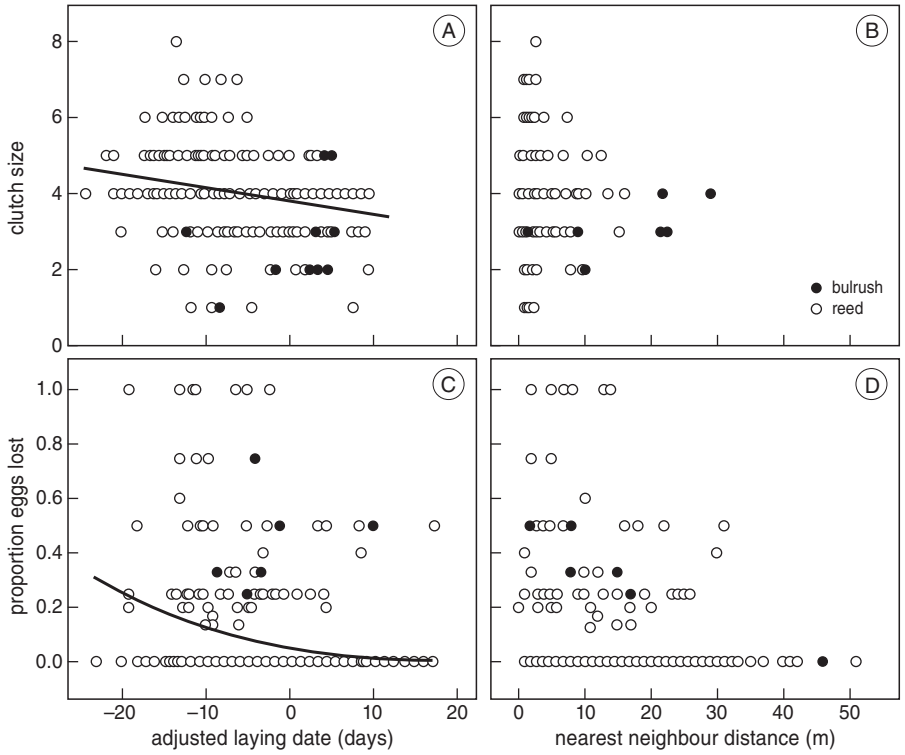


Figure 4. (A, B) Clutch size and (C, D) the proportion of eggs lost depending on (A, C) the adjusted laying date and (B, D) the nearest neighbour distance. See Table 2 for GLMs; adjusted laying date (corrected for differences between years) had significant effects as indicated by the lines.

Table 2. Clutch size and the proportion of eggs lost depending on the adjusted laying date, nearest neighbour distance NND, year and habitat.

	df	Clutch size[d] (n = 381)		Proportion egg loss[e] (n = 381)	
		Wald χ^2	*P*	Wald χ^2	*P*
Adjusted laying date[a]	1	24.7	<0.001	46.1	<0.001
NND	1	0.5	0.46	0.5	0.46
Year[b]	3	13.5	0.004	20.3	<0.001
Habitat[c]	1	2.2	0.13	1.0	0.32

[a]Adjusted laying date = laying date minus the average for that year. [b]Breeding season 2003, 2004, 2005 or 2006. [c]Bulrush or Reed. [d]Fitted as Poisson-distribution with log-link. [e]Number of eggs lost / clutch size fitted as weighted-binomial distribution with probit-link.

Pairs breeding early in the season were more productive and had more time to raise their chicks or produce replacement clutches, compared to pairs breeding late in the season. Many studies found a decline in Great Crested Grebe clutch size through the breeding season (Goc 1986, Ulfvens 1988, Ulenaers & Dhondt 1991, Dittberner 1996), whether nesting colonially or solitary (this date

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Figure 5. An example of two close nests with both Great Crested Grebe pairs incubating (mid-April 2006; photo A. Konter).

effect is a general phenomenon in birds; see review Verhulst & Nilsson 2008). In grebes, the advantage of early breeding needs to be off-set against seasonal changes in risk of flooding, with storms and flooding more likely to occur early in the season. I have shown that early breeders experienced higher egg losses, probably mostly due to more nests being flooded compared to nests active later in the season. This may be one of the reasons why early nesting pairs delayed the production of their first egg (on average ca. 28 days), whereas late laying pairs almost started laying immediately after nest occupation (ca. 3 days delay). Variability in the arrival and timing of breeding of pairs may be due to individuals returning from different wintering grounds, some close by, others far away (Ulenaers & Dhondt 1991).

