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Factors affecting clutch size and duckling survival in the common goldeneye *Bucephala clangula*

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Female age and condition as well as nesting schedule may affect clutch size and chick survival, which both are important factors affecting the annual reproductive output. Clutch size and chick survival are often interrelated in altricial birds but in precocial species the interrelation is dubious. To study factors affecting clutch size and the survival of ducklings in the common goldeneye *Bucephala clangula*, we examined ringing-recovery data, supplied by ringers, from seven intensively studied goldeneye populations from different parts of Finland. Due to large sample sizes it was possible to distinguish the effects of interrelated variables, e.g. female age and hatching date. Clutch size was significantly associated with both female age and hatching date; first-time breeders and late breeders had small clutches. Clutch size was not associated with female condition. The recovery rate of ducklings was associated with hatching date (low in late broods) but not with female age, condition or brood size. The natal brood sizes of recruited female ducklings did not differ from annual averages, but the natal hatching date of recruited females was earlier and their mothers were older than annual averages in the populations into which the recruited females were born. The timing of nesting was the most important factor affecting the reproductive output of common goldeneye females in a given year.

Key words: brood size, *Bucephala clangula*, clutch size, common goldeneye, duckling survival, reproductive output

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Clutch size and chick survival are important factors affecting the annual reproductive output of individual birds. In addition to environmental circumstances these two factors may be influenced by the age and condition of the birds as well as the timing of nesting. Clutch size and chick survival have been shown to be interrelated in altricial birds (reviews in Lindén & Møller 1989, Dijkstra, Bult, Bijlsman, Daan, Meijer & Zijlstra 1990, Lessells 1991) but in precocial species the effect of brood-size dependent mortality

on reproductive success is controversial (see Milonoff, Pöysä & Virtanen 1995).

The common goldeneye *Bucephala clangula* is a cavity-nesting duck species with nidifugous chicks. Because it readily uses boxes for breeding and females are philopatric (e.g. Dow & Fredga 1983, Savard & Eadie 1989, Pöysä, Runko & Ruusila 1997a) the species provides excellent opportunities for studying which factors affect reproductive output in precocial birds. Sirén (e.g. 1952, 1957) was the

first to take advantage of this possibility and since then the results of many intensive studies have been published (see e.g. references in Milonoff et al. 1995). Although the reproductive performance of goldeneye is one of the most intensively studied among precocial species, some of the main results are still dubious. For example, the independent effects of brood size and hatching date on duckling survival have not been studied (Dow & Fredga 1984). Moreover, many of the conclusions of earlier studies cannot be generalised because they are based on results from one population only (e.g. the effect of female age on clutch size and duckling survival). Other studies have attempted to answer other important but also controversial questions, e.g. whether or not chick survival is dependent on brood size (Milonoff et al. 1995).

In this article we use data from seven intensively studied goldeneye populations from different parts of Finland. Mainly using ringing-recovery data, we study factors affecting clutch size and the survival of ducklings. The factors examined are the age, weight and condition of the females and the hatching date and size of the broods. Differential recruitment may also reveal factors affecting chick survival. We compare the number of brood members, birth dates and age of mothers of recruited females with the mean brood size, mean hatching date and mean age of breeding females in the recruits' population in their year of birth.

Material and methods

The material consists of Finnish ringing-recovery data supplied by ringers. We used data from seven populations (Fig. 1) that had been studied for a period of at least eight consecutive years during 1965-1993 and on which we had the most extensive and complete information. However, the availability of information varied among populations and among individuals in each population. In every analysis we used the populations and individuals of which we had the information needed (see Results).

Incubating females were caught at nest boxes and unringed females were ringed with alloy or steel rings. For several years, some of the females were controlled when breeding, but only one randomly selected observation per female was used in our analyses. The exact age of the breeding females was usually not known, so we used breeding years as an

