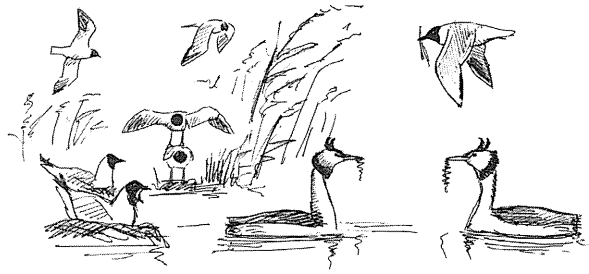
Costs and benefits to Great Crested Grebes *Podiceps cristatus* nesting in association with Black-headed Gulls *Larus ridibundus*

KELD HENRIKSEN



(Med et dansk resumé: Toppet Lappedykker Podiceps cristatus *ynglende i selskab med Hættemåger* Larus ridibundus*: omkostninger og fordele)*

Introduction

Some grebe and duck species nest in association with aggressive gulls or terns. This habit is usually explained as an adaptation to reduce nest predation because gulls and terns provide early warning of approaching predators (Bergman 1957, Nuechterlein 1981, Burger 1984) and actively defend their own nests (e.g. Kruuk 1964, Lemmetyinen 1971, Fuchs 1977). Reproductive costs to birds nesting in close association with gulls may be competition for nest sites and egg and/or chick predation from the gulls (Vermeer 1968, Dwernychuk & Boag 1972, Burger 1974, Götmark & Åhlund 1988).

In some areas, the proportion of Great Crested Grebes *Podiceps cristatus* nesting within colonies of Black-headed Gulls *Larus ridibundus* is very high (Goc 1986, Ulfvens 1988, Henriksen 1992). However, quantitative data on costs and benefits associated with this habit are scarce.

In this paper I compare the hatching success of Great Crested Grebe nests placed among Black-headed Gull nests (associated nests) with those placed away from gull nests (solitary nests).

Study area and methods

The study was carried out in 1985-89 and 1991-92 in eastern Jutland, Denmark, in Lake Brabrand, a shallow hypereutrophic lake with an area of 1.5 km^2 (see Henriksen (1992) for further description of the lake).

The number of breeding pairs of Black-headed Gulls in 1985-89 was 3200-4100, decreasing to 2200 and 1900 in 1991 and 1992, respectively (A. Janniche pers. comm.). The general pattern of nest placement was high-density nesting in stands of reeds *Phragmites australis* surrounded by open water during early April, more dispersed nesting at the outer edges of the reed bed along the lakeside later in April, and nesting in scattered groups of 10-200 pairs in the numerous stands of bulrushes *Scirpus lacustris* emerging outside the reed bed in May. In years with high water levels in late April (as in 1991), many pairs also nested on the flooded meadows; however, these nests were always unsuccessful and gave rise to an extended egg-laying period due to subsequent relaying.

In 1985-89, I searched for grebe nests by boat weekly from mid-April to about 1 June. The nest content was recorded when the nest was first found and on subsequent visits every week. The positions of all nests were plotted on a detailed map and I also repeatedly mapped the distribution of active gull nests.

From mid-April to mid-June in 1991-92 associated grebe nests were located and checked by boat every two or three days in two areas with bulrushes (58 nests) and two with reeds (38 nests). All eggs in a clutch were marked according to laying order. The distance to the nearest active gull nest was either estimated with an accuracy of 1 m or measured.

Daily survival of grebe nests was calculated separately for the period of egg-laying (P1) and for

Tab. 1. Estimated daily survival (±SE) during egg-laying (P1) and after egg-laying (P2) of Great Crested Grebe nests placed among (associated) and away from (solitary) Black-headed Gull nests, 1985-89. Nest-days are the total number of days for which the sample of nests was under observation.
Overlevelse pr dag (±SE) under æglægningen (P1) og efter æglægningen (P2) af reder af Toppet Lappedykker placeret mellem hættemågereder og for sig selv 1985-89. Rededage er summen af observationsperioderne for de enkelte reder.

	During egg-laying *Under æglægningen*			After egg-laying *Efter æglægningen*		
Nest placement *Redeplacering*	Nests *Reder*	Nest-days *Rededage*	P1	Nests *Reder*	Nest-days *Rededage*	P2
Associated *Mellem hættemågereder*	298	1221	0.961 (±0.006)	347	4575	0.990 (±0.002)
Solitary *For sig selv*	45	206	0.884 (±0.022)	38	453	0.958 (±0.009)

the period after egg-laying (P2) according to Mayfield (1975). Incubation was assumed to take 28 days (7 days during egg-laying and 21 days after egg-laying), so hatching success was calculated as $P1^7 \times P2^{21}$. In 1991-92, when grebe eggs were marked, daily loss rates of individual eggs were calculated according to Mayfield (1975). Calculation of standard errors of daily nest survival and egg loss followed Hensler & Nichols (1981), and I tested for differences by using two-tailed z-tests. Other statistical tests referred to are described in Siegel & Castellan (1988).