The nearest neighbour distance progressively decreased through the season, as expected from a passive filling-up of the breeding habitat by nesting pairs (Fig. 5). If early pairs target anti-predator benefits from colonial breeding (effects of active protection or dilution), they should aggregate from the start on, but no evidence was found to support this prediction. Also, grebes could not benefit from other species deterring predators, since they were either absent from the area (e.g. gulls) or too few in numbers and asynchronous breeding (e.g. Coots). While the 'Dilution effect' hypothesis must, therefore, be refuted for the site studied, it may nevertheless hold true for other populations of Great Crested Grebes located at places where predators are more common.

The 'Information centre' hypothesis suggests that grebes benefit from colonial breeding, since grebes may be quicker to locate good fishing areas by following successful foragers. Smelt *Osmerus eperlanus* is the main food of the Great Crested Grebes at Lake IJssel. This species accounts for 40–85% of the total numbers of fish, or for over

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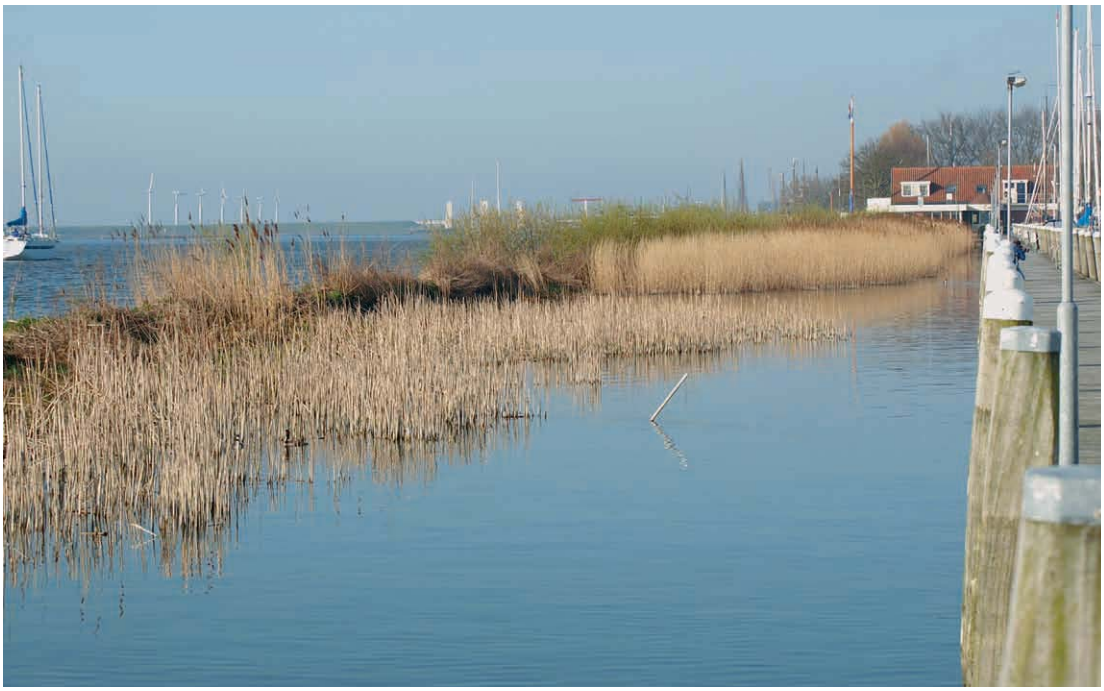


Figure 6. View of the Footbridge colony in early April with Lake IJssel, the dam separating the lake from the harbour, the Bulrush and the Reed areas and the footbridge (from left to right; photo A. Konter).

