

Nest characteristics and nest survival in the horned grebe *Podiceps auritus* and great crested grebe *Podiceps cristatus* in a Finnish archipelago

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Ulfvens, J. 1988: Nest characteristics and nest survival in the horned grebe *Podiceps auritus* and great crested grebe *Podiceps cristatus* in a Finnish archipelago. — Ann. Zool. Fennici 25:293–298.

The study is based on three observations: (1) grebes expanding into the archipelagoes of the Baltic Sea experience a straining water regime, as the water level amplitude is higher than in lakes (up to 75 cm during the breeding season in the area studied); (2) grebes breeding in the archipelago seem to build larger nests than in lakes; and (3) larger nests seem to survive better in the archipelago than small nests.

Successful and flooded nests seemed to be structurally similar, although on average successful nests were significantly larger. However, among the flooded nests there were more atypical nest types than among the successful nests; this is probably due to a local lack of nest material and suitable nest sites, but could not be related to any differences in nesting habitat. The large nests are probably favourable as they can withstand wave action and rising sea water better. The greater investment in nest-building among grebes in the archipelago is probably not due to a specific “strategy”, but to the mechanical reactions to the continuous changes in sea water level.

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1. Introduction

A common feature of grebes is their habit of building floating or semi-floating nest-rafts, which is a sophisticated way of adapting to the morphological specialization of the birds and of protecting the clutch against terrestrial predators. Nevertheless, the floating nests suffer frequent losses during periods of adverse weather, e.g. storms or heavy rain (cf. Chabreck 1963, De Smet 1987, Glover 1953).

During recent decades grebes have colonized large areas of the archipelago in the Baltic Sea (see Andersson & Staav 1980). In Finland, the great crested grebe *Podiceps cristatus* in particular has increased markedly in numbers and locally extended its range throughout the archipelago (see Lammi 1983). The red-necked grebe *Podiceps grisegena*, and particularly the horned grebe *Podiceps auritus*, have also local populations breeding in the archipelago (cf. Multala 1983, Kylänpää 1984). These grebe populations are subjected to a considerably more unstable

water regime than in the birds' more traditional habitats on lakes and ponds. The water level amplitude in the archipelago during the breeding season is as much as 75 cm. As a consequence, significantly more eggs are lost due to flooding in horned and great crested grebes breeding in the archipelago than in grebes breeding on lakes, and flooding is the major cause of egg loss in grebes in the archipelago (Ulfvens 1988).

In an earlier paper (Ulfvens 1988), I found that those nests that survived in horned and great crested grebes breeding in the archipelago were larger than flooded nests. This raises the question as to whether grebes have adapted to the unstable water regime in the archipelago by building larger and perhaps different kinds of nests from those in more traditional habitats.

The main objective of this study therefore is to answer the questions: (1) Is there a real difference in nest-building between successful and flooded nests; and (2) How does nest quality affect the survival of the nests?

2. Study area, material and methods

This study forms part of a long-term population study of horned and great crested grebes carried out in 1979–1986 in four different study areas along the coast of Ostrobothnia, western Finland (red-necked grebes are scarce in this area and were not included in the study).

The observations analysed here were made in the main study area in the Korsnäs archipelago (62°49'N, 21°10'E). The area is about 20 km² in extent and consists of two shallow bays (maximum water depth about 4 m), which are surrounded by small groups of low moraine islets.

In May–August, the amplitude of the sea water level was 58–76 and 55–69 cm, respectively, at two closely lying measuring points along the coast (Lisitzin 1959). During eight years of study in the Korsnäs archipelago, I recorded an average amplitude of 64 cm in May–August, a figure significantly larger than that for the lakes (e.g. 19 cm in unregulated lakes; for details, see Ulfvén 1988).

Conventional nest measurements (nest diameter, total height and height above the water line; cf. Melde 1973) were recorded to the nearest cm. The nests were usually monitored during the whole incubation period, or until they failed. The material includes 142 nests of the horned grebe and 446 nests of the great crested grebe.

In order to quantify the nests' ability to rise and fall with the sea water, a measurement which I call the "floating amplitude" was introduced. It was measured simply by rising the nest with one hand and measuring the maximum distance that the nest could move upwards without becoming unattached. The floating amplitudes were recorded using the scale 0, 1, 3, 5, 7, 10, 15 and >20 cm. The precision of the measurements may have varied (e.g. due to the practical difficulty involved in lifting the nests and measuring their amplitude at the same time), which should be kept in mind when interpreting results from comparisons between small samples.

