Nesting ecology and production of young in the Great Crested Grebe *Podiceps cristatus* in a hypereutrophic Danish lake

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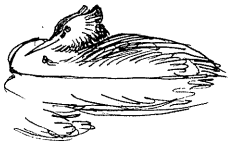

(Med et dansk resumé: Redeøkologi og ungeproduktion hos Toppet Lappedykker Podiceps cristatus *i en hypereutrof dansk sø)*

Introduction

Lake Brabrand in eastern Jutland, Denmark, is a typical example of a shallow formerly naturally eutrophic lake which has become nutrient-loaded due to urban run-off. For decades the lake has been in a state characterized by turbid water and food chains dominated by planktonic algae, zooplankton and small cyprinid fishes (Århus Amtskommune 1985, 1989). This state favours the piscivorous Great Crested Grebe *Podiceps cristatus* as long as no oxygen deficiency followed by reduced fish density occurs (e.g. Asbirk & Dybbro 1978, Nilsson 1978).

In this paper I present basic data on the breeding biology of Great Crested Grebes in the hypereutrophic Lake Brabrand. Spring arrival, breeding density, nest site, egg-laying, clutch size, nest success, and production of young were studied in five breeding seasons from 1985 to 1989.

Study area

Lake Brabrand is 3 km long and 0.25-1 km wide, covering an area of 1.5 km^2. Fringing vegetation of reeds *Phragmites australis* at least 10 m wide is present along three-fifths of the shore, and from early May numerous small stands of bulrushes *Scirpus lacustris* emerge outside the reedbed. Nowadays there is hardly any submerged vegetation left in the lake.

In summer, the average depth is 0.9 m, maximum depth 1.8 m, the transparency 0.3-0.4 m, and mean concentration of total-phosphorus 0.95 mg per liter (Århus Amtskommune 1985). The mean amplitude of the water level in May was 17 cm (range 12-26 cm). The lake was frozen in the first three winters, ice break-up taking place in the last few days of March.

Roach *Rutilus rutilus* and bream *Abramis brama* dominate the fish populations, making up 83% by weight and 71% by number of the total fish catch in a study by Århus Amtskommune (1989). Mean length of roach was 9 cm (range 3-26 cm) and of bream 17 cm (range 3-33 cm).

In addition to the Great Crested Grebe there were 10 other waterfowl species breeding in the lake, with a total of 85-117 pairs. Coot *Fulica atra* and Mallard *Anas platyrhynchos* dominated with 50-60 pairs and 20-25 pairs, respectively. The number of Black-necked Grebe *Podiceps nigricollis* was 5-15 pairs. The Black-headed Gull *Larus ridibundus* colony numbered 3200-4100 pairs (A. Janniche pers. comm.).

Recreational activities included some boat racing in scullers and kayaks along a route marked in the middle of the lake. About 40 persons carried out fishing from early spring, mainly with eel traps.

Methods

Grebes were counted at least every third day from the first days of March, or from ice break-up, to the end of April. By the end of April some of the grebes were incubating and some nests were not visible from the shore.

Nests were located by systematically searching the shoreline by boat. I recorded the status of each nest, mapped its position, and covered the eggs with nest material before leaving. Neither nests nor eggs were marked. I counted and checked nests once each week from mid-April to about 1 June. During these repeated nest counts I tried to detect possible non-breeding grebes. In 1987 I also made an almost complete nest count on 29 June. To avoid biases in comparisons between years these late June-nests were not included in the following analyses.

The number of breeding pairs was defined as the maximum number of simultaneously active nests, plus nests failed in the period between the day of this maximum occupancy and the preceding nest count. Clutch size was defined as the maximum

