



Co-parasites preferentially lay with kin and in safe neighbourhoods: experimental evidence from goldeneye ducks



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ARTICLE INFO

Article history:

Received 1 November 2013

Initial acceptance 16 January 2014

Final acceptance 28 February 2014

Available online 14 April 2014

MS. number: 13-00912R

Keywords:

Bucephala clangula

common goldeneye

conspecific brood parasitism

kinship

nest predation risk

philopatry

social interaction

Conspecific brood parasitism (CBP) is an alternative reproductive tactic in several animal taxa. Recently the role of kinship in CBP has been in focus, and some studies have demonstrated high host–parasite relatedness in avian CBP systems. However, high natal and breeding site fidelity of hosts and parasites complicates the interpretation of previous observational findings, and the mechanisms leading to high host–parasite relatedness remain unknown. Some recent findings suggest that broadening the scope of the study of interactions may cast light on these mechanisms. We studied relatedness between parasites laying in the same nest (co-parasites) and factors possibly driving relatedness patterns between co-parasites in the common goldeneye, *Bucephala clangula*. Based on a field experiment, controlling for site fidelity and host role, we report here that both relatedness and safety of the nest site, and their interaction, affected the likelihood of two females engaging in co-parasitism. At the population level, parasites indeed seemed to lay eggs preferentially with kin. Analyses at a finer spatial scale revealed that high relatedness between co-parasites was not due to the philopatry effect only. Parasites engaging in co-parasitism also laid in safer neighbourhoods than parasites that did not engage in co-parasitism; the number of nondepredated nesting attempts the previous year was higher for the parasites engaging in co-parasitism. However, the interaction between relatedness and safety of the nest site suggests that co-parasitism at dangerous lakes was more likely to involve relatives. Our results provide the first experimental evidence that nest predation risk and interaction between related parasites are associated with kin-biased co-parasitism in a CBP system.

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In conspecific brood parasitism (CBP) a female lays eggs in the nest of another individual of the same species who takes care of incubation and rearing the young. CBP occurs in several animal taxa (Sato, 1986; Summers & Amos, 1997; Tallamy, 2005) but is particularly widespread in birds (Yom-Tov, 2001) in which it potentially plays an important role in a wide range of behavioural processes such as determination of optimal clutch size (Lyon, 1998) and lifetime reproductive success (Åhlund & Andersson, 2001), and the evolution of breeding systems (Lyon & Eadie, 2008). Knowing the evolutionary and ecological drivers of CBP essentially adds to our understanding of these fundamental behavioural phenomena. Moreover, as the decision whether to parasitize or not is made by the parasite in the first place, identification of proximate cues

affecting laying decisions of parasites may help to explain the evolution and occurrence of CBP.

Recent intriguing findings of high host–parasite relatedness in some avian CBP systems suggest that kinship plays a role in CBP (Andersson & Åhlund, 2000; Andersson & Waldeck, 2007; Jaatinen, Jaari, O'Hara, Öst, & Merilä, 2009; Jaatinen, Öst, Gienapp, & Merilä, 2011; Tiedemann et al., 2011; Waldeck, Andersson, Kilpi, & Öst, 2008; see also Eadie & Lyon, 2011). In general, kin selection and cooperation can promote the evolution of CBP if the costs of parasitism are sufficiently low (Andersson, 2001; Jaatinen, Lehtonen, & Kokko, 2011; López-Sepulcre & Kokko, 2002). However, the mechanisms leading to high host–parasite relatedness remain unknown. Some earlier findings suggest that relatedness between parasites laying in the same nest may also be high (Roy Nielsen, Semel, Sherman, Westneat, & Parker, 2006, p. 495), and visits to nest sites in pairs or small groups by non-nesting females (i.e. potential parasites) have been observed in many brood-parasitic species (Eadie & Gauthier, 1985; Semel & Sherman, 2001; Zicus & Hennes, 1989). Moreover, there is evidence from

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goldeneyes (Åhlund, 2005) and other brood-parasitic species (Semel & Sherman, 1986) that two or more parasites may visit a nest and lay eggs jointly or in quick succession.

Regarding avian CBP systems, high relatedness between hosts and parasites was first documented in the common goldeneye, *Bucephala clangula* (hereafter, goldeneye), a hole-nesting duck (Andersson & Åhlund, 2000). As is typical for several avian species in which CBP is frequent (Lyon & Eadie, 2000), goldeneye females have high natal and nest site fidelity, resulting in local female lineages with high relatedness (Ruusila, Pöysä, & Runko, 2000). A successful female may use the same nest site for several years (Dow & Fredga, 1985), and female offspring have even been observed to return to nest in their birth nest site, if unoccupied, 2 or more years later (Pöysä, Runko, & Ruusila, 1997). In such a system parasitism of kin can occur incidentally as a by-product of random host (nest) choice (McRae & Burke, 1996) or because both host and parasite independently prefer to lay in the same high-quality nest site (e.g. low nest predation risk; Paasivaara, Rutila, Pöysä, & Runko, 2010; Pöysä, 1999, 2003a, 2006). Regarding goldeneyes, Andersson and Åhlund (2000) concluded that natal and breeding philopatry of females was not enough to explain the high host–parasite relatedness in their study; instead, they suggested that kin recognition and discrimination by host females was involved. Indeed, Andersson and Åhlund (2000) reported on observations in which host females, while in the nest, prevented other females from entering the nest (see also Åhlund, 2005). However, because goldeneye females do not attend the nest but visit it for egg laying only once per day or every 2 days (Åhlund, 2005; Pöysä, 2004; Zicus & Hennes, 1995), opportunities for host females to prevent other females entering the nest and in this way discriminate against unrelated parasites are limited during the egg-laying period (see Pöysä, 2004). Hence, kin recognition and discrimination by host females alone may not suffice to explain patterns of relatedness in parasitized nests.