A methodological problem arises owing to the fact that the nest measurements change during incubation as nest material is added to the nest (this applies to both species observed; see Fjeldså 1973, Ulfvén 1988, Uusitalo 1969). In order to compare nest measurements for different groups of nests, the records should either be made during the same part of the incubation period or be equally distributed over the whole incubation period. In practice, the latter method has to be used in order to obtain meaningful samples. I tested the correspondence of the times of measuring successful and flooded nests (the measurements for the flooded nests are those recorded prior to failure) in both species and there was no significant difference regarding their respective distribution over the incubation period (in the horned grebe: $\chi^2=3.8$, $df=5$, $P=0.58$; in the great crested grebe: $\chi^2=10.8$, $df=5$, $P=0.06$). Thus the series of nest measurements should be comparable with each other.

For the multiple regression analysis the survival of the nests was used as a constant, and successful nests were given the value 1, whereas flooded nests were equal to 0.

Nest types were mainly adopted from Clase et al. (1960) and Fjeldså (1973), who found at least four different nest types in the horned grebe ssp. *arcticus* (see Table 2 for definitions).

The term "successful" is here used for nests that survived without becoming flooded, but does not exclude egg losses due to other causes (these losses were specified by Ulfvén 1988).

Table 1. Nest characteristics of successful and flooded nests in the horned grebe and the great crested grebe (measurements in cm; means \pm SD). Sample sizes in brackets. Differences between success and species tested with *t*-test. The floating amplitudes are treated in the text.

	Horned grebe	<i>P</i>	Great crested grebe
Nest diameter			
Successful	53.7 \pm 10.3 (125)	<0.001	72.8 \pm 12.3 (394)
<i>P</i>	<0.01		<0.01
Flooded	45.7 \pm 13.1 (17)	<0.001	67.1 \pm 14.3 (52)
Total nest height			
Successful	28.3 \pm 7.4 (119)	<0.05	26.7 \pm 7.3 (385)
<i>P</i>	<0.05		<0.05
Flooded	33.5 \pm 10.8 (15)	<0.01	23.3 \pm 8.8 (37)
Height over water line			
Successful	8.4 \pm 3.9 (120)	<0.001	11.8 \pm 5.6 (387)
<i>P</i>	<0.001		<0.001
Flooded	4.6 \pm 2.6 (15)	<0.001	8.9 \pm 5.1 (37)

3. Results

3.1. Nest dimensions of successful and flooded nests

In both species, the successful nests differed from the flooded ones (Table 1). In general, the successful nests were larger than the flooded nests (this does not, however, apply to total nest height in the horned grebe).

The pattern is the same when all the measurements for the flooded nests (i.e. also those that were obtained during several visits prior to flooding) are included; the differences between the two groups of nests are generally more accentuated (e.g. $P<0.001$ for nest diameter in the great crested grebe), as the nests are mostly smaller early on in the incubation period (see below).

The floating amplitudes of successful nests and flooded nests showed no difference in the great crested grebe ($\chi^2=5.5$, $df=6$, $P=0.48$); this was also the case when all measurements for the flooded nests were included ($\chi^2=10.3$, $df=7$, $P=0.17$). In the horned grebe, on the other hand, there were significant differences in both cases, successful nests showing smaller floating amplitudes (χ^2 tests, $P<0.01$). However, the sample was small ($n=9$).

3.2. Nest characteristics of the two species

On the whole the nests of the great crested grebe were larger than those of the horned grebe (Table 1). However, the total nest height was larger for both successful and lost nests in the horned grebe. The floating amplitudes of the great crested grebe nests were significantly smaller, both in successful and flooded nests, than in the horned grebe (successful nests: $\chi^2=61.0$, $df=6$, $P<0.001$; flooded nests: $\chi^2=14.6$, $df=6$, $P<0.05$). In the latter case the sample was small ($n=9$).

