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Brief report

Association between conspecific nest parasitism and the timing of breeding in the Common Goldeneye *Bucephala clangula*: an alternative interpretation

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1. Introduction

Conspecific nest parasitism is common in birds, especially among Anatidae (Rohwer & Freeman 1989). Several hypotheses have been put forward to explain its adaptive significance in waterfowl but there are no satisfactory explanations (for a review, see Sayler 1992). Dow and Fredga (1984) found in the Common Goldeneye *Bucephala clangula* that parasitism is more frequent in clutches that are larger and laid earlier in the season. They also found that early-hatched young survive better than late-hatched young (see also Milonoff et al. 1998) and suggested that by laying in the early clutches parasitic females increase the chances of their young being raised successfully. However, Dow and Fredga (1984) did not consider the actual timing of parasitic egg-laying. For example, if parasitic egg-laying mainly occurs early in the breeding season, the prevalence of parasitized nests among early breeding attempts may simply be due to the fact that they were the only nests available for parasitic egg-laying. On the other hand, if parasitic egg-laying also occurs later in the season one might expect that, if hatching date *per se* is important, nests still in the laying phase late in the season should be parasitized randomly. This is because, in this case, all nests have a late hatching date.

In practice it is difficult to distinguish if earliness *per se*, availability or some other factor is the reason why some nests are prone to be parasitized. Here I address this problem by comparing the occurrence of parasitic egg-laying between early but deserted nests (i.e. available for parasitic laying also later in the season) and late nests that are still in the laying phase. Deserted nests are suitable for the comparison, because parasitic females seem not to be able to assess whether the nest has been deserted or whether egg-laying is still in progress (Eriksson & Andersson 1982), i.e. they perceive deserted nests also as being in the laying phase.

2. Methods

In the breeding season 1998 I followed the occurrence and timing of parasitic egg-laying in a goldeneye population in south-east Finland (61°35´N, 29°40´E). Sixtyfour nest-boxes were available for goldeneyes on 30 lakes. Each box was visited several times in May and June (first visit between 4–6 May), all nesting attempts and their fate were recorded (similar procedure was used each year between 1992–1998; described in detail in Pöysä

1999). Here I report on data from 10 nests that were identified as parasitized or non-parasitized based on egg-laying interval, a reliable and commonly used indicator of conspecific nest parasitism in birds (MacWhirter 1989), including goldeneyes (Eriksson & Andersson 1982, Dow & Fredga 1984, Eadie 1989). There were eight additional breeding attempts in 1998, but direct data of the occurrence of parasitic egg-laying in those nests were not obtained. I considered a nest parasitized if more than one egg was laid within 24 hours (nest-boxes 5 and 7–10, Table 1) or if a long skip occurred in egg-laying (nest-box 6, a skip of ≥12 days). Regarding the latter criterion Eriksson and Andersson (1982) used a skip of three days or more to determine nest parasitism and Eadie (1989) used a skip greater than six days so my criterion should be considered conservative. In the nest with the long skip in egg-laying, the first breeding attempt with six eggs was deserted but another female (or several females) laid four additional eggs, incubated the eggs, and the brood hatched successfully. Criterion developed by Eadie (1989) for goldeneyes to identify parasitized nests (based on width, length and weight of eggs) also confirmed that the nest had eggs from more than one female. The date of the appearance of each parasitic egg in each nest was determined as accurately as possible. If the interval between successive visits to a nest was longer than one day I assumed that the parasitic egg was laid in the middle of the visits. The remaining four nests were non-parasitized, i.e. normal egg-laying interval. Two of them were successful and two were depredated during the incubation phase. The initiation date of egg-laying was determined by backdating from the first observation of eggs in the nest, using the criterion that average egg-laying interval is 1.32 days (Fredga & Dow 1983). Mean number of eggs per nest during the first observation was 3.2 (S.D. = 1.4) and did not differ between parasitized and non-parasitized nests (Mann-Whiney U-test, $U = 5.5$, $P = 0.31$). I removed eggs from the deserted nests (nest-boxes 5 and 7–10, Table 1) on 13 June; ducklings left the nest-box number 6 on 12 July.

Statistical tests were run with SYSTAT procedures (Wilkinson 1992). All significance levels are two-tailed.

3. Results and discussion

As in Dow and Fredga (1984), egg-laying was initiated earlier and clutch size was larger in parasitized nests than in non-parasitized nests (egg-laying, Mann-Whitney U-test, $U = 0$, $P = 0.022$; clutch size, Mann-Whitney U-test, $U = 1$, $P = 0.036$; Table 1). However, in five of the parasitized nests (nest-boxes 6–10, Table 1) parasitic egg-laying

Table 1. Summary of nesting parameters in non-parasitized and parasitized nests in 1998. The fate of the previous (year t–n) nesting attempt in each box is also given; 'no' means that the box had not been used for nesting before. The periods during which parasitc egg-laying was observed in the parasitized nests are given (date of the last recognized parasitic egg-laying for each nest in parentheses).