Previous studies documenting high relatedness between hosts and parasites have not been able to separate the roles of host relatedness and nest site quality in affecting the egg-laying decision of parasites. While the outcome of kinship-driven and nest site quality-driven parasitic laying may be the same, the identification of actual mechanisms is essential for understanding how behavioural decision rules in the context of CBP evolve. In addition, we argue that investigating only host–parasite interaction may lead one to miss potentially important components in the social context of CBP. It has been found in many brood-parasitic species that more than one parasite may lay in a given nest (e.g. Andersson & Åhlund, 2001; McRae & Burke, 1996; Roy Nielsen et al., 2006; Waldeck et al., 2008). For example, Andersson and Åhlund (2001) reported for the goldeneye that up to five different parasites laid in the same clutch that was incubated by the host female and eventually hatched. Previous analyses have focused on relatedness between host and parasite, whereas relatedness and interaction among parasites has received no attention at all.

We suggest that studying laying decisions of and relatedness between parasites, while simultaneously controlling for any effects of the host, may provide useful information on the mechanisms resulting in the patterns of relatedness observed in parasitized nests. In this paper we focus on factors that potentially explain why parasitic goldeneye females lay in the same nest, i.e. engage in co-parasitism. We experimentally induced parasitic egg laying in decoy nests that did not have a host at all and that had never produced offspring. Our experimental design thus allowed, for the first time, control of any effects of host–parasite interactions and birth nest fidelity of parasites on the laying decisions of parasites. Specifically, we addressed two main questions. First, does relatedness explain the tendency of females to engage in co-parasitism?

Second, is the occurrence of co-parasitism associated with nest predation risk? In the connection of these questions we also examined whether there is any interaction between relatedness and nest predation risk in explaining the tendency of females to engage in co-parasitism, i.e. could the safety of the nest site affect the likelihood that the parasites engaging in co-parasitism are related? In addition, to assess the possible role of philopatry in driving relatedness between co-parasites, we examined changes in the degree of relatedness between parasites in relation to the distance between the experimental nests used for egg laying by the parasites.

METHODS

Experimental System and Parasitic Eggs

The study was carried out in 2001–2007 in southeast Finland (61°35' N, 29°40' E) using the same experimental system as in an earlier experiment (Pöysä, 2003a, Pöysä, 2003b). Two new nest-boxes (hereafter, experimental nests) were erected in a visible place at the shoreline of each of the 15 lakes (Fig. 1). The position of each experimental nest was recorded with a GPS device (Garmin GPS Map 60CSx). Mean \pm SE distance between the two experimental nests within a lake was 132 ± 8 m (range 69–199 m, $N = 15$), and mean \pm SE distance from the two experimental nests within a lake to the nearest experimental nest on a different lake was 702 ± 59 m (range 302–1613 m, $N = 30$; the maximum distance between any two experimental nests was 7371 m, i.e. lakes A and I in Fig. 1). The experimental nests were open for parasitic egg laying only (a 35-day period each year, starting immediately after egg laying in real goldeneye nests in the area began), and were not used for normal nesting between 1999 and 2007. Access of goldeneye females to the experimental nests was controlled with a door on the entrance hole; the door was removed when the experiment started and put back again after the experiment (i.e. there was open access for the 35-day period).

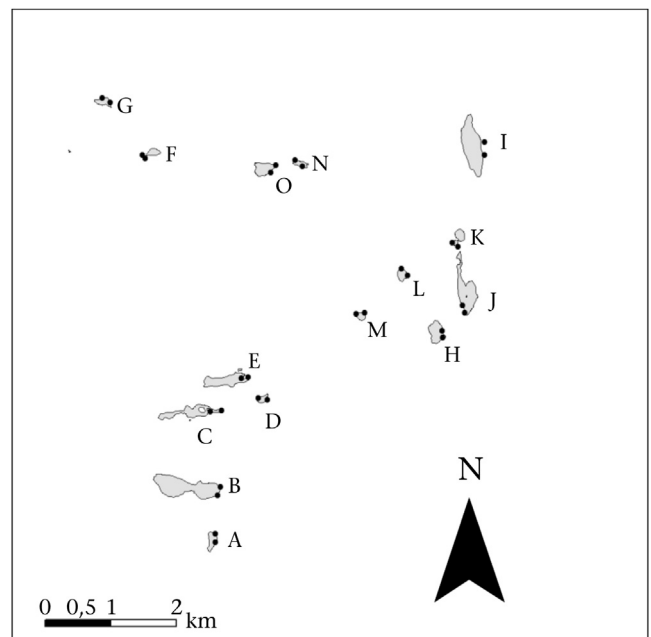


Figure 1. Map of the study area, showing the distribution of the experimental nests at the 15 lakes used in the experiment (A–O; each lake had two experimental nests).

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