Among successful nests in both species, the nest characteristics relate to each other in a nearly similar way: the nest diameter correlates significantly with the total height ($P<0.001$ in both species) and with the height over the water line ($P<0.001$ in both species), and negatively with the floating amplitude ($P<0.001$ in both species); the total height is not significantly correlated with the height over the water ($P=0.28$ in the great crested grebe; $P=0.43$ in the horned grebe); the total height and the height over the waterline are negatively correlated with the floating amplitude ($P<0.05$ in the great crested grebe, $P=0.09$ in the horned grebe in respect of the former relation; $P<0.001$ for both species in respect of the latter).

The trends are similar in the flooded nests (tests made only on the great crested grebe because of the smallness of the sample in the horned grebe), although the correlations for most relations are not significant (in contrast, $P<0.05$ for the correlation of nest diameter against total nest height).

A multiple regression analysis showed that the nest measurements have very low partial regression coefficients (in the horned grebe: 0.00069–0.011; in the great crested grebe: 0.00095–0.0053). Only the coefficients for the total nest height (horned grebe) and the height over the water line were significant (great crested grebe) ($P<0.05$; see also Table 1). Together the differences in the four nest measurements between successful and flooded nests explained only 13.9% of the survival of the nests in the horned grebe and 2.2% in the great crested grebe. The significance of the multiple regression analysis was $F=4.9$, $P<0.001$ in the horned grebe and $F=2.22$, $P=0.05$ in the great crested grebe.

3.3. Relations between nest and shore types

The barrenness of the shores in the study area differs greatly and increases towards the more

Table 2. Frequencies (percent in brackets) of nest types among the successful and flooded nests of the horned grebe and the great crested grebe. The nest types are: floating nest (usually anchored in helophytes), bottom nest (usually not anchored in helophytes), stone top nest (built on top of stones or boulders), shore nest (built on the bottom at the waterline or situated on dry land).

Nest types	Horned grebe		Great crested grebe	
	Successful	Flooded	Successful	Flooded
Floating	71 (73.2)	6 (35.3)	210 (68.6)	38 (61.3)
Bottom	25 (25.8)	10 (58.8)	79 (25.8)	9 (14.5)
Stone top	1 (1.0)	1 (5.9)	11 (3.6)	12 (19.4)
Shore	0	0	6 (2.0)	3 (4.8)
Totals	97	17	306	62

maritime parts of the area (see Ulfvens 1988). Thus, there are both local and gradual differences in the availability of nest material (barren boulder shores generally offer no large stands of helophytes). This might be reflected in the flooded nests, if these nests were situated at more barren sites than the successful nests.

I tested this by comparing the nest types represented in the two groups of nests. In both species there was a significantly higher number of nest types 2–4 among the flooded nests than among the successful ones (in the horned grebe: $\chi^2=10.2$, $df=2$, $P<0.01$; in the great crested grebe: $\chi^2=25.4$, $df=3$, $P<0.001$; see Table 2). However, in relation to habitat the flooded nests did not differ from the successful ones; on average they were not situated on more barren stony or boulder-strewn shores (for habitat classification, see Ulfvens 1988) than the nests that survived (in the horned grebe: $\chi^2=9.0$, $df=5$, $P=0.11$; in the great crested grebe: $\chi^2=7.2$, $df=8$, $P=0.52$).

Neither did the flooded nests seem to be situated at more exposed sites than the successful ones. The nests grow in size but their floating amplitude decreases during the incubation period, and in both species they are markedly larger in the archipelago than on nearby lakes (for details, see Ulfvens 1988).

4. Discussion

4.1. Water levels

Nest-building in grebes has been well studied from a structural and qualitative point of view (e.g.

Ahlén 1966, Clase et al. 1960, Fjeldså 1973, Leys & de Wilde 1968, Melde 1973, Vlug 1983). No study has dealt in detail with the survival value of different nest types in differing environmental conditions (however, see Fjeldså 1986). Yet an unstable water regime, e.g. in the archipelagoes of the Baltic, is a major constraint to breeding in grebes, which is reflected in the high and variable rate of egg losses caused by flooding (Ulfvens 1988).

During episodes of rising sea water level, large shore areas on islets in the Finnish archipelago may be flooded, causing large-scale nest losses among several species of waterbirds (cf. Merilä et al. 1975). Thus it is not surprising to find that many waterbirds (including grebes; Broekhuysen & Frost 1968) commence to elevate their nests on such occasions (cf. von Haartman 1984, Merilä et al. 1975, 1981); this behaviour also saves some nests from flooding.

