

Offshore breeding in the Great Crested Grebe *Podiceps cristatus*: two offshore areas examined in relation to an inshore area in western Finland

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Offshore areas in the Baltic Sea offer extreme conditions for breeding Great Crested Grebes (e.g. lack of helophytes, strong wave action, and high sea water amplitudes). Yet nowadays Great Crested Grebes nest fairly commonly in offshore archipelagoes in both Finland and Sweden. In this study several breeding parameters were compared in Great Crested Grebes nesting in a rocky and in a boulder-rich moraine archipelago in western Finland. The breeding of offshore grebes is on average successful (1.55–1.60 young per pair and year) due to such factors as protection from larid colonies, good availability of food and opportunistic modifications of the breeding. However, the egg-laying seems to be clearly later than in a traditional habitat, and the habitat and nest site selection differs between the areas studied. Areas with irregular shores may offer grebes protected microhabitats, which promotes the exploitation of even very barren archipelagoes.

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Introduction

Offshore breeding in the archipelagoes of the Baltic Sea is nowadays common in several bird species whose traditional habitats are shallow coastal bays or even eutrophic bird lakes. Species belonging to this group are, for instance, the Black-headed Gull *Larus ridibundus*, the Mute Swan *Cygnus olor*, the Great Crested Grebe *Podiceps cristatus* and several dabbling ducks (for references, see Ulfvens 1988).

Some of the species have colonized the offshore areas fairly recently, apparently due to a population increase in the birds' traditional habitats and to eutrophication of the archipelago, which facilitates nest building and feeding even in offshore areas (see von Haartman 1984).

The archipelago differs both geomorphologically and ecologically from eutrophic lakes. Thus it is not surprising that many of the new archipelago birds meet straining conditions, which reduce their breeding performance (e.g. Hildén 1964). In some species, failure to become established on certain types of islets have been noted (Bergman 1953, Kilpi 1984).

However, in an earlier paper on grebes' ecology I found that the Great Crested Grebe exploits even very barren offshore areas successfully, and that its net production of young in these areas does not differ

markedly from that in an inshore area (Ulfvens 1988). This may seem surprising when we consider the difficulties that high waves or rapid changes in the sea water level may cause for birds that build their nests in the water or near the shoreline.

Great Crested Grebes are quite numerous in some archipelagoes today; in the archipelago off Stockholm, for instance, there were about 3 700 Great Crested Grebe pairs in the mid-1970s, and of these about 110 pairs bred on isolated groups of offshore islets (Andersson & Staaav 1980). Great Crested Grebes breeding in the archipelago must thus be able to cope with the vagaries of this habitat (unless the offshore populations are maintained solely by immigration).

In this paper I summarize my observations of the Great Crested Grebe made in two archipelago areas off the Finnish west coast. I looked for possible differences related to nesting between grebe populations in archipelagoes that clearly differ geomorphologically.

Study areas, material and methods

The observations were chiefly made in the offshore areas of Bergö and Kaldonskär in southern Os-

trobothnia, W Finland, in 1983–1986. Some data from 1987–1988 are also included.

The Bergö area (approximately 63°N, 20°55'E) is a vast offshore archipelago, about 150 km² in extent, in the westernmost part of the communes of Korsnäs and Malax/Maalathi. It consists of several hundred of small skerries, mainly with stones or boulders (maximum diameter up to 10 m) along the shores. The shores are irregular, which gives a labyrinthic structure to most of the island groups; thus there are many small protected bays behind ridges of stones or boulders. There are also some large central islands, in which the protected bays have clear mainland features. Within the groups of skerries the water is seldom deeper than 3–4 m.

The Kaldonskär area (approximately 62°26'N, 21°07'E) is situated in the commune of Närpes/Närpiö, about 60 km south of the Bergö area. This archipelago, about 16 km² in extent, has an inner part with some larger forested islands, mainly with rocky shores. The outer part consists of swarms of polished rock islets around a forested central island. The islets are generally treeless and have relatively steep rocky shores. Along and between some islets are deposits of loose moraine. Between the islets the water depth is usually less than 5 m. The area is mainly representative of the rocky type of archipelago found in the Archipelago Sea and Stockholm archipelago.

In the Bergö area, Great Crested Grebes started breeding in some numbers in the late 1970s (Ulfvens 1988). From Kaldonskär, no information on the colonization by grebes is available.

The methods have been explained in detail elsewhere (Ulfvens 1988). Here, I only wish to mention that two measurements, called the floating amplitude of the nests and the exposition index, were introduced to quantify the ability of the nest to sink and rise with the water level and to quantify the exposure of the nests to hard winds and open water areas. One or two censuses were made in mid-June and one or two in late July or early August (for details, see Ulfvens 1988).

The term "net result" here refers to the number of young fledged for each pair that were encountered with eggs. It is an estimate that was calculated as follows: from the number of eggs laid in each area a 41% deduction was made for egg mortality and a 40% deduction for chick mortality. The following result was then divided by the number of pairs observed to have eggs. I assume that the figures for egg and chick mortality are approximately the same as in the inshore

archipelago of Korsnäs (Ulfvens 1988); no other available data have been published.