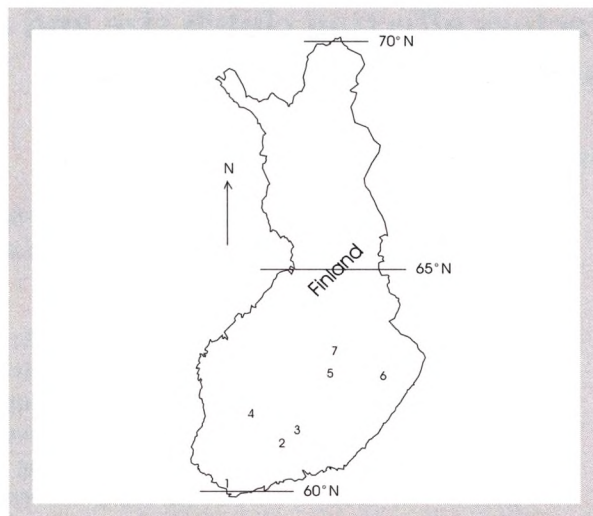


Figure 1. Location of the seven populations studied for at least eight consecutive years during 1965 - 1993.

estimate of age. The age of 33 females was known; they were ringed at the age of 1-2 days. The average age of these females when recorded breeding for the first time was 2.8 years ($SE = \pm 0.2$). Thus, a female of unknown age was considered to be three years old when it was recorded breeding for the first time. Because the weight of a female changes during incubation, we only used weight measurements taken during the last five days of incubation. As a condition index we used the residuals from a regression of weight on wing length, the wing length being the maximum length of the flattened wing.

Clutch sizes larger than 19 were regarded as parasitised and were left out of the analyses. Also smaller clutches may include parasitic eggs (see Dow & Fredga 1984). The effects of parasitism on results related to clutch size will be discussed later (see Discussion), but we assume that other reproductive parameters were probably not affected by parasitic eggs. Newly hatched chicks were ringed with special chick bands (see Pöysä et al. 1997a). Brood size was defined as the number of chicks leaving the nest.

The recovery rate, i.e. the proportion, of banded ducklings after the age of one month was used to measure the survival of broods; high recovery rates should indicate high survival at least to the age of one month. Unnatural deaths (mostly through hunting) between the age of 1-3 months and all later controls were considered. Most duckling mortality occurs during the first weeks of life (Milonoff et al. 1995, Pöysä, Virtanen & Milonoff 1997b and references therein). To study factors affecting the recruitment of

the young we compared the natal brood size and hatching date of female ducklings (N = 31) recruited into the natal population with the average (excluding observations of recruited birds) of the natal year in the respective population. Also the ages of the recruited females' mothers were compared with mean ages of breeding females in the natal populations.

Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used for testing, excluding tests dealing with recruitment rate (see below). Female age was divided into nine classes; age classes 3-10 refer to the corresponding age in years and age class 11 to an age of >10 years (in tables and figures referred to as age classes 3-11, respectively) and brood size was divided into four classes: <7, 7-9, 10-12, >12 ducklings (in figures referred to as 1-4, respectively). Hatching date was divided into three classes (early, average and late, in tables and figures referred to 1-3, respectively), and so was female weight (light, average and heavy) and condition (poor, average, good). This was done by dividing the range between minimum and maximum values into three classes of equal length. To use the data as thoroughly as possible we used two different data bases when testing the effects of independent variables on the recovery rates of ducklings; the smaller one included only broods with captured and identified females (recovery rate A in Table 1) and the larger one also included broods of females which were not captured (recovery rate B). Whenever an ANOVA was statistically significant, we used Fisher's LSD test to do planned comparisons between contiguous variable classes. When necessary, logarithmic transformation was used to make the data fit to normal distribution. Due to significant differences among populations (see Table 1), population was used as a factor in ANOVAs whenever necessary; differences between populations are not within the topics of the present paper and will be

addressed elsewhere. Also the influence of the year was tested but it had no significant effects. Because of the high number of levels (classes) within each factor, especially in female age and population, there were empty cells and cells in which there was only one observation and thus it was not possible to perform ANOVAs with all interaction terms included. Therefore, we used the population with the largest data set (population 7) and calculated partial correlations using continuous variables to confirm results derived from ANOVAs. In ANCOVAs, variables used as covariates were continuous. The factors affecting the recruitment rates of ducklings were tested using Mann-Whitney U-test. All significance levels refer to two-tailed tests. The means are given with standard errors. The statistical analyses were made using SYSTAT procedures (Wilkinson 1992).