4.2. Nest structure in the two species

This study shows that size differences exist between successful and flooded nests in grebes breeding in the archipelago of W Finland. The survival of the nests seems to be correlated with this difference; the nests "survive" better the larger they are.

In both species studied, both successful and flooded nests were, on average, structurally similar. For instance, it is easily understood that a higher nest needs to be stabilized by adding to its diameter, and that large nests lose some of their floating amplitude as a consequence of greater weight (this may also be caused by the fact that the air-filled stems become water-logged as incubation proceeds).

However, there is one puzzling difference between the nest measurements in the great crested and horned grebes: nests of the horned grebe have a significantly larger total height (the floating amplitudes are also higher, but this is clearly a consequence of the smaller overall nest size in the horned grebe). This difference may be understood as resulting from the differences in habitat selection in the two species: the horned grebe breeds on shores with a more luxuriant vegetation. Thus, horned grebes have access to nest sites that offer both dense reeds in which to anchor the nest and an abundance of nest-building materials, and they may build higher nests than the great crested grebes in more sterile habitats.

4.3. Nest type differences

The difference in the nest type distribution of successful and flooded nests may be explained in a similar way to the above. Typical floating nests are usually found at luxuriant sites. On sterile shores in exposed areas of the archipelago there are, however, no such facilities and the nests have to be built at other kinds of sites (stones, boulders or the shore). As the shores are often markedly sterile, there is also a lack of nest-building material and consequently the nests in the offshore areas are mostly smaller than those in inshore areas (see Ulfvens 1988).

The study revealed, however, no difference as regards the general shore type of the successful and flooded nests, which may seem contradictory to this interpretation; but large differences exist in the abundance of helophytes even within small areas of the same shore type, owing to differences in the degree of exposure of the shores.

4.4. The survival value of large nests

We may easily understand that large nests are least liable to be lost during episodes of inclement weather. These nests are often the highest, so that flooding of the eggs is less probable. They also possess a large mass, and this may be favourable with respect to the wave action, which may be violent on open shores during cyclonic depressions. As high winds from the south and southwest often accompany the rising sea water level in early summer, the large nests are advantageous from at least these two points of view.

It is therefore not surprising to find that the nests in both the horned grebe and the great crested grebe on the whole are larger in the archipelago than in lake habitats (for comparisons from Ostrobothnia, cf. Ulfvens 1988; see also Fjeldså 1973, Melde 1973, Lammi 1985, Olsoni 1928, Uusitalo 1969). We might interpret such a difference as an adaptation to the unstable water regime in the archipelago, but I rather think it is the result of an ever-present plasticity in the nest-building behaviour of grebes. As the sea water level changes almost constantly in the archipelago, this may stimulate continuous and intense nest-building in the grebes breeding along the coast; consequently, the grebes in the archipelago invest more in nest-building than do grebes on lakes,

although nest-building continues during the whole incubation period in both habitats.

The multiple regression analysis showed, however, that the differences between nest measurements of successful and flooded nests accounted for the survival of the nests only to a minor degree. This might indicate that it would not be especially important for grebes in the archipelago to build large nests.

The result of the analysis should, in my opinion, be understood in two ways: (1) regardless of their qualities nests may be destroyed during episodes of inclement weather; and (2) the selection of protected nest sites is of primary importance.

The first statement is easy to understand, as it is a fact that some summer storms cause extremely high water level changes (up to 50–60 cm in one or two days). However, investment in large nests is certainly important *per se* also with regard to smaller, but less disastrous changes in the sea water level (such

changes occur 2–4 times during the main breeding period in May–July; cf. Ulfvens 1988).

The latter explanation is also conceivable, as the archipelago studied generally offers protected micro-habitats (such as small bays or impounded areas behind ridges of stones or boulders) and the great crested grebe pairs breeding in the sterile offshore areas clearly use such places as nesting sites (Ulfvens 1988). However, the occurrence of extensive nest losses in waterbirds, as well as the very great annual variations in the egg losses due to flooding in grebes in the archipelago (see Ulfvens 1988), reveal that the present limits of accommodation of the birds are sometimes exceeded.

Acknowledgements. I am indebted to Jon Fjeldså, Esa Lammi, Hans Källander, Samuel Panelius, Veikko Salonen and an anonymous referee for discussions and comments on the manuscript.

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Received 20.IV.1988

Printed 30.XII.1988