Nest-box number	Initiation of egg-laying	Initiation of incubation	Clutch size	Previous nesting attempt
Non-parasitized nests				
1	15 May	23 May	6	Depredated
2	16 May	25 May	6	Depredated
3	22 May	4 June	8	No
4	23 May	1 June	6	Depredated
Parasitized nests				
5	1 May	6–15 May (14 May)	19	Successful
6	3 May	1–13 June (11 June)	10	Deserted
7	4 May	9–29 May (28 May)	17	Successful
8	5 May	12–22 May (21 May)	12	Deserted
9	6 May	12–27 May (25 May)	14	Successful
10	13 May	16–20 May (18 May)	7	Depredated

occurred also much later in the season, in some cases even several weeks after the initiation of egg-laying. These observations indicate that earliness *per se* cannot be the sole explanation for the occurrence of parasitism in a given nest. It is noteworthy that, at the same time, there were other nests available for parasitism, i.e. nests in which incubation had not yet started (nest-boxes 1–4, Table 1). It is unlikely that, as compared with non-parasitized nests in which egg-laying started later, longer exposure time of early nests was the reason for these nests to be parasitized because parasitic egg-laying usually started 3–7 days after the initiation of normal egg-laying and non-parasitized nests were available for parasitism for 8–12 days (see Table 1). Furthermore, in the parasitized nests, the length of the period of parasitic egg-laying did not increase with the earliness of the nesting attempt ($r_s = -0.143$, $n = 6$, $P > 0.50$). Nor was the date of the last recognized parasitc egg-laying associated with the date of the initiation of normal egg-laying ($r_s = -0.086$, $n = 6$, $P > 0.50$), meaning that last parasitic eggs were not laid in those nests that had been available for a longer time. These observations indicate that longer exposure did not affect the rate of parasitism. Similarly, Morse and Wight (1969) found in the Wood Duck *Aix sponsa*, another diving duck in which conspecific nest parasitism is common, that parasitic laying occurred during all periods of the breeding season when there were active nests available.

I have shown elsewhere (Pöysä 1999) that the occurrence of nest parasitism in a nest-box is associated with nest predation risk in the Common Goldeneye, i.e. nests with lower predation risk will be parasitized more frequently. Also data from year 1998 suggest the same, though sample sizes are small. The previous breeding attempt in all the nest-boxes that were not parasitized in 1998 were depredated, while this was the case only in one of the nest-boxes that did have a parasitized nest in 1998 (Fisher's test, $P = 0.048$, see Table 1, nest-box number 3 excluded because there had not been a previous breeding attempt). Late parasitic egg-laying occurred in those nest-boxes that had not been depredated during the previous nesting attempt, while those nest-boxes that were previously depredated did not get parasitic eggs.

Also the initiation of egg-laying was associated with the fate of the previous breeding attempt: egg-laying initiated later in nest-boxes in which the previous breeding attempt was depredated than in nest-boxes in which it was not depredated (Mann-Whitney U-test: $U = 0$, $P\pi = 0.028$, Table 1; nest-box number 3 excluded). This may be explained by the fact that females that have been unsuccessful in their nesting, especially due to nest predation, usually change their nest site (Dow & Fredga 1984, H. Pöysä unpubl.), leaving the nest-box empty. Those females that change the nest site have later laying dates than those which stay in the same nest-box (Dow & Fredga 1984).

In conclusion, direct observations of the timing of parasitic egg-laying suggest that earliness *per se* does not explain the occurrence of parasitism in a given nest in the Common Goldeneye, at least not in the population studied by me. It seems that nest predation is an important factor affecting both the initiation of egg-laying and the occurrence of conspecific nest parasitism. A breeding attempt in a nest-box that has not been previously depredated is both early and more likely parasitized.

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Selostus: **Loismuninnan ja pesintäaikataulun välinen yhteys telkällä: vaihtoehtoinen tulkinta**

Aikaisemmissa tutkimuksissa on havaittu, että loismunintaa esiintyy telkällä yleisemmin aikaisissa kuin myöhäisissä pesinnöissä. Tämän on tulkittu johtuvan siitä, että loisivat telkkänaaraat pyrkisivät näin parantamaan jälkeläistensä selviytymismahdollisuuksia, sillä yleensä aikaiset pesinnät tuottavat parhaiten jälkeläisiä. Tämän työn tulokset kuitenkin viittaavat siihen, että pesintäaikataulu sinänsä ei vaikuta loisituksi tulemiseen. Sen sijaan loismuninnan esiintyminen oli yhteydessä edellisen pesintäyrityksen kohtaloon; loismunintaa esiintyi erityisesti niissä pöntöissä, joita ei oltu ryöstetty edellisen pesinnän aikana. Pesäpredaatio näyttäisi vaikuttavan sekä pesintäaikatauluun että loismuninnan esiintymiseen: pesintä alkaa aikaisemmin ja tulee todennäköisimmin loisituksi pöntössä, jota ei ole edellisvuonna ryöstetty.

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