Results

Clutch size

Clutch size was significantly associated with female age (Table 1, Fig. 2). However, the only significant difference in the sample of the four populations was between age classes 3 and 4, first-time breeders having smaller clutches. Clutch size was also significantly associated with hatching date, late breeders having small clutches (see Table 1, Fig. 3). Furthermore, in three of the four populations involved in the test early breeders had the largest clutches. Clutch size was not associated with female condition (Table 2).

To confirm the individual effect of female age and hatching date on clutch size we also calculated partial correlations in the largest population (7) by controlling for the effect of each of the variables (partial correlations, female age: $r = 0.206$, $F = 7.33$, $N = 169$, $P < 0.01$; hatching date: $r = -0.231$, $F = 9.34$, $N = 169$, $P < 0.01$; data from population 7 only).

Table 1. Analysis of variance testing for effects of population, female age, hatching date and brood size on clutch size and recovery rate of the young. Samples differ depending on information needed (clutch size: data from populations 1, 2, 3 and 7, N = 417; recovery rate A, only broods for which females were captured: populations 2 and 7, N = 330; recovery rate B, including also broods for which females were not captured: populations 2, 4, 5, 6 and 7, N = 511). Population numbers refer to those in Figures 1-4. Variable classes (see Methods and Figures 2-4) which differ significantly from each other are shown in parentheses.

| Source | Clutch size | | | Recovery rate A | | | Recovery rate B | | |
|---------------|-------------|----|------------|-----------------|----|------------|-----------------|----|------------|
| | F | df | P | F | df | P | F | df | P |
| Population | 9.14 | 3 | 0.00 | 4.95 | 1 | 0.03 | 3.10 | 4 | 0.02 |
| Female age | 2.08 | 8 | 0.04 (3-4) | 0.85 | 8 | 0.56 | | | |
| Hatching date | 14.72 | 2 | 0.00 (2-3) | 8.39 | 2 | 0.00 (2-3) | 7.69 | 2 | 0.001(2-3) |
| Brood size | | | | 0.72 | 3 | 0.54 | 1.01 | 3 | 0.39 |

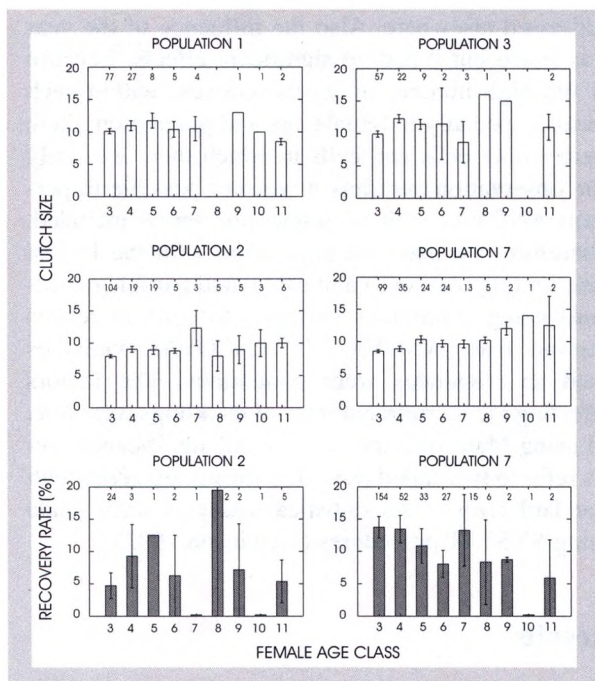


Figure 2. Mean (\pm SE) clutch size and recovery rate of ducklings for females belonging to age classes 3-11 in population 1, 2, 3 and 7. Age classes 3-10 refer to the corresponding age in years and age class 11 to females >10 years old. Population numbers refer to those given in Figure 1. Numbers above bars indicate sample sizes.

Recovery rate

Recovery rate of young was not associated with female age or condition (see Tables 1 and 2 and Fig. 2). The low recovery rate of late broods made the association between hatching date and recovery rate highly significant (see Table 1 and Fig. 3). In most of the populations the recovery rate was highest in the early broods. Recovery rate was not associated with brood size (see Table 1, Fig. 4).

