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COMMENTARY

Female-biased natal philopatry, social parallels, and conspecific brood parasitism in New World quails and waterfowl

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ABSTRACT

Brood merging and conspecific brood parasitism are common in some waterfowl and New World quails. A previously unrecognized, unusual similarity between them—female-biased natal philopatry and local relatedness—may enable indirect inclusive fitness gains in brood parasitism and merging. New World quails offer a rare possibility to test the role of female-biased natal philopatry in brood parasitism, brood merging, and other aspects of sociality and to help clarify the evolution of these traits.

Keywords: brood merging, conspecific brood parasitism, female philopatry, inclusive fitness, quail, relatedness, waterfowl

Filopatría natal sesgada de la hembra, paralelos sociales y parasitismo de nidada de individuos conespecíficos en codornices del Nuevo Mundo y en aves acuáticas

RESUMEN

La unión de nidadas y el parasitismo de nidada de individuos conespecíficos son comunes en algunas aves acuáticas y en codornices del Nuevo Mundo. Una similitud inusual previamente no reconocida entre ellas, la filopatría natal sesgada de la hembra y el parentesco local, pueden permitir ganancias indirectas en la adecuación biológica inclusiva en el parasitismo y la unión de nidadas. Las codornices del nuevo mundo ofrecen una rara posibilidad de evaluar el rol de la filopatría natal sesgada de la hembra en el parasitismo de nidada, en la unión de nidadas y en otros aspectos de sociabilidad, y pueden ayudar a clarificar la evolución de estos rasgos.

Palabras clave: Adecuación biológica inclusiva, aves acuáticas, codornices, filopatría de la hembra, parasitismo de nidada de individuos conespecíficos, parentesco, unión de nidadas

Waterfowl (Anatidae) are