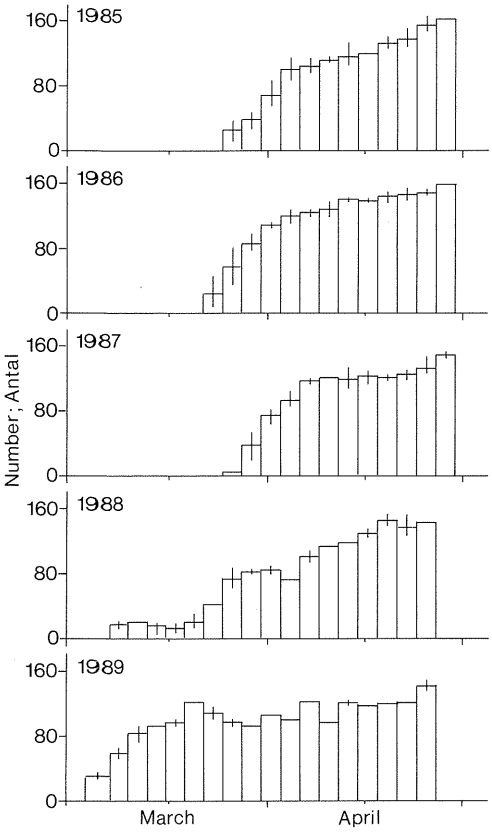

Fig. 1. Spring arrival of Great Crested Grebe in Lake Brabrand. Mean number and range per three-day period. The lake was frozen in the first three winters.
Ankomst af Toppet Lappedykker om foråret til Brabrand Sø. Søen var isdækket de første tre vintre.

number of eggs found in a given nest. Clutches where it was obvious that two females were involved in egg-laying were not included in the clutch size analysis. Clutches partly reduced by predators etc. were likewise excluded. Without doubt, however, some replacement clutches were incluced. Ninety-two percent of all clutches were found during or shortly after egg-laying, and for most of the other clutches laying dates could be estimated from the hatching date.

Daily loss rates of clutches (m) were calculated according to Mayfield's (1975) exposure method. Because loss rates are likely to vary with nesting stage, they were calculated separately for the period of egg-laying (7 days) and for the period after egg-laying (21 days). For each period clutch survival was calculated by raising the daily survival rate (1 - m) to a power equal to the length of the period in days; clutch survival from laying of the first egg to hatching was estimated as the product of the clutch survival estimates for the two periods. Nest success was thus defined as the probability that a newly initiated clutch would survive to produce at least one hatched young. Variance estimates of the daily survival rates followed Hensler & Nichols (1981), and I tested for differences by using two-tailed z-tests. Other statistical analyses followed procedures in Sokal & Rohlf (1981).

I made four to eight brood counts each year from late July to mid-August. The broods were plotted on a map, and the size of the young grebes was estimated in proportion to adult size. Production of young was measured as the number of young at least half adult size per pair per year.

Results

Spring arrival, breeding numbers and nest sites

In the springs of 1985-87 the Great Crested Grebes arrived in late March during ice break-up (Fig. 1), and the numbers increased steadily almost day by day. A few grebes wintered during the ice-free conditions in the winters 1987/88 and 1988/89, and spring arrival was much more irregular in

Tab. 1. Numbers of breeding pairs, breeding density (pairs per 10 ha water surface), and per cent distribution of nests according to surrounding nest vegetation, of Great Crested Grebe in Lake Brabrand.
Antal ynglepar, yngletæthed (par pr 10 ha vandflade) og procentvis fordeling af rederne med hensyn til redevegetation hos Toppet Lappedykker i Brabrand Sø.

	1985	1986	1987	1988	1989
No. of pairs *Antal par*	74	87	107	103	98
Density *Yngletæthed*	4.9	5.8	7.1	6.9	6.5
No. of nests *Antal reder*	81	102	133	118	124
Nest vegetation *Redevegetation* (%)					
Reed *Tagrør* (*Phragmites australis*)	84	57	35	76	53
Bulrush *Søkogleaks* (*Scirpus lacustris*)	11	24	46	18	40
Reedmace *Bredbladet dunhammer* (*Typha latifolia*)	4	16	12	6	7
Other *Andet*	1	3	7	0	0

1988 and 1989 (Fig. 1). The arrival of the breeding population in 1985-86 was complete by the end of April, about 30 days after break-up of the ice. However, in 1987-89 only about 75% of the breeding population had arrived by the end of April.

The number of breeding pairs increased during the first study years (Tab. 1), and breeding density ranged from 4.9 to 7.1 pairs per 10 ha water surface. Systematic search for non-breeders during the nest counts revealed that all grebes present attempted to breed.

Eightyeight percent of all nests found were placed in reeds or bulrushes, the two dominating emergents in the lake. The proportions of these two plant species as nest vegetation varied significantly between years ($G = 59.74$, $df = 4$, $p < 0.001$, Tab. 1). Most nests (84-93%) were placed less than 30 m away from gull nests (K. Henriksen in prep.).