As above, we calculated partial correlations in population 7 to confirm the results derived with female age, hatching date and brood size. When other vari-

Table 2. Separate analyses of covariance for testing the effect of female condition on clutch size (female age and hatching date as covariates) and recovery rate of the young (female age, hatching date and brood size as covariates). See Methods for an explanation of female condition index. Data from population 7, only ($N = 59$).

| Source | Clutch size | | | Recovery rate | | |
|------------------|-------------|----|------|---------------|----|------|
| | F | df | P | F | df | P |
| Female condition | 0.39 | 2 | 0.68 | 1.01 | 2 | 0.37 |
| Female age | 5.54 | 1 | 0.02 | 2.44 | 1 | 0.12 |
| Hatching date | 2.02 | 1 | 0.16 | 0.47 | 1 | 0.50 |
| Brood size | | | | 0.43 | 1 | 0.52 |

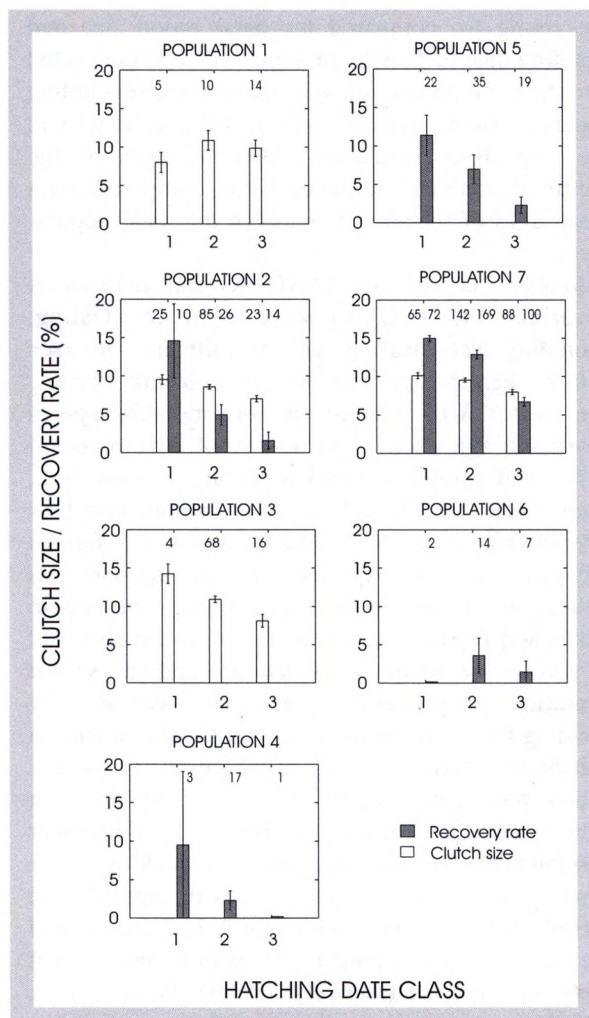


Figure 3. Mean (\pm SE) clutch size and recovery rate of ducklings for hatching date classes 1-3 in populations 1-7. Hatching date classes 1, 2 and 3 refer to early, average and late hatching date, respectively. Population numbers refer to those given in Figure 1. Numbers above bars indicate sample sizes.

ables were held constant, the recovery rate was significantly associated with hatching date (partial correlations, recovery rate A: $r = -0.259$, $F = 20.77$, $N = 292$, $P < 0.001$; recovery rate B: $r = -0.209$, $F = 15.42$, $N = 341$, $P < 0.001$). Recovery rate was associated also with female age (partial correlation, recovery rate A: $r = -0.166$, $F = 8.17$, $N = 292$, $P < 0.01$) but not with brood size (partial correlations, recovery rate A: $r = -0.091$, $F = 2.42$, $N = 292$, $P > 0.10$; recovery rate B: $r = -0.070$, $F = 1.69$, $N = 341$, $P > 0.10$).

