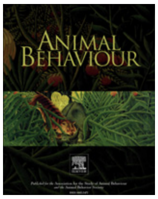
Animal Behaviour 80 (2010) 881–886

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



# Response of parasitically laying goldeneyes to experimental nest predation

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ARTICLE INFO

*Article history:*
Received 30 March 2010
Initial acceptance 29 April 2010
Final acceptance 9 August 2010
Available online 16 September 2010
MS. number: 10-00225R

*Keywords:*
*Bucephala clangula*
common goldeneye
conspecific brood parasitism
information reliability
nest predation
personal information
protein fingerprinting
public information

Conspecific brood parasitism (CBP) has been identified as an integral life history component in birds. Recent empirical and theoretical studies suggest that nest predation is an important ecological factor affecting the occurrence and evolution of CBP; however, behavioural responses of parasites to nest predation remain unexplored. Here we report on a field experiment addressing the ability of parasitically laying common goldeneye, *Bucephala clangula*, females to respond to nest predation, based either on their own experience or on public information. Females that started parasitic laying in a nest and afterwards experienced partial clutch predation stopped laying in the nest. However, nests that faced partial clutch predation earlier in the season were not avoided by other parasitically laying females later in the season; these later-laying females had not themselves experienced the partial clutch predation in the nest. Hence, considering within-season responses to nest predation, a parasite uses its own experience, rather than public information, in laying decisions and nest choice. The rate of parasitic laying in the experimental nests decreased from the first to the last year of the experiment. Because the experimental nests never produced a successful clutch, this finding suggests that parasites used information on the ever-failing nature of the nests and avoided laying in them. Our results offer new experimental evidence to support the hypothesis that safety and success of nest sites play important roles in CBP.

Conspecific brood parasitism (CBP) is an alternative reproductive tactic in which a female lays one or more eggs in the nest of another individual of the same species who takes care of incubation and rearing the young. CBP is widespread in birds (Yom-Tov 2001), but only recently has it been recognized as an important life history component, whereby females can increase their reproductive output (Petrie & Møller 1991; Arnold & Owens 2002; Lyon & Eadie 2008). A good empirical example of the importance of CBP in a life history context is Åhlund & Andersson's (2001) finding that common goldeneye, *Bucephala clangula* (hereafter, goldeneye) females that combine parasitic laying with normal nesting are able to double their fledgling production.

Early hypotheses proposed to explain the occurrence of CBP considered nest depredation as an important determinant of CBP in both evolutionary (Payne 1977; Rubenstein 1982) and ecological time (Hamilton & Orians 1965; Yom-Tov 1980). Indeed, nest depredation may have promoted the evolution of CBP, although not through random risk spreading, as suggested earlier (Payne 1977; Rubenstein 1982), but through informed risk spreading, whereby parasites are able to assess nest predation risk and lay accordingly (Pöysä & Pesonen 2007). Moreover, a recent model focusing on partial clutch predation and predator dilution effects within a clutch found that distributing eggs among multiple nests would result in higher fitness, underscoring the potential role of nest predation in the evolution of CBP (Roy Nielsen et al. 2008). In ecological time, parasitic laying may occur as a within-season response to nest loss (Hamilton & Orians 1965; Yom-Tov 1980). This type of short-term response to nest destruction has been demonstrated in several species (e.g. Haramis et al. 1984; Emlen & Wrege 1986; Feare 1991; Stouffer & Power 1991; McRae 1998); more generally, it has been considered under the 'nest loss' hypothesis in which parasitic laying is seen as a salvage strategy (Eadie et al. 1988; Lyon & Eadie 2008).

In general, breeding birds have a remarkable capacity to assess and respond to changes in nest predation risk (reviewed in Lima 2009; Martin & Briskie 2009). Similarly, the response of parasitically laying females to nest predation may be more sophisticated than previously anticipated and considered in the 'nest loss' hypothesis. For example, McRae (1997) found in the moorhen, *Gallinula chloropus*, that, under a high level of nest predation, females that had not been brood parasites before laid some eggs parasitically before initiating their own nest. However, the mechanism through which parasitically laying females assessed nest

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doi:10.1016/j.anbehav.2010.08.009

predation risk remained unknown, and at least some of the females had lost their own nest before they started laying parasitically (McRae 1998). Parasitic goldeneye females have been found to discriminate between risky and safe nest sites and lay parasitic eggs accordingly (Pöysä 1999a, 2003a). This ability appears to be based on the information about nest success gathered by prospecting females the year before actual parasitic laying (Pöysä 2006), exemplifying use of public information (i.e. information derived from the performance of others; see Danchin et al. 2001, 2004, 2008) in the choice of target nests by parasites.

There are no studies attempting to clarify whether individuals pursuing a parasitic tactic are able to respond immediately to nest predation during the laying period. Nor do we know whether information on nest predation is transferred among parasites within the laying period and what kind of information is needed to induce a response. For example, is information on clutch predation in a particular nest transmitted, within the same season, to individuals that have not themselves experienced the clutch predation, a phenomenon that would involve use of social information (see Danchin et al. 2008)? An earlier experiment, in which partial clutch predation was simulated before parasites started egg laying and in which the parasites did not have experience of predation in a given nest site, suggested that previous experience of nest predation is an important factor in parasitic laying (Pöysä 2003a).