95% of the fish occurring in the upper layer of the water according to a trawl-sampling effort in 1985–1988 (van Eerden *et al.* 1993). Fish appeared to be distributed regularly with summer Smelt stocks comprised between 30 and 56 kg ha-^{1} (van Eerden *et al.* 1993). Willemsen (1983 in Piersma *et al.* 1997) estimated total fish mass to be 300–500 kg ha-^{1}. The regular distribution of the prey makes the hypothesis of the colony as an information centre unlikely to apply in my study area. Moreover, the grebes fed individually, not in groups, spreading out all over the area. Cooperative hunting as often performed by Cormorants *Phalacrocorax* sp. or witnessed in the African Crested Grebe *P. c. infuscatus* (pers. obs.) has never been observed in Great Crested Grebes at Lake IJssel (pers. obs.).

On Lake IJssel, water levels are quite stable as they are regulated by a lock to the Waddensea. Under such circumstances, flooding of nesting habitat is only due to occasional storms and thus may permit a greater dispersal of platforms. Nevertheless, the habitat available for nesting must be in short supply compared to the food basis offered by the lake, since the Lake IJssel is so large, but breeding is only possible along the shoreline (Fig. 6). This was already the case in the 1960s when Leys *et al.* (1969) found up to 100 colonial nests near Lelystad at a body of water cut from the IJsselmeer. The place was not suitable for breeding; nests were frequently washed away during bad weather and local food was scarce. Adults had to get food from the Lake IJssel by flying back-and-fro, and starvation of chicks was frequent. The average number of fledglings produced per breeding pair was as low as 0.41 (compared to a maximum of 1 in other areas). The abundance of fish at Lake IJssel in combination with a general scarcity of suitable nesting habitat forces the grebes to aggregate their nests, provoking extremely high densities at better quality sites. My data suggest

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that social attraction or other benefits, at least *a priori*, do not determine where the pairs settle.

This study did not directly test the hypothesis that individual grebes prefer to nest in colonies or singly. Nevertheless, I found that early breeders did not aggregate, and corrected for other effects, differences in clutch size and egg loss were due to differences in laying date and not to nearest neighbour distance. Similarly, Bukacińska *et al.* (1993) found that territorial grebes started breeding later in the season with smaller clutches compared to colonial pairs, which is typical of younger breeders. Goc (1986) suggested that late small clutches stemmed from younger females, too. Koshelev (1977) found single nests to be located at untypical places and this could be a hint that such pairs were unable to gain access to a colony, possibly as a consequence of lack of experience or body condition. The general scarcity of nesting sites around Lake IJssel promoted both the aggregation of breeding grebes and competition among settling pairs. Differences in competitive ability among pairs must have an impact on individual breeding strategies, and this could explain why some pairs occupied the less favourable Bulrush habitat, instead of the Reed habitat (Fig. 6). In this sense and given the constraints of the habitat, the individual trait would not be a preference for solitary nesting but an incapability to gain a foothold inside a colony. In addition, even though Moskal and Marszałek (1986) thought breeding habitat to be plentiful available, the differences in reproductive success they found depending on the 'type' of habitat is in line with my interpretation.

From the start of the breeding season onwards, the Great Crested Grebes present tended to use the entire area of vegetation available for platform building and vigorously defended access to the area of their platform. The sustained pressure stemming from yet unsettled grebes let new settlers in between established pairs and distances between neighbouring breeders gradually decreased in time unlike in the Eared Grebe where breeding spreads out from a nucleus (McAllister 1956). Koshelev and Chernichko (1985) also found colony formation to start with a few pairs in loose aggregation at some distance; especially with the start of egg laying, they become less aggressive permitting other pairs to nest in between them. This is also in line with Kuchinskaya (2001) who concluded that numbers occurring on any body of water depend on the feeding basis while their nesting distribution is largely influenced by the extent and the characteristics of the emerging water vegetation used for building platforms.