Recruitment rate

The natal brood sizes of recruited females (8.9 ± 2.4)

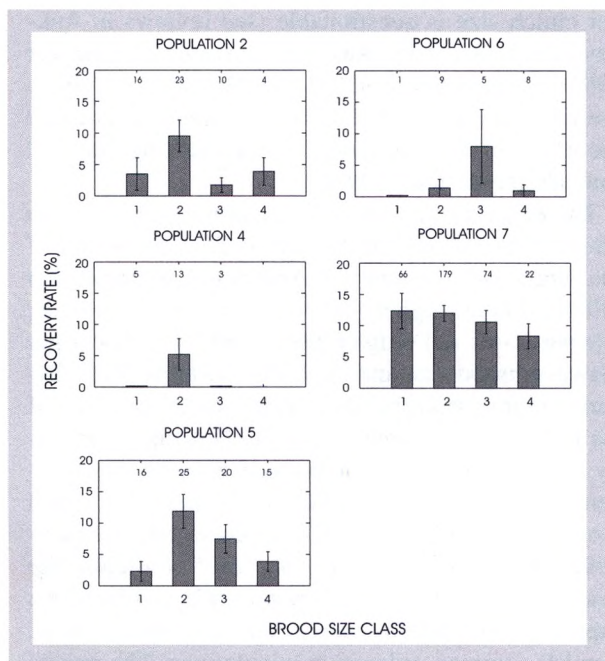


Figure 4. Mean (\pm SE) recovery rate of ducklings in brood size classes 1-4 in populations 2 and 4-7. Brood size classes 1-4 refer to brood sizes of <7, 7-9, 10-12, and >12 ducklings, respectively. Population numbers refer to those given in Figure 1. Numbers above bars indicate sample sizes.

did not differ from annual averages in the populations into which they were born (8.6 ± 0.9 , $Z = 0.60$, $N = 31$, $P > 0.5$) but the date of birth of recruited females (5 June \pm 8 days) was earlier than population averages (11 June \pm 7 days, $Z = 3.98$, $N = 31$, $P < 0.001$; data from populations 2, 4 and 7). The age of mothers of recruited female ducklings (4.8 ± 1.6 years) was higher than the average annual age of mothers in the populations into which the recruited females were born (4.1 ± 1.3 , $Z = 2.49$, $N = 27$, $P < 0.05$).

Discussion

Young first-time breeders laid smaller clutches than older ones. Dow & Fredga (1984) made similar observations in a Swedish goldeneye population. The pattern is general in wildfowl (review in Sæther 1990, see also Forslund & Larsson 1992) although it may not be universal (see MacInnes & Dunn 1988, Hepp & Kennamer 1993). Furthermore, differences in nesting time may confuse the situation. Young females often nest later than older females (Sæther 1990, see also Gauthier 1989, Forslund & Larsson

1992, Hepp & Kennamer 1993) and this pattern was also observed in our populations as well as in a Swedish goldeneye population (Dow & Fredga 1984). Because late clutches generally are small, the observed differences in clutch size between young and old females could merely have been due to the time effect. In our study, first-time breeders had small clutches also after controlling for the hatching time. It seems that breeding age or experience (see Forslund & Pärt 1995 for difficulties in distinguishing these from each other) *per se*, and not e.g. time constraints (*cf.* Curio 1983, Sæther 1990), are important factors affecting the clutch size of young first-time breeders in goldeneye. Contrary to Dow & Fredga (1984), we found no clear tendency towards increasing clutch sizes in older age classes. Similarly, no signs of senescence could be seen in the clutch sizes of the oldest females (review in Forslund & Pärt 1995).

The age or experience of a female did not affect the survival of the young, though, surprisingly, a decrease in recovery rate with increasing female age was found in population 7. However, due to a small sample size of old females (see Fig. 2) the result from population 7 may be incidental. Similarly Dow & Fredga (1984) found no association between the recovery rate of young, indicating survival, and female age although their data were only indicative. Neither did Pöysä et al. (1997b) find any indication in a preliminary analysis that duckling mortality would depend on female age. In many species older females fledge more young than young females (review in Sæther 1990, see also Gauthier 1989, Forslund & Larsson 1992), but this may simply be due to larger clutch sizes of experienced females. The importance of brood rearing experience may also be smaller in nidifugous species than in nidicolous species (*cf.* Sæther 1990, for the common goldeneye see Pöysä et al. 1997b). On the other hand, in our populations the recruited ducklings were mainly from the broods of experienced females, so the effect of female age and experience on fledgling success and recruitment in the common goldeneye needs further research.

