

NEWS AND VIEWS

PERSPECTIVE

The relative role of relatives in conspecific brood parasitism

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Conspecific brood parasites lay their eggs in the nests of other females in the same population, leading to a fascinating array of possible 'games' among parasites and their hosts (Davies 2000; Lyon & Eadie 2008). Almost 30 years ago, Andersson & Eriksson (1982) first suggested that perhaps this form of parasitism was not what it seemed—indeed, perhaps it was not parasitism at all! Andersson & Eriksson (1982) observed that conspecific brood parasitism (CBP) was disproportionately common in waterfowl (Anatidae), a group of birds for which natal philopatry is female-biased rather than the more usual avian pattern of male-biased natal philopatry. Accordingly, Andersson (1984) reasoned (and demonstrated in an elegantly simple model) that relatedness among females might facilitate the evolution of CBP—prodding us to reconsider it as a kin-selected and possibly cooperative breeding system rather than a parasitic interaction. The idea was much cited but rarely tested empirically until recently—a number of new studies, empowered with a battery of molecular techniques, have now put Andersson's hypothesis to the test (Table 1). The results are tantalizing, but also somewhat conflicting. Several studies, focusing on waterfowl, have found clear evidence that hosts and parasites are often related (Andersson & Åhlund 2000; Roy Nielsen *et al.* 2006; Andersson & Waldeck 2007; Waldeck *et al.* 2008; Jaatinen *et al.* 2009; Tiedemann *et al.* 2011). However, this is not always the case (Semel & Sherman 2001; Anderholm *et al.* 2009; and see Pöysä 2004). In a new study reported in this issue of *Molecular Ecology*, Jaatinen *et al.* (2011a) provide yet another twist to this story that might explain not only why such variable results have been obtained, but also suggests that the games between parasites and their hosts—and the role of kinship in these games—may be even more complex than Andersson (1984) imagined. Indeed, the role of kinship in CBP may be very much one of relative degree!

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Jaatinen *et al.*'s (2011a) study highlights several intriguing and as yet not fully resolved issues. First, they confirm results from an earlier study (Jaatinen *et al.* 2009) showing that relatedness influences conspecific brood parasitism (CBP) in the Barrow's goldeneye (*Bucephala islandica*; Fig. 1), a species of cavity-nesting sea duck well known to engage in parasitic egg-laying (Eadie 1989; Eadie & Fryxell 1992). CBP in this species was more frequent among related females that nested in close proximity (Jaatinen *et al.* 2009, 2011a). Female natal philopatry is pronounced in the Barrow's goldeneye (Eadie *et al.* 2000), and it is possible the spatial proximity of kin could account for this pattern. However, Jaatinen *et al.* (2011a) show that relatedness and distance independently affected the extent of parasitism, suggesting that natal philopatry alone cannot provide an explanation. Similar patterns of elevated host–parasite relatedness after controlling for spatial proximity of kin have been reported for other species (Table 1). The novel observation of Jaatinen *et al.*'s newest study is that the nesting status of the parasite profoundly altered the influence of relatedness on host–parasite interactions. Parasitic females that also had a nest of their own ('nesting parasites') increased the number of eggs laid in a host nest with increasing relatedness to the host, whereas parasites without a nest of their own ('non-nesting parasites') did not. Apparently, females within the same population may be using different decision rules with respect to relatedness, and the effects of kinship on CBP may be far more subtle than previously appreciated.

The observation that nesting and non-nesting females differ in aspects of their parasitic behaviour is not, in itself, surprising—parasitic females in these two contexts face different constraints and life history trade-offs (Lyon & Eadie 2008; e.g. nesting females have the option of laying eggs in their own nests, whereas non-nesting females do not). Indeed, empirical results to date, including those of Jaatinen *et al.* (2011a), indicate that non-nesting parasites typically have lower fecundity and reproductive success relative to both nesting parasites and females that nest without parasitizing (Lyon 1993; Åhlund & Andersson 2001). Truly surprising is Jaatinen *et al.*'s (2011a) observation that nesting and non-nesting parasites show different responses to host–parasite relatedness. Why do they differ? One possibility is that this pattern is simply a consequence of the observed differences in fecundity of the two groups

Table 1 A summary of recent studies that have tested for evidence of relatedness between hosts and parasites in avian conspecific brood parasites

