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Clutch size, productivity and population changes in a population of the Horned Grebe *Podiceps auritus* in an exposed habitat

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The Horned Grebe *Podiceps auritus* has decreased markedly in Finland during recent decades. Merikallio (1958) estimated the total population at 3 000 pairs, Lammi (1983) at 1 500 pairs. A recent census of 29 eutrophic lakes and coastal bays in Finland showed that the population of Horned Grebes continued to decrease from the late 1970s to 1986–87. The decrease amounted to 67% and was highly significant (Esa Lammi and Risto A. Väisänen, pers. comm.).

The reasons for the decrease are largely unknown, but drowning in fishnets and hunting gear, and deterioration of the breeding lakes (for instance because of acidification and increasing humus content) have been proposed as explanations. Cold winters deplete the population, but the effect seems to be only temporary (Lammi 1983). In Lake Hornborgasjön in Sweden, Skidell (1980) observed that local habitat impairment caused a marked population decline in the Horned Grebe.

Consequently, there is an urgent need to study the breeding, productivity, population dynamics, habitat changes and wintering of Finnish Horned Grebes in detail. I have earlier (Ulfvens 1988) presented some results on the breeding and population dynamics of Horned Grebes along the west coast in Finland. Here I will summarize data collected over a period of ten years, from 1979 to 1988.

Study area, material and methods

The study was carried out in the archipelago of Korsnäs (62°49'N, 21°10'E) in southern Ostrobothnia. In this area, the Horned Grebes breed in "semitraditional" habitats, such as shallow bays or lagoon-like areas behind ridges of stones or islets (for details, see Ulfvens 1988).

In 1979–86 the grebes were censused by passing slowly close to the shores in a boat and by walking along the shores in some areas. The census was performed in mid or late May, and the nests and broods

were monitored by repeated visits throughout the breeding season. In 1987–88 the breeding population was censused in early June; repeated visits were made to some of the nests and the broods were counted in late July and early August.

As the birds were not marked, and the broods tend to be mobile, it was mostly impossible to distinguish between broods of initial, replacement or second clutches; all broods are thus pooled in the following calculations.

The net productivity is an approximation based on the observed number of breeding pairs, clutch size and survival of the eggs and young. The number of pairs that failed to produce young could not be counted directly, as some of the pairs that lost their eggs deserted the area early in the summer and may have re-nested somewhere else. However, the figure for egg losses accounts for at least some of the total failures.

The number of pairs observed totalled 172.

Results

The general outline of the breeding is as follows (for details, see Ulfvens 1988): Egg-laying commences around 27 May and the laying interval is 1.8 days. The clutch size decreases by 0.05 eggs per day. The incubation lasts for 23.7 days. Thus the young are mostly hatched around midsummer, and the broods contain up to 6 young each. 40.8% of the eggs are lost during the incubation period, and the egg mortality rate varies significantly between years (11–72%), mainly due to storms and rises in the sea water level. The survival rate of the young can be estimated at about 60%, but is probably slightly higher.

The mean clutch size (Table 1) for the ten years of study is larger than in lake populations in Finland (cf. Uusitalo 1969, 1976, Ulfvens 1988). The range of the annual mean clutch sizes is 4.7–5.3, but the variation between years is not significant ($F = 0.59$, $df_1 = 7$, $df_2 = 67$, $P = 0.76$).

Table 1. Clutch size (completed initial clutches only) and brood size in the population of Horned Grebes in the Korsnäs archipelago in 1979–1988. The broods comprise initial, replacement and second clutches; the observations mostly concern well-grown young aged 4–7 weeks.

	Mean	SD	n	Range
Clutch size	5.06	1.12	78	2–7
Brood size	2.93	1.13	59	1–6

The broods are also large in comparison with broods in Finnish lakes (Table 1). For instance, Horned Grebe broods in the lakes in Ostrobothnia contain only 1.5 young each (Ulfvens 1988). The mean brood size ranged from 2.7 to 3.8 in the years studied; there was no significant variation between years ($F = 1.30$, $df_1 = 6$, $df_2 = 48$, $P = 0.28$).

The population was largest in 1979, when 24 pairs were encountered. After that it decreased to 11 pairs in 1983, and then began to recover: 13 pairs in 1984, 12 pairs in 1985, 15 pairs in 1986, 20 pairs in 1987 and 22 pairs in 1988.

I have earlier (Ulfvens 1988) calculated the productivity per pair and year at 1.9 young (according to the Mayfield method: 1.5). Over the ten years of study, the net result is 1.8 young per pair and year, assuming that 59% of the eggs and 60% of the young survive. The scanty observations from 1987–88 do not allow an extended calculation according to the Mayfield method.