Henriksen (1996) reported conspecific brood parasitism in the Great Crested Grebe. He found 8% of 51 clutches at Lake Brabant to contain parasitic eggs. Such eggs were never added to complete clutches and the author suggested as a possible explanation that females losing the entire clutch during the egg laying phase could decide to continue laying in foreign nests. In Eared Grebe *Podiceps nigricollis californicus*, Lyon and Everding (1996) and Hill *et al.* (1997) found high rates of intra-specific brood parasitism in densely packed colonies becoming possible through high rates of aggression that leave clutches often unobserved. In the study by Lyon and Everding, non-parasitized nests had full clutches of four eggs or less and the authors concluded that four eggs is representative of a normal full clutch in the species; clutches containing more than four eggs have a high likelihood to stem from more than one female. To some extent, this could also hold true for this study although clutches of seven eggs laid by one female have been reported for the Great Crested Grebe (Bandorf 1982). Although this study only found limited evidence for clutch destruction or egg loss in the context of intra-specific competition, clutch size may have been affected by intra-specific nest parasitism. The often observed seasonal decrease in average egg numbers in colonial Great Crested Grebes does not solely depend on breeding experience or individual conditions of early and late breeders, but it can be biased by cuckoldry and egg loss, especially under high nesting density.

More generally, colonial breeding recorded at Enkhuizen or at other sites does not seem to have any social or otherwise beneficial component for the Great Crested Grebes, on the contrary, they

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bear the risk of increased nest parasitism and egg loss. However, if the birds were to reproduce under favourable conditions, they may not have a choice. In other members of the family, this could be different. Thus, Hooded Grebes in Patagonia profit from aggregated nesting as the construction of large and closely packed platforms offers more protection from wind and wave action (Fjeldså 1986). In the Eared Grebe, high rates of predation on eggs by American Coots *Fulica americana* resulted from more dispersed nesting (Hill *et al.* 1997). Although Western Grebes have higher minimum distances between nests than Great Crested Grebes, they seem to prefer nesting in the vicinity of conspecifics. Could it be that in the grebes colonial nesting follows a fixed evolutionary path? First birds are forced to breed together, then economic benefits add, and finally these may trigger a socialisation of behaviours. That Great Crested Grebes are capable of more gregarious manners is proved by common loafing of territorial breeders or the huge moulting aggregations in autumn. The African subspecies *P. c. infuscatus* may already be one step ahead as it regularly hunts communally (pers. obs.). Perhaps colonial breeding in the nominate Great Crested Grebe, as it exists today, is still at an early evolutionary stage, so to say at the starting point of a more social living together.

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SAMENVATTING

Aan het IJsselmeer bij Lelystad broeden Futen *Podiceps cristatus*, een soort die bekend staat om geringe verdraagzaamheid tegenover soortgenoten, in kolonies. In de onderhavige studie is onderzocht waarom ze soms in kolonies broeden. De Futen broedden in het onderzoeksgebied in twee habitattypes: Riet *Phragmites australis* en plekken die door Grote Lisdodde *Typha latifolia* werden gedomineerd. Stroken met Lisdodde lijken een tweederangs habitat. De Futen begonnen er later eieren te leggen dan in Riet en de legsels waren er kleiner. Tussen paren bestond grote variatie in het tijdstip van aankomst in de kolonie, en daarmee ook in het moment van nestbouw en eileg. Paren die vroeg in het seizoen een nest maakten, deden er langer over om het legsel te voltooien, ook als rekening gehouden werd met het groter aantal eieren dat ze produceerden. Bovendien hadden vroege vogels meer te lijden van eiverlies dan Futen die later begonnen. Wanneer rekening gehouden werd met legdatum, jaar en habitat waarin het nest lag, bleek er geen verband te bestaan tussen de afstand tot de naaste buren en legselgrootte en eiverlies. Op grond hiervan wordt geconcludeerd dat broeden in kolonies door Futen voortkomt uit gebrek aan geschikte nestplaatsen, zonder dat het groepsgewijs nestelen de kansen op nakomelingen vergroot. (DH)

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