Hatching date had the most pronounced effect on clutch size. Late clutches were small, as they also were in two Swedish populations (Eriksson 1979, Dow & Fredga 1984). The same pattern has been demonstrated also in other waterfowl populations (reviews in Toft, Trauger & Murdy 1984, Briggs 1993, see also Forslund & Larsson 1992, Hepp &

Kenamer 1993). However, because young females often breed later than older females, the results may stem from age differences (see above). In our study the effect of hatching date was significant also after controlling for female age (see also Hepp & Kenamer 1993). Small clutches may result from small nutrient reserves of late breeding females (for a review of hypothesis see Hamann & Cooke 1989). We found no association between clutch size and female condition after controlling for hatching date and female age. Thus, late breeding females may have hatched smaller clutches to retain normal weight and condition at the end of incubation. Although there are only few observations of re-nesting in the goldeneye (Mäntysola 1954, Zicus 1990), at least some of the decline in clutch size may also be due to small replacement clutches.

The observed differences in clutch sizes may partly be due to differences in nest parasitism. The proportion of parasitised eggs in a Swedish goldeneye population was high in large and early clutches (Dow & Fredga 1984). However, because the proportion of parasitised eggs varies independently of clutch size parasitism cannot entirely account for the differences in clutch sizes (for more detailed analyses see Dow & Fredga 1984).

Hatching date, after controlling for female age and brood size, also had a pronounced effect on recovery rates of young, late broods having low recovery rates. Dow & Fredga (1984) reached the same conclusion although they did not have enough data to analyse the effect of hatching date directly by controlling for the effect of other variables. The lower survival of late broods has also been observed in black ducks *Anas rubripes* (Ringelman & Longcore 1982) and lesser snow geese *Chen caerulescens caerulescens* (Cooke, Findlay & Rockwell 1984), but in these studies the effect of other variables was not controlled for. Furthermore, the recruitment rate of goldeneye young in early broods was higher than in late broods. The same pattern has been observed in buffleheads *Bucephala albeola* (Gauthier 1989), lesser snow geese (Cooke et al. 1984) and wood ducks *Aix sponsa* (Grice & Rogers 1965, but see Hepp, Kenamer & Harvey 1989).

Female condition at the end of incubation was not related to clutch size or the recovery rate of young. In wood ducks measurements at the end of incubation showed that heavy females laid large clutches (Hepp & Kenamer 1993) but in general the connection between the condition of an incubating female and

her clutch size is questionable (see reviews in Ankney, Afton & Alisauskas 1991, Arnold & Rohwer 1991 and Drobney 1991). To our knowledge, this is the first time waterfowl research takes into account the effect of female condition on duckling survival (but see Pöysä et al. 1997b).

There has been a long lasting controversy about the effect of brood size on the survival of ducklings of the common goldeneye. Andersson & Eriksson (1982) found higher mortality in larger broods, whereas Dow & Fredga (1984) found no association between brood size and duckling mortality. This disparity is important because these studies are two of the few that discuss the brood-size dependent mortality in nidifugous birds and because brood-size dependent mortality has effects on the evolution of clutch size (reviews in Lessells 1991, Rohwer 1992, Stearns 1992). Recently, Milonoff et al. (1995) criticised the results of Andersson & Eriksson (1982) and found no support for brood-size dependent mortality in three Finnish common goldeneye populations. The results of the present study, based on extensive data, are in accordance with Dow & Fredga (1984) and Milonoff et al. (1995). Brood-size manipulation experiments in blue-winged teal *Anas discors* (Rohwer 1985), Canada goose *Branta canadensis* (Lessells 1986) and common goldeneye (Milonoff & Paananen 1993) have given the same result (see also Heusmann 1972, Clawson, Hartman & Fredrickson 1979, but see Safrieli 1975).

The most important factor affecting the reproductive output of common goldeneye females in a given year was the timing of nesting. At high latitudes, ducklings hatching late may have insufficient time to mature before migration (Hepp et al. 1989). Therefore, the value of late offsprings is low, on average. Females which succeed in commencing nesting late may not invest as much into laying and brood rearing as early nesting females (but see Pöysä et al. 1997b). This would lead to small late clutches and low survival and recruitment of young from late broods. However, direct effects of quality differences between early and late nesting females and deteriorating rearing conditions may lead to the same outcome. The importance of the costs of reproduction for the survival and future fecundity of goldeneye females (see Dow & Fredga 1984, Milonoff & Paananen 1993) as well as the influence of re-nesting and continued laying on size differences between early and late clutches are still open questions.

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