Discussion

Two significant findings emerge from the study: 1) the productivity of a population of Horned Grebes may be good, despite difficult physical conditions for breeding (in this case: rapid changes in the sea water level), and 2) a population of Horned Grebes may recover from an over 50% decrease in only a few years.

Unfortunately, the population studied is somewhat atypical of Finnish Horned Grebes as regards the general breeding performance and population trend. There are, however, several coastal populations of Horned Grebes in Finland (Lammi 1983) and the high productivity observed in this study may thus apply to at least a part of the Finnish population. The present productivity is slightly better than in the stable population in Iceland (Fjeldså 1973). In Canada, Ferguson & Sealy (1983) observed a population

of Horned Grebes with large clutches and broods, but high egg losses; they suggested that it is advantageous for Horned Grebes in unpredictable habitats to maximize their reproductive effort (e.g. in the form of large clutches and several nesting attempts). This raises the question whether the lake and coastal populations in Finland differ in their breeding strategies, paralleling the differences observed between the populations in Iceland and the North-American marshlands. If this is the case, the lake populations may be more vulnerable to habitat changes, having become adapted to a moderate reproductive effort.

It is possible that the population decline in Korsnäs in 1979–83 (a period in which, on the other hand, the local population of the Great Crested Grebe *Podiceps cristatus* increased by 74%) was mainly caused by emigration and vagrancy, as I have proposed earlier (Ulfvens 1988). Similarly, the population increase in 1984–88 may have primarily been due to immigration, rather than to recruitment of locally produced birds. Of course, these questions cannot be solved satisfactorily without marking some of the birds. The extremely cold winter of 1984/85 had no markedly negative effect on the population size. Predation was not observed to have caused any deaths of adult Horned Grebe, although egg predation was fairly common in the area (Ulfvens 1988).

The demographic data so far available for the Horned Grebe are insufficient for conclusive calculations of the "balance" of different populations. As regards the annual mortality rate, there is only the guess of Fjeldså (1973) that the rate may be about 50%. When this value is applied to the population in Korsnäs, it results in an annual decrease of 5%. Fjeldså's value may be too high, as the annual mortality in the Great Crested Grebe varies from 25 to 41% (see Fuchs 1982, van der Poel 1984).

My data from the lakes in southern Ostrobothnia showed that the smaller clutch size in these habitats and the smaller broods resulting from it were most probably caused by food shortage in the mainly oligotrophic or dystrophic lakes (Ulfvens 1988). The data do not, however, reveal any change in the feeding conditions, a result which would be essential in order to substantiate the suggested link (e.g. Lammi 1983) between the decline in the Horned Grebe populations and acidification and/or increasing humus content of the lakes.

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Sammanfattning: Kullstorlek, produktivitet och populationsförändringar hos svarthakedoppingar i en atypisk miljö

En population av svarthakedopping (11–24 par) som undersöktes under tio år i skärgården i Korsnäs i södra Österbotten hade en medelkullstorlek på 5,1 ägg (tabell 1). Ungkullarnas storlek var i medeltal 2,9. Båda värdena är klart högre än motsvarande värden hos svarthakedoppingar som häckar i små, näringsfattiga sjöar i Sydösterbotten. Den undersökta populationen minskade från 24 till 11 par för att sedan under åren 1984–88 åter öka till 22 par.

Resultaten visar att lokala bestånd av svarthake kan ha en god häckningsframgång och att reducerade bestånd kan återhämta sig över blott några år. Emellertid är uppgifterna om till exempel vinterdödligheten hos svarthakedoppingen och effekterna av eventuella förändringar i traditionella häckningsmiljöer bristfälliga, vilket gör att orsakerna till artens märkbara minskning i Finland alltjämt är höljda i dunkel.

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Solitary pairs of Great Black-backed Gulls *Larus marinus* prevent strangers from mobbing a predator model at their nest site

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Mobbing (i.e. flocking around a predator, see Kruuk 1964) is a typical feature of colonial gulls. The function and adaptive value of this behaviour have remained elusive, though many facets of the problem have been studied (Conover 1987). The benefits or costs of "communal" mobbing for a particular territory owner in a colony are also obscure.

Large gulls, such as the Great Black-backed Gull *Larus marinus*, breed both solitarily and in colonies in the same area (see Bergman 1982, Götmark 1982). As strange gulls are often attracted to mobbing

events, even at sites of solitary pairs (see Kilpi 1988), we might expect that such solitary pairs would either accept "help" in mobbing (thus behaving as colonial gulls) or reject any strange gulls.

I recently suggested (Kilpi 1988) that solitary pairs of nesting Great Black-backed Gulls actively defend the air "territory" around their breeding islet against strange gulls attracted to the site during temporary disturbances. Thus, Great Black-backs seemed to actively prevent any "communal" defence by strangers recruited to the site.