We carried out an experiment addressing the ability of parasitic goldeneye females to respond immediately to nest predation. The goldeneye is a medium-sized hole-nesting diving duck that readily accepts nestboxes (e.g. Pöysä & Pöysä 2002; Åhlund 2005). CBP is frequent in goldeneyes, and parasitic eggs start to appear in a nest early in the host's own laying sequence (see Åhlund 2005). A nest may be parasitized by more than one female, and a single parasite may lay up to seven eggs in the same nest (Andersson & Åhlund 2001; Åhlund 2005). In our experiment, parasites were allowed to start egg laying in experimental nests and partial clutch predation was simulated in the nests during the laying period in 4 successive years. Specifically, the experiment addressed two main questions. (1) Does a parasite stop egg laying in a nest that suffers partial clutch predation during the laying period? (2) Does partial clutch predation result in an overall aversion towards the predated nest sites among parasites within the same season? In addition, as earlier work in the species suggests that information about previous nesting success affects the probability that a given nest site is parasitized (Pöysä 1999a, 2006), we examined whether the attractiveness of individual experimental nest sites decreases across years; this trend is to be expected because the experimental nests did not produce a successful nest in any year.

## METHODS

### *Experimental Setting*

The study was carried out in 2001–2004 at 15 lakes in southeast Finland (61°35′N, 29°40′E) using the same experimental system as in an earlier experiment conducted in 1999–2000 (see Pöysä 2003a, b for details). In brief, in spring 1999 two new nestboxes (hereafter, experimental nests) were erected in a visible place at the shoreline of each of the 15 lakes. The position of each experimental nest was recorded with a GPS device (Garmin GPS Map 60CSx). The mean ± SE distance between the two experimental nests within a lake was 132 ± 8 m (range 69–199 m, $N = 15$), and from the two experimental nests within a lake to the nearest experimental nest on a different lake 702 ± 59 m (range 302–1613 m, $N = 30$; maximum distance between any two experimental nests 7371 m). Access of goldeneye females to the experimental nests was controlled with a door on the entrance hole; the experimental nests were open for parasitic egg laying only (a 35-day period each year, starting immediately after egg laying in real common goldeneye nests in the area began), and were not used for normal nesting between 1999 and 2004 (i.e. the door on the entrance hole was removed when the experiment started and put back again when the experiment ended in each year, see also Pöysä 2003a).

The experiment started and ended on the same day at all the experimental lakes in a given year (Table 1). On the first day of the experiment, three decoy eggs (chicken eggs dyed to mimic the colour of goldeneye eggs) were positioned close together in the middle of the experimental nests. An earlier experiment revealed that real nests and nests with only decoy eggs were equally parasitized by goldeneye females (Pöysä 2003b). In 2001, before the experiment started, one of the two experimental nests at a given experimental lake was randomly chosen as a treatment nest. Each year between 2001 and 2004 (same treatment nests every year), two of the three eggs in the treatment nests were destroyed, that is, the eggs were emptied and about one-third of the shell was removed to simulate a goldeneye egg destroyed by pine marten, *Martes martes*, or mink, *Mustela vison*, during the egg-laying period. Because the rate of parasitic laying in the experimental nests varied between years (see below), we adjusted on an annual basis the timing of this predation simulation (12–16 days since the start of the experiment; see Table 1). The other experimental nest with three eggs was left intact (control nest). A given nest was either a treatment nest or a control nest in all the 4 years to avoid confusion from possible carryover effects. Allocation of the experimental nests to the two groups (treatment or control) was random with respect to parasitic activity in an earlier experiment conducted in 1999–2000, in terms of the mean number of parasitic eggs laid per nest and the mean number of females that laid parasitically per nest in that experiment (data from Pöysä 2003a; mean ± SE number of parasitic eggs: treatment nests: 1.5 ± 0.6, $N = 15$; control nests: 1.6 ± 0.6, $N = 15$; two-tailed, paired-sample $t$ test: $t_{14} = 0.191$, $P = 0.852$; mean ± SE number of parasitic females: treatment nests: 0.5 ± 0.2, $N = 15$; control nests: 0.4 ± 0.2, $N = 15$; two-tailed, paired-sample $t$ test: $t_{14} = -0.494$, $P = 0.629$).

Checking and restoring the experimental nests were done as described for the earlier experiment (Pöysä 2003a). In brief, both the treatment nest and the control nest at a given lake were checked on each visit, at a mean ± SE interval of 1.4 ± 0.01 days (range 1–2 days). On each visit, we numbered new parasitic goldeneye eggs, removed them (under licence from The Ministry of Agriculture and Forestry, Finland) from the experimental nests for later analyses (see Egg albumen sampling and analyses below), and restored the

**Table 1**

Timing of the experiment, timing of parasitic laying and total number of parasitic eggs laid (treatment nests/control nests) before and after the predation simulation in each year

| Year | Timing of the experiment | | | Timing of parasitic laying | | Number of parasitic eggs laid | | |
|---|---|---|---|---|---|---|---|---|
| | Start | Predation simulation | End | First egg | Last egg | Before | After | Total |
| 2001 | 25 April | 7 May | 30 May | 26 April | 29 May | 33 (13/20) | 38 (18/20) | 71 |
| 2002 | 25 April | 10 May | 30 May | 1 May | 26 May | 17 (13/4) | 15 (6/9) | 32 |
| 2003 | 28 April | 14 May | 2 June | 29 April | 1 June | 14 (10/4) | 10 (4/6) | 24 |
| 2004 | 25 April | 10 May | 30 May | 4 May | 18 May | 7 (6/1) | 3 (3/0) | 10 |