Species	Evidence of host-parasite relatedness?	Evidence of local kin structure?	Relatedness > expected spatially	r Host-Parasite	r Population	Costs or benefits measured?	Method	Source
Common moorhen (<i>Gallinula chloropus</i>)	Mixed	Yes	No	—	—	No	DNA minisatellite fingerprints	McRae & Burke (1996)
Common goldeneye (<i>Bucephala clangula</i>)	Some parasitism between relatives	Limited dispersal of both sexes	Not greater than expected	—	—	(but discussed)		
	Yes	Not tested; high female philopatry	Yes	0.132	—	No	Protein fingerprints 50 bands	Andersson & Åhland (2000)
Wood duck (<i>Aix sponsa</i>)	Number of parasitic eggs also increased with relatedness	No (parasites avoid relatives)	No	—	—	No	Behavioural observation	Semel & Sherman (2001)
Common goldeneye (<i>B. clangula</i>)	No	Not tested	Significantly less likely to parasitize local kin	—	—	Yes	Field measures	Pöysä (2004)
Wood duck (<i>A. sponsa</i>)	Relatedness unlikely to explain CBP	Not tested	Not measured	—	—	Yes	Field measures	Pöysä (2004)
	Yes (for primary parasites)	No	Yes (for primary parasites)	0.04 (all) 0.11 (primary parasites)	0.01–0.02	No	5 microsatellites	Roy Nielsen <i>et al.</i> (2006)
Common eider (<i>Mollissima somateria</i>)	Yes	No	Yes	0.122 (all) 0.126, 0.162 (two colonies)	–0.065 (neighbours 1–10 m)	No	Protein fingerprints 30 bands	Andersson & Waldeck (2007)
Common eider (<i>M. somateria</i>)	Yes	Yes	Possibly Host-parasite relatedness > close neighbours in 1 of 2 analyses	0.18–0.21	0.09 (neighbours)	No	Protein fingerprints 51 bands	Waldeck <i>et al.</i> (2008)
Barnacle goose (<i>Branta hucopis</i>)	No	Weak	No	0.04	–0.0008	No	Protein fingerprints 28 bands	Anderholm <i>et al.</i> (2009)
Barrow's goldeneye (<i>Bucephala islandica</i>)	Yes	Females within 40 m more closely related	No	0.08	–0.015	No	19 microsatellites	Jaatinen <i>et al.</i> 2009
Common eider (<i>M. somateria</i>)	Number of parasitic eggs increased with relatedness	Slight decline in relatedness with distance	Host-parasite relatedness similar to neighbours	0.39 (mean) 0.48, 0.28 (different sites)	0.11 (neighbours)	No	7 microsatellites	Tiedemann <i>et al.</i> (2011)
Common eider (<i>M. somateria</i>)	Yes	No	Yes	0.39 (mean) 0.48, 0.28 (different sites)	0.0	No	7 microsatellites	Tiedemann <i>et al.</i> (2011)

CBP, conspecific brood parasitism.



Fig. 1 A pair of Barrow's goldeneyes (*Bucephala islandica*) in central British Columbia. Photo credit: Bruce Lyon.

of females. Because non-nesting parasites typically realize only 1–2 total offspring, their opportunity to differentially allocate parasitic eggs in relation to host relatedness should, on average, be more limited than that of nesting parasites (7–8 offspring). This 'ceiling effect' could be tested with randomization methods to assess whether parasites lay eggs randomly with respect to host characteristics (Emlen & Wrege 1986), given their potential fecundity and pool of available hosts.

A second possibility—that these responses reflect fundamental differences in parasitic tactics—is much more intriguing and puzzling. An important issue here is whether the benefits of kinship apply to the brood parasite (laying eggs parasitically) or to the host (accepting brood parasitic eggs from a donor)? It is easy to see why relatedness might be relevant from a host's perspective: if parasitic offspring are relatives, then the host gains some indirect fitness from raising related offspring, and she may also enable some reproduction in a relative where otherwise none might be possible (Andersson 1984). This latter benefit seems unlikely in Jaatinen *et al.*'s (2011a) study because it predicts that the non-nesting females would be more likely to parasitize relatives, opposite to the pattern detected. The key question, then, is why would nesting brood parasites lay more parasitic eggs when the hosts are relatives? Jaatinen *et al.* (2011a) offer several suggestions, including: (i) nesting parasites have better information about females in the surrounding nests and so can target relatives more reliably, (ii) nesting parasites are constrained to area-restricted search of host nests and, with fewer potential host nests available, preferentially parasitize relatives whose resistance may be lower, (iii) non-nesting parasites may have lower egg-laying capacity, perhaps due to lower production of key hormones, or (iv) nesting parasites employ a cooperative strategy, whereas non-nesting parasites are truly parasitic.

These hypotheses are interesting and plausible, but they fail to fully elaborate the fitness benefits or costs to each group of parasites, and so a complete explanation for this intriguing pattern remains elusive. This highlights a second

issue of growing importance in the study of kinship and CBP—the need for a full understanding of the direct and indirect fitness benefits of CBP to *both* hosts and parasites. Most recent work has focused only on the assessment of r , testing the hypothesis that hosts and parasites are related and looking for elevated measure of kinship against background levels imposed by patterns of local kin structure (Table 1). This is an important start. Yet, Hamilton's (1964) rule, the foundation for studies of kin selection, is about more than just r —it is equally about the costs and benefits of the behaviour to all individuals involved. Very few studies have fully quantified the direct and indirect fitness benefits of CBP, yet such assessments will be critical, as several recent models reveal (Zink 2000; Andersson 2001; Lopez-Sepulcre & Kokko 2002; Jaatinen *et al.* 2011b). If parasitism is costly to the host, parasitic females would increase their indirect fitness by avoiding relatives (Zink 2000); conversely, if costs are low, parasitism of relatives may be favoured (Andersson 2001; Lopez-Sepulcre & Kokko 2002; Jaatinen *et al.* 2011b). Empirical studies of the costs and benefits of parasitism to both hosts and parasites are clearly needed if we are to fully evaluate the role of kinship in the evolution of CBP [for an informative example, see Pöysä (2004)]. In addition, such information will allow us to determine whether kinship is central to the evolution of CBP itself, or whether it simply enables parasitic females to fine-tune their parasitic tactics to obtain additional fitness than would otherwise be possible. The former would be supported if the costs and benefits interact such that parasitism is only beneficial when host and parasite are related.