Results

Nest placement and frequency of association

In 1985-89, all the associated grebe nests were placed less than 30 m away from gull nests and usually in groups of 3-36 nests. Median group size of associated nests did not differ significantly between years (Kruskal-Wallis test, H = 2.14, df = 4, n.s.) and was six nests for all years combined. All the solitary nests were well-dispersed and during all years the mean distance to gull nests was 240 m (range 60-560 m, N = 63).

The mean proportion of grebe pairs associated with gulls was 88% (range 81% in 1989 to 93% in 1985, 69-94 pairs); the difference between years is not significant ($\chi^2 = 9.22$, df = 4, n.s.).

Clutch size and hatching succes

Overall, the start of egg-laying in solitary nests ranged from 11 April to 20 May and mean clutch size ± SD was 4.2±0.83 (N = 25); mean size of clutches in associated nests initiated during the same period was 4.0±0.89 (N = 146). In 1987 (mean clutch size 4.6±0.52, N = 8 for solitary nests vs. 4.4±0.89, N = 53 for associated nests) and 1988 (4.1±0.78, N = 9 vs. 3.8±0.89, N = 54), sample sizes permitted a statistical comparison of clutch size. The median clutch size, however, did not differ significantly between solitary and associated nests (Wilcoxon test, two-tailed, z = 0.73, n.s. in 1987 and z = 1.21, n.s. in 1988).

Mean nest survival of associated nests during egg-laying and after egg-laying was 0.961 and 0.990 nests surviving per day, respectively; for solitary nests it was 0.884 and 0.958 nests surviving per day, respectively (Tab. 1). Hatching success, thus, was 61% for associated nests and 17% for solitary nests. The difference in daily nest survival between associated and solitary nests is statistically significant, both during egg-laying (z = 3.35, $p < 0.001$) and after egg-laying (z = 3.30, $p < 0.001$). Egg predation accounted for 89% (124/139) of all nest failures and wave action accounted for 11% (15/139). A few nests, however, may have been abandoned before predation of eggs took place.

Egg losses in associated nests

In 1991-92, the mean distance from associated nests to nearest gull nest was 3.3 m (range 0.6-16 m, N = 96), with 83% of nests less than 5 m away from gull nests.

Egg losses due to flooding only occurred in 1991 following a rapid and prolonged increase in the water level in late April (mean 9 cm per day for seven days). Usurpation of grebe nests by gulls accounted for 46% (0.030/0.065) of total daily egg loss rate during egg-laying (Tab. 2). Nine grebe nests were usurped by gulls (in two, the grebe eggs were covered with new nest material; in another two, one grebe egg was found nearby in the water; in five, the grebe eggs disappeared completely). One gull egg was found in an active

Tab. 2. Estimated daily rates of egg loss (±SE) in nests of Great Crested Grebes placed among Black-headed Gull nests, 1991-92. Egg-days are the total number of days for which the sample of individual eggs was under observation.
Dagligt ægtab (±SE) i reder af Toppet Lappedykker placeret mellem hættemågereder 1991-92. Ægdage er summen af observationsperioderne for de enkelte æg.

	During egg-laying *Under æglægningen*	After egg-laying *Efter æglægningen*
Causes of losses *Årsager til ægtab*		
Nest flooded *Rede oversvømmet*	0.006 (±0.003)	0.010 (±0.002)
Nest usurped by gulls *Rede overtaget af måger*	0.030 (±0.007)	0.001 (±0.001)
Egg predated *Æg præderet*	0.009 (±0.004)	0.003 (±0.001)
Clutch predated *Ægkuld præderet*	0.013 (±0.005)	0.002 (±0.001)
Egg rolled out *Æg trillet ud af rede*	0.007 (±0.004)	0
No. egg-days *Ægdage*	540	3369
Total daily rate of loss *Totale daglige ægtab*	0.065 (±0.011)	0.017 (±0.002)

grebe nest, but was missing three days later. Daily egg loss due to nest usurpation by gulls was significantly higher during egg-laying than after egg-laying ($z = 3.89$, $p < 0.001$; Tab. 2).