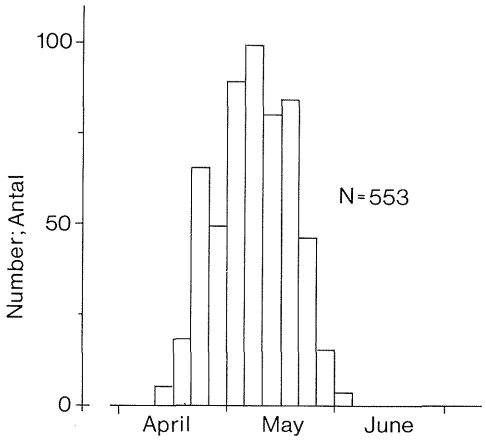

Fig. 2. Distribution of first-egg dates in the Great Crested Grebe, Lake Brabrand 1985-89.
Æglægningen hos Toppet Lappedykker i Brabrand Sø 1985-89.

Egg-laying and clutch size

For all years combined, a peak of egg-laying occurred in the first week of May (Fig. 2). This pattern was apparent in all years although a minor peak occurred in the third week of April in 1988 and 1989. Seven well incubated and six hatching clutches were found on 29 June 1987.

Full clutches varied from two to seven eggs (Tab. 2), but clutches of two, six and seven were relatively rare. Clutch size varied significantly between years (Kruskal-Wallis test, $H = 13.41$, $df = 4$, $p < 0.01$). However, multiple comparisons showed that median clutch size only differed significantly between the two years 1987 and 1989. Apart from 1986 there was a significant decline in clutch size in the course of the season ($r = -0.65$, $p < 0.001$ in 1985; $r = -0.06$, $p > 0.5$ in 1986; $r = -0.32$, $p < 0.01$ in 1987; $r = -0.33$, $p < 0.01$ in 1988; $r = -0.23$, $p < 0.05$ in 1989; sample sizes as in Tab. 2).

Nest success and production of young

Mean clutch survival for all years was 0.950 clutches surviving per day during the period of egg-laying and 0.987 clutches surviving per day during the period after egg-laying (Tab. 3). Overall clutch survival during the two periods was 0.696 and 0.754, respectively, and the nest success, i.e. the probability that a breeding attempt produced at least one hatched young, was 0.525 or 52.5%.

Even though confidence limits overlap (Tab. 3), daily survival rate during the period of egg-laying was significantly higher in 1986 than in 1989 ($z = 2.42$, $p < 0.02$). Comparing the other years gave $z = 0.13$-1.72, $p > 0.08$-0.8. Daily survival rate of clutches during the period after egg-laying did not vary significantly between years ($z = 0.20$-1.63, $p > 0.1$-0.8). However, in all years except 1986 ($z =$

Tab. 2. Clutch size of the Great Crested Grebe in Lake Brabrand.
Kuldstørrelse hos Toppet Lappedykker i Brabrand Sø.

	Clutch size *Kuldstørrelse*								
Year *År*	2	3	4	5	6	7	N	$\bar{x}$	SD
1985	1	9	22	7	2	2	43	4.14	1.04
1986		9	37	15	2	1	64	4.20	0.78
1987	6	4	38	23	6		77	4.25	0.96
1988	4	18	34	14	2		72	3.89	0.88
1989	8	16	43	8	1		76	3.71	0.85
1985-1989	19	56	174	67	13	3	332	4.02	0.92

Tab. 3. Daily survival rates of clutches during egg-laying and after egg-laying in the Great Crested Grebe in Lake Brabrand. Nest-days based on number of days nests were under observation.
Overlevelsesrater af kuld under æglægningen og efter æglægningen hos Toppet Lappedykker i Brabrand Sø. Rededage er summen af dage i de perioder, hver enkelt rede blev kontrolleret.

	During egg-laying *Under æglægningen*				After egg-laying *Efter æglægningen*			
Year *År*	Nests *Reder*	Nest-days *Rededage*	Daily survival *Overlevelse pr dag*	95% CI	Nests *Reder*	Nest-days *Rededage*	Daily Survival *Overlevelse pr dag*	95% CI
1985	51	199	0.945	0.913-0.977	48	547	0.991	0.983-0.999
1986	74	334	0.973	0.956-0.990	80	1021	0.987	0.980-0.994
1987	87	380.5	0.950	0.928-0.972	84	935.5	0.988	0.981-0.995
1988	60	224.5	0.942	0.912-0.973	83	1228	0.989	0.983-0.995
1989	71	289	0.931	0.902-0.960	91	1296.5	0.982	0.975-0.989
1985-89	343	1427	0.950	0.939-0.961	386	5028	0.987	0.984-0.990

1.47, $p > 0.1$) the daily survival rate was lower during the period of egg-laying than during the period after ($z = 2.57$-3.31, $p < 0.001$-0.05).