Jaatinen *et al.*'s (2011a) study highlights a third area of increasing interest to the study of kinship and CBP—the role of kin recognition. The fact that parasitism occurred more often than expected given the spatial proximity of kin, in both this and other studies (Table 1), and that some but not all groups of parasites respond differentially to their degree of relatedness to hosts, implies some method of kin discrimination. Further evidence derives from observations for several species that the parasitic females that lay the majority of eggs in a host nest are more closely related to the host than parasites that lay only a few eggs (Andersson & Åhlund 2000; Roy Nielsen *et al.* 2006; Waldeck *et al.* 2008; Jaatinen *et al.* 2009). These observations raise two questions: (i) how do females recognize kin (and who does the recognizing—parasite, host or both) and (ii) is kin recognition essential for kin selection to operate? Little research has explored the mechanisms of kin discrimination in conspecific brood parasites. Possibilities include familiarity through previous experience, perhaps via growing up together as brood mates as suggested by Andersson & Åhlund (2000) for common goldeneyes (*Bucephala clangula*), or some form of self-referent phenotype matching in the absence of previous experience (e.g. Hauber & Sherman 2001; and see Dickinson 2007). Alternatively, shared traits among kin such as timing of breeding (Andersson & Waldeck 2007) or similar nest site preferences (e.g. natal habitat preference induction; Davis & Stamps 2004) might simply predispose individuals to interact nonrandomly with

relatives in the population, but without actual kin recognition. This is a rich area for future research.

To what extent is kin recognition necessary to promote CBP via kin selection? Recent models by Andersson (2001), Lopez-Sepulcre & Kokko (2002) and Jaatinen *et al.* (2011b) suggest that kin recognition may be critical, again depending on the costs to the host. If CBP is costly, parasites should avoid relatives unless the costs are small and hosts can accurately recognize (and differentially accept) eggs laid by relatives (Lopez-Sepulcre & Kokko 2002). Intriguingly, one model predicts that, in the presence of relatedness and recognition, hosts would achieve higher fitness by reducing their own clutch size and gaining the indirect benefits of eggs laid in their nest by relatives (Jaatinen *et al.* 2011b). This is consistent with Jaatinen *et al.*'s (2009) observation that hosts reduced their clutch size in response to parasitism and the magnitude of reduction increased with host–parasite relatedness. Nonetheless, it is important to keep clear the distinction between kin selection and kin recognition. In general, kin selection does not require kin recognition—in sufficiently kin-structured populations, kin selection can occur without kin recognition (Hamilton 1964; West & Gardner 2010). Conversely, the occurrence of kin recognition does not necessarily mean that kin selection is at work—kin recognition might simply be part of a fine-tuning strategy of brood parasites, as noted above.

Recent efforts to develop more integrated models of CBP illustrate clearly that there is considerable richness and depth to this seemingly surreptitious behaviour; indeed, it is now apparent that a broad spectrum of interactions is possible, ranging from purely parasitic to completely cooperative, regulated by the interplay between relatedness and recognition, and depending on the prevailing ecological and social conditions (de Valpine & Eadie 2008; Jaatinen *et al.* 2011b). Theoretical models have currently outpaced empirical studies, but the novel studies of Jaatinen *et al.* (2011a) and others (Table 1) are starting to fill the gap. Three things are clear: (i) relatedness unquestionably plays some role in CBP for many, but not all species (Table 1); (ii) there is tantalizing evidence of kin recognition and discrimination, but the mechanisms are not well explored and (iii) there is a marked paucity of information on the direct and indirect benefits of CBP to both parasites and hosts in relation to kinship. A challenge for future research will be to determine whether the evolution of brood parasitism *per se* requires kin selection or, instead, if the inclusive fitness obtained from parasitism between relatives merely augments fitness already gained from parasitism. New models provide fertile grounds for future empirical work, and molecular tools will undoubtedly play a central role in this research. However, we echo our previous call to collect the critical data not only on relatedness, but also on the social and ecological constraints and the costs and benefits of the behavioural alternatives (Lyon & Eadie 2000). As Dickinson (2007) summarized succinctly, the most interesting results will come from coupling the genetics to behaviour and demography. Given the considerable range of possible costs and benefits of CBP among and within species, it is

perhaps not unexpected that we find different patterns of parasitism in relation to kinship (Table 1). The role of relatives is indeed relative.

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