Great Crested Grebes also dumped eggs in nests of conspecifics. This occurred in 5% (5/96) of nests (in one during egg-laying, in four after egg-laying). Finally, three grebe eggs were dumped in active gull nests.

Discussion

In Lake Brabrand, Great Crested Grebes nesting in association with Black-headed Gulls were more successful in hatching their eggs than solitarily nesting grebes. Similar results were obtained in Poland by Goc (1986), who found a higher survival of associated nests (58%) than of solitary nests (28%). In a coastal area in western Finland, however, there was no difference in total egg loss between associated and solitary pairs, but losses due to egg predation were smaller among associated pairs (Ulfvens 1988).

So far only hatching success has been considered as a measure of reproductive success, and there remains the possibility that grebe chicks from associated nests suffer predation from the gulls during the hatching period. Other measures of reproductive success (e.g. the probability that a nesting attempt will produce chicks leaving the nesting area) may therefore lead to a somewhat different result. However, although some individual Black-headed Gulls in some colonies seem to specialize in eating eggs and small chicks of associated Sandwich Terns *Sterna sandvicensis* (e.g. Van den Assem 1954, Fuchs 1977, Veen 1977) serious preying upon grebe chicks has never been seen.

The frequency of solitary pairs did not decrease during the study years although they fared worse with regard to hatching success. Solitary pairs often had large well-built nests in well-developed stands of reeds, bred early, and had large clutches, indicating that they were not inferior to associating pairs in quality, age or other respects. Because of high breeding density in Lake Brabrand it was impossible without individually marked birds to determine whether pairs were consistently solitary or associated with gulls when renesting during successive years or during the same season. However, in places where single pairs nested, Ulfvens (1988) found that nesting in the same suitable sites during successive years was common, even after one or two years of total nest failure.

Usurpation of nests by gulls was a major cause of egg loss in associated grebe nests during egg-laying. Other reproductive costs to associated pairs due to the presence of gulls were egg dumping in nests of conspecifics (probably due to clumped nesting near gulls) and gulls. Since most egg dumping in conspecific nests was observed in nests containing complete clutches it was probably accidental and dumped eggs were unlikely to produce hatchlings. In ducks egg dumping can reduce hatching success through egg breakage, egg displacement, inefficient incubation, or nest desertion (e.g. Weller 1959, Joyner 1976, Pienkowski & Evans 1982).

Even if nesting in close proximity to gulls inflicted some loss of eggs or nests on Great Crested Grebe pairs, these reproductive costs were more than offset by other factors, leading to a higher nest survival of associated nests. Nesting in association with Black-headed Gulls, thus, seems to be beneficial, at least to Great Crested Grebes.

Resumé

Toppet Lappedykker *Podiceps cristatus* ynglende i selskab med Hættemåger *Larus ridibundus*: omkostninger og fordele

Nogle ande- og lappedykkerarter yngler ofte i mågekolonier og drager antagelig fordel af mågernes advarselsskrig og aggressive forsvar af egne reder. Toppet Lappedykker *Podiceps cristatus* yngler nogle steder hyppigt i hættemågekolonier, men få har kvantitativt undersøgt omkostninger og fordele ved denne adfærd.

Hos Toppet Lappedykker i Brabrand Sø ved Århus blev succesen af reder placeret mellem hættemågereder og reder placeret for sig selv undersøgt i 1985-89. I 1991-92 blev årsagerne til ægtab i reder placeret mellem mågereder undersøgt nærmere. Feltarbejdet hvert år omfattede redeoptælling og -kontrol fra robåd, ugentligt fra midten af april til omkring 1. juni i 1985-89 og hver anden eller tredje dag fra midten af april til midten af juni i 1991-92. Redesuccesen blev beregnet i henhold til Mayfield (1975) og angiver sandsynligheden for, at der klækkes mindst én unge pr rede.

De fleste par (81-93%, 69-94 par) ynglede i selskab med Hættemåger, og oftest var grupper på 3-36 reder placeret mellem mågerederne. Reder placeret for sig selv var spredt fordelt i søen i en afstand af 60-560 m (gennemsnit 240 m) fra nærmeste mågerede. Kuldstørrelsen var den samme i de to redetyper.

Yngleforsøgene mislykkedes hyppigere i reder placeret for sig selv (Tab. 1); forskellen er statistisk signifikant både under og efter æglægningen ($p < 0{,}001$). Årsagerne til mislykkede yngleforsøg var ægprædation (89%) og bølgegang (11%). Den gennemsnitlige succes af reder placeret mellem mågereder var 61%, mens den kun var 17% i reder placeret for sig selv.