In Bergö, the number of pairs recorded totals 122 for the four years of study, and in Kaldonskär 33.

Results

The main results (Table 1) will be commented upon in the discussion. Here comments are given only on some points:

Firstly, comparison of the distribution among breeding habitats is awkward, as most of the "stony" shores in Kaldonskär differ from those in Bergö; in Kaldonskär there are mostly scattered stones along the shores of rocky islets. Therefore up to 80–90% of the nests in Kaldonskär are situated along chiefly rocky islets. The difference between the habitats used in the two areas is thus clear (for data on the availability of habitats, see Ulfvens 1988, Table 2).

Secondly, the nests in Kaldonskär lie in shallow water, in consequence of the grebes' habit of nesting near the shore in this area. In Bergö, the grebes often build their nest on a stone or a boulder at the waterline some metres off the shore.

Thirdly, the proportion of nests in protected microhabitats (defined as sites exposed to wind from at most two directions, and a stretch of open water of less than 20 m) is significantly higher in Bergö, which naturally is reflected in the lower exposition indices in this area.

It should also be noted that almost all the grebe pairs are associated with larids; in a typical Finnish lake, the corresponding proportion is only 20–25% (Esa Lammi, pers. comm.). The nests in both Bergö and Kaldonskär usually have no vegetation cover, and the grebes breed near the shoreline more often than in the traditional habitats (cf. Ulfvens 1988). The nests differ clearly from nests in traditional habitats: the offshore nests are higher above the waterline and their floating amplitude is lower. This is the result of a shortage of air-filled plant stems, because of which the nests cannot adjust to changes in the water level, but have to be enlarged instead.

It was not possible to determine the mean laying date of the offshore grebes, as most of the clutches were completed when found. However, up to 55% of the clutches in Bergö had been started at a late date, in mid-June or even later. In an inshore area in Ostrobothnia the mean laying date was 25–26 May (Ulfvens 1988).

Table 1. Nest site characteristics and reproductive success of the Great Crested Grebe populations in the Bergö and Kaldonskär offshore archipelagoes. Means \pm SD indicated when possible. The sample sizes are in parentheses. Only completed clutches are included. The statistical tests used are indicated in parentheses after the P value (t=t-test, $\chi^2=\chi^2$ test, U=Mann-Whitney U-test). All P values are two-tailed.

	Bergö	Kaldonskär	P	
Habitat distribution	(84)	(26)		
— mud shore	1%	4%		
— stone shore	22%	77%	<0.001	(χ^2)
— boulder shore	77%	0%		
— rock shore	0%	19%		
Nest site distribution				
— water depth (cm)	30.3 \pm 18.1 (72)	14.5 \pm 12.9 (24)	<0.001	(t)
— distance to the shoreline (m)	3.4 \pm 4.2 (75)	1.9 \pm 2.3 (25)	0.08	(t)
Exposition indices	16.7 \pm 24.9 (66)	39.9 \pm 30.6 (26)	<0.001	(U)
Nests in protected microhabitats	80% (66)	54% (26)	<0.05	(χ^2)
Nests near the shoreline (<0.5 m)	28% (75)	40% (25)	0.26	(χ^2)
Nests without cover	91% (76)	76% (25)	0.06	(χ^2)
Frequency of associations with larids	96% (94)	97% (29)	0.85	(χ^2)
Nest types	(76)	(25)		
— floating nest	0%	0%		
— bottom nest	20%	28%	0.11	(χ^2)
— stone top nest	70%	48%		
— shore nest	10%	24%		
Nest sizes				
— diameter (cm)	61.1 \pm 12.7 (65)	70.5 \pm 19.3 (28)	<0.05	(t)
— total height (cm)	20.6 \pm 11.2 (63)	16.1 \pm 9.6 (28)	<0.05	(t)
— height above the waterline (cm)	13.0 \pm 7.3 (63)	15.4 \pm 4.3 (28)	<0.05	(t)
— floating amplitude (cm)	0.4 \pm 0.7 (62)	0.2 \pm 0.4 (28)	0.36	(χ^2)
Clutch size	4.39 \pm 0.82 (38)	4.53 \pm 0.99 (15)	0.56	(t)
Brood size	3.25 \pm 1.04 (8)	2.19 \pm 1.06 (26)	<0.05	(t)
Net result (number of young per breeding pair and year)	1.55	1.60		

Discussion

Several explanations have been proposed for the poor breeding outcome in new archipelago birds. In the Black-headed Gull, for instance, steep shores in some areas may prevent the young from returning to their breeding skerry after they have fled out on to the water (Bergman 1953). In the Mute Swan, offshore pairs may be faced with a food shortage, which in combination with other constraints results in small broods (Tenovuo 1976).

Hildén (1964; see also Koskimies 1957) presented extensive data sets on the breeding result of several dabbling and diving ducks in an offshore archipelago

in the Finnish Quark. His conclusions were that the broods are smaller, the proportion of hens that lose their entire brood is greater and the annual variations in the breeding result are wider than in inland waters. This may be connected with several characteristics of the offshore archipelago: spells of chilly weather with high waves lead to a lowered surface water temperature and poorer feeding conditions for the young, and large gulls and diseases may deplete the broods.