In all years combined, nest success of grebes breeding in association with gulls was 60.5%; in grebes not doing so it was only 17.1% (K. Henriksen in prep.).

An empty but intact nest was the most common evidence of nest failure. Of 139 failed nests only 15 disappeared or were damaged; all but one of these were placed in weak emerging bulrush stands in early May. The causes of nest failure thus appeared to be desertion/egg predation (89%) and wave action (11%). It was impossible to distinguish between failure due to predation and failure due to abandonment followed by scavenging of nest contents. However, I never found a nest with a set of cold eggs, suggesting that nest abandonment was rare. Twelve percent (48/390) of clutches with eggs controlled more than once were partly depredated. Eight of these clutches nevertheless succeeded, 26 were still incubated, and 14 failed during the time spanned by observations.

Nest success varied from 63.1% in 1986 to 40.9% in 1989, and production of young likewise differed considerably between years (Tab. 4). Very few young less than half adult size were counted during the brood counts (2-4% of total yearly numbers).

Tab. 4. Breeding performance of Great Crested Grebe in Lake Brabrand. Nest success is the probability that a clutch will survive to produce at least one hatched young. Production of young is the number of young at least half adult size per pair.
Yngleresultat hos Toppet Lappedykker i Brabrand Sø. Redesucces angiver sandsynligheden for, at der klækkes mindst én unge pr rede. Ungeproduktionen er antallet af mindst halvvoksne unger pr par.

Year *År*	Nest success (%) *Redesucces (%)*	Production of young *Ungeproduktion*
1985	55.4	0.89
1986	63.1	1.46
1987	54.5	1.08
1988	51.8	0.37
1989	40.9	0.47
1985-1989	52.5	0.84

Discussion

The clear effect of ice conditions on spring arrival was expected. It was more surprising to find that a quarter of the breeding population in three of the study years had not yet arrived by the end of April. This happened in 1987-89 when the breeding numbers were high. The late-arriving grebes probably did not come directly from their winter quarters. My guess is that they inspected potential breeding lakes and finally ended up in Lake Brabrand during May, when plenty of nest sites are available in the emerging bulrushes. At any rate it appears likely that the most suitable nest sites were those occupied early in the breeding season.

The breeding density in Lake Brabrand is one of the highest in Denmark for a lake of that size (Asbirk & Dybbro 1978) and is also very high compared to other European lakes of similar size (Leys & de Wilde 1969, Berndt & Drenckhahn 1974, Goc 1986). Nesting in old reed stems in association with gulls from mid-April, "solitary" nesting in old and new reed stems from late April, and nesting in emerging bulrushes in association with gulls from mid-May was the general pattern

Omkring 90% af de Toppede Lappedykkere i Brabrand Sø ynglede nær Hættemågekolonier, og her var ynglesuccesen mere end tre gange så høj som for ensomt beliggende reder. Foto: John Larsen.

of nest placement in Lake Brabrand. A higher proportion of nests were placed in bulrushes in 1987 and 1989, the two years with the lowest water level i May. My study thus supports the suggestion by Simmons (1974) that the need for cover or other protection for the nest is the chief determinant of egg-laying dates and dispersion of nests.

The only factor shown to influence clutch size in my study was laying date, with the largest clutches normally occurring in April and early May. Similar seasonal changes occur in other parts of northern and eastern Europe (Lawniczak 1982, Goc 1986, Ulfvens 1988) and are thought to be due to smaller replacement clutches and late breeding of young grebes that lay smaller clutches. If so, the non-significant decline in clutch size with season in 1986 may be explained by the high clutch survival, hence few replacement clutches, in 1986. A higher proportion of breeding young grebes, producing small clutches, probably occurred after the mild winters in 1988 and 1989, resulting in the low mean clutch sizes in these years.