Årsagerne til ægtab i reder placeret mellem mågereder og deres relative betydning ses af Tab. 2. Den tætte kontakt med ynglende Hættemåger medførte, at måger overtog aktive lappedykkerreder, og at lappedykkere lagde æg i mågereder. Ægtab forårsaget af mågers overtagelse af lappedykkerreder dominerede under æglægningen (Tab. 2) og var hyppigst i denne periode ($p < 0{,}001$). Der blev desuden i fem procent af lappedykkerrederne (5 af 96) konstateret ægdumpning fra artsfæller, sandsynligvis p.g.a. den høje tæthed af reder mellem mågerederne.

Disse ægtab i reder placeret mellem hættemågereder, der direkte eller indirekte skyldtes tilstedeværelsen af ynglende Hættemåger, mere end opvejedes dog af andre faktorer, der medførte en bedre redesucces end i reder placeret for sig selv. Det kan således konstateres, at Toppet Lappedykker i Brabrand Sø har stor fordel af at yngle i selskab med Hættemåger.

References

Bergman, G. 1957: Zum Problem der gemischten Kolonien: Die Reiherente (*Aythya fuligula*) und die Lariden. – Vogelwarte 19: 15-25.

Burger, J. 1974: Breeding biology and ecology of the Brown-hooded Gull in Argentina. – Auk 91: 601-613.

Burger, J. 1984: Grebes nesting in gull colonies: protective associations and early warning. – Amer. Nat. 123: 327-337.

Dwernychuk, L. W. & D. A. Boag 1972: Ducks nesting in association with gulls – an ecological trap? – Can. J. Zool. 50: 559-563.

Fuchs, E. 1977: Predation and anti-predator behaviour in a mixed colony of terns *Sterna* sp. and Black-headed Gulls *Larus ridibundus* with special reference to the Sandwich Tern *Sterna sandvicensis*. – Ornis Scand. 8: 17-32.

Goc, M. 1986: Colonial versus territorial breeding of the great crested grebe *Podiceps cristatus* on Lake Druzno. – Acta Orn. 22: 95-145.

Götmark, F. & M. Åhlund 1988: Nest predation and nest site selection among Eiders *Somateria mollissima*: the influence of gulls. – Ibis 130: 111-123.

Henriksen, K. 1992: Nesting ecology and production of young in the Great Crested Grebe *Podiceps cristatus* in a hypereutrophic Danish lake. – Dansk Orn. Foren. Tidsskr. 86: 163-168.

Hensler, G. L. & J. D. Nichols 1981: The Mayfield method of estimating nesting success: a model, estimators and simulation results. – Wilson Bull. 93: 42-53.

Joyner, D. F. 1976: Effects of interspecific nest parasitism by redheads and ruddy ducks. – J. Wildl. Mgmt 40: 33-38.

Kruuk, H. 1964: Predators and anti-predator behaviour of the Black-headed Gull *(Larus ridibundus* L.). – Behaviour, Suppl. 11: 1-129.

Lemmetyinen, R. 1971: Nest defence behaviour of Common and Arctic Terns and its effects on the success achieved by predators. – Ornis Fenn. 48: 13-24.

Mayfield, H. F. 1975: Suggestions for calculating nest success. – Wilson Bull. 87: 456-466.

Nuechterlein, G. L. 1981: Information parasitism in mixed colonies of Western Grebes and Forster's Terns. – Anim. Behav. 29: 985-989.

Pienkowski, M. W. & P. R. Evans 1982: Clutch parasitism and nesting interference between shelducks at Aberlady Bay. – Wildfowl 33: 159-163.

Siegel, S. & N. J. Castellan Jr 1988: Nonparametric statistics for the behavioral sciences. – McGraw-Hill, New York.

Ulfvens, J. 1988: Comparative breeding ecology of the Horned Grebe *Podiceps auritus* and the Great Crested Grebe *Podiceps cristatus*: archipelago versus lake habitats. – Acta Zool. Fenn. 183: 1-75.

Van den Assem, J. 1954: Kokmeeuwen als belagers van Grote Sterns. – Levende Natuur 57: 141-145.

Veen, J. 1977: Functional and causal aspects of nest distribution in colonies of the sandwich tern *(Sterna s. sandvicensis* Lath.). – Behaviour, Suppl. 20: 1-193.

Vermeer, K. 1968: Ecological aspects of ducks nesting in high densities among larids. – Wilson Bull. 80: 78-83.

Weller, M. W. 1959: Parasitic egg laying in the Redhead *(Aythya americana)* and other North American Anatidae. – Ecol. Monogr. 29: 333-365.

Accepted 14 December 1992

Keld Henriksen
Kærvej 17
8230 Åbyhøj