For the Great Crested Grebe, the offshore areas are "technically" more difficult for breeding than the traditional habitats. There are often no helophytes which could be used to anchor the nests in or to protect the nests from predators, and the open water areas

are large enough to allow strong wave action and frequent destruction of nests at the waterline.

The lack of protection from helophytes is obvious in both areas studied (Table 1) and could result in high egg predation (cf. Salonen & Penttinen 1988; see also von Haartman 1975, Tenovuo 1963). However, the risk of frequent egg predation is clearly reduced and perhaps compensated for by the common association with terns and gulls (Ulfvens 1988).

In the Bergö area many of the offshore Great Crested Grebes start breeding late, sometimes only a week before midsummer. This is presumably caused by the fact that many suitable nest sites are inaccessible earlier in the summer when the sea water level is usually low (Ulfvens 1988).

Yet the nesting outcome of Great Crested Grebes breeding in the archipelago is generally good, and the broods that I observed in the two offshore areas did not differ significantly between years (data from both areas pooled; F-test, $p=0.8$). In contrast to most other waterbirds, the grebes carry their young on their backs even for several weeks. Grebe young are thus protected against attack by large gulls and kept warm in cold weather. Other factors that may contribute to the success are good availability of food (Lammi & Ulfvens 1988), a long breeding season, opportunistic habitat selection and selective learning to use atypical nest sites (cf. Ulfvens 1988).

In fact, the net result in an inshore area in Ostrobothnia was 1.55 young per pair and year (1.59 according to the Mayfield method; Ulfvens 1988), which is practically the same as in the two offshore areas studied. Even large grebe broods may survive in the offshore areas; I observed several broods with three or four well-grown young. This does not, however, prove that the mean result is good, as an unknown proportion of females may have failed to produce young.

The net figures presented here are only estimates. It is possible that the figure for average egg mortality includes the females that lost their nests and produced no young, but some of the unsuccessful females that deserted one of my study areas may have re-nested in another area. Thus it is not possible to determine the net result more precisely at present.

When this is borne in mind, it seems that differences in the geomorphology of certain archipelagoes do not necessarily lead to differences in the net result of breeding in Great Crested Grebes. In contrast, the habitat and nest site distribution and the nest building are clearly affected.

The modifications of the breeding in response to the differing geomorphology certainly conform to expectation, but I wish to emphasize that grebe pairs breeding in the barren boulder-rich archipelago in Bergö usually succeed in finding protected microhabitats for their nests. This is an important observation, as it may imply that moraine archipelagoes with an irregular shore configuration are more suitable for breeding grebes than groups of rocky islets with more regular shores. The benefit is presumably accentuated in extreme situations with hard winds and high waves, when the most exposed nests can be demolished, while nests in protected sites may survive.

The process of colonization of offshore areas by Great Crested Grebes is taking place *ad oculos* and deserves attention as an example of how animals may adjust their ecological amplitude to accord with local conditions.

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Sammanfattning: Skäggdoppingens häckning i ytterskärgården i Österbotten

Hög vågbildning, stora vattenståndsväxlingar och brist på helofyter är några faktorer som gör att ytterskärgården är en extremt påfrestande häckningsmiljö för skäggdoppingar. Trots allt förekommer numera häckande skäggdoppingar rätt allmänt i ytterskärgårdar både i Finland och Sverige. Till exempel i Stockholms skärgård fanns det under åren 1974–75 ca 3 700 skäggdoppingspar, av vilka minst 110 häckade i ytterskärgårdsmiljö.

Denna undersökning behandlar skillnader i häckningsparametrar hos skäggdoppingar i ytterskärgårdarna i Bergö och Kaldonskär i södra Österbotten. Det förra området består av blockrik moränkskärgård med ett gott utbud av skyddade vikar, det senare området är i huvudsak en storskalig klippskärgård av samma branta typ som finns i sydvästra Finland.

Ett centralt fynd är att skäggdoppingarna i ytterskärgården har en relativt god häckningsframgång: 1,55 ungar per par och år i Bergö och 1,60 i Kaldonskär. Siffrorna skiljer sig inte från motsvarande värde i en innerskärgård i Österbotten. Kullstorleken skiljer sig inte mellan de två undersökta ytterskärgårdarna, inte heller mellan ytterskärgårdarna och den nämnda inre skärgårdsmiljön.

Däremot påverkas andra drag i häckningen klart av miljöns kvalitet i ytterskärgården: en stor del av paren börjar lägga ägg först i mitten av juni, de flesta doppingpar är associerade med måsfåglar och biotop- och boplatstvalet anpassas efter förhållandena i respektive område.

En orsak till doppingarnas framgång i yttre skärgården är bland andra förekomsten av skyddade småbiotoper som kan erbjuda lämpliga boplatser bakom ryggar av stenar eller små grupper av skär. Även här häckar skäggdoppingarna i atypiska förhållanden och största delen av bona byggs på stenar i vattenbrynet eller direkt på stranden.

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