Nest failure was most likely during the egg-laying period. Reduced nest attendance and vigilance during the egg-laying period were the likely reasons. Also, the habit of covering the clutch with nest material when disturbed is less developed during the early stages of the egg-laying period (Simmons 1955, Goc 1986); recent studies showed that the proportion of experimental nests destroyed by Hooded Crows *Corvus corone* (Salonen & Penttinen 1988) and by Coots (Keller 1989a) decreased when the eggs were covered.

Predation from Hooded Crows was probably the main cause of nest failure, as egg shell dumps near crow nests revealed that egg predation was common. How often predation by crows occurred in consequence of the disturbance created by the activity of fishermen is unknown, but it may have been quite frequent. In a study by Keller (1989b) incubating grebes on lakes with recreational activities left their nest at shorter distances from approaching rowing boats, but covered their clutch less frequently, than grebes in less disturbed lakes. On the other hand, disturbance of incubating grebes during nest counts was a minor problem concerning egg predation. I always covered the eggs after inspection, and the incubating birds usually returned within a few minutes when I left the nest area. During 153 hours of nest counts I saw two grebe eggs being taken by Hooded Crows, most likely caused by my presence in the nest area.

Fuchs (1982) estimated the first-year survival at 59% and the annual adult survival at 65-75% for

Great Crested Grebes in Switzerland. Annual survival of adult grebes in Holland was estimated at 60% (van der Poel 1984). It would thus seem that 0.8-1.4 fledged young per pair is needed to maintain a stable population; and that young production in Lake Brabrand in some years is too low to balance average mortality, but more than sufficient in other years.

Resumé

Redeøkologi og ungeproduktion hos Toppet Lappedykker *Podiceps cristatus* i en hypereutrof dansk sø

Brabrand Sø ved Århus er i de seneste årtier blevet stærkt eutrofieret som følge af fosfortilførsel fra spildevand; algemængden i vandet er stor, og undervandsplanterne er forsvundet. Skalle *Rutilus rutilus* og brasen *Abramis brama* er blevet favoriseret af denne udvikling; men væksten hos begge arter er langsom, og individerne bliver ikke særligt store (Århus Amtskommune 1989). Søer af denne type rummer oftest de tætteste ynglebestande af Toppet Lappedykker *Podiceps cristatus* (f.eks. Asbirk & Dybbro 1978). I fem ynglesæsoner 1985-89 blev redeøkologien og ungeproduktionen hos Toppet Lappedykker i Brabrand Sø undersøgt.

Feltarbejdet hvert år omfattede registrering af ankomsten om foråret ved optællinger mindst hver tredje dag, ugentlige redeoptællinger fra robåd fra midten af april til omkring 1. juni og 4-8 kuldtællinger fra slutningen af juli til midt i august. Redesuccesen blev beregnet ved hjælp af en metode, der bygger på forholdet mellem antallet af mislykkede kuld og antallet af rededage (se evt. Mayfield 1975).

Forløbet af ankomsten til søen om foråret afhang af vintervejret (Fig. 1). Overraskende var det, at kun omkring 75% af søens ynglebestand var ankommet i slutningen af april i årene 1987-89, årene med de højeste yngletætheder (Tab. 1).

De fleste reder var anbragt i tagrør *Phragmites australis* og søkogleaks *Scirpus lacustris* (Tab. 1), og 84-93% var anbragt mindre end 30 m fra reder af Hættemåge *Larus ridibundus*.

Æglægningen startede midt i april og kulminerede i første uge af maj (Fig. 2). Kuldstørrelsen var 2-7 æg (Tab. 2) og mindskedes signifikant gennem ynglesæsonen ($p < 0{,}001$-$0{,}05$), undtagen i 1986 ($p > 0{,}5$).

Yngleforsøgene mislykkedes hyppigere under æglægningen end i perioden efter æglægningen (Tab. 3); forskellen var signifikant ($p < 0{,}001$-$0{,}05$), undtagen i 1986 ($p > 0{,}1$). Den gennemsnitlige redesucces for alle årene var 52,5%, men varierede betydeligt (Tab. 4). For alle årene var redesuccesen hos lappedykkerpar, der ynglede i selskab med Hættemåger, i gennemsnit 60,5%; hos par, der ynglede for sig selv, var den kun 17,1%. Årsagerne til mislykkede kuld var ægprædation (89%) og bølgegang (11%).

Ungeproduktionen (Tab. 4) var tilstrækkelig til at opretholde ynglebestanden uden immigration i 1986 og måske også i 1987 og 1985, men ikke i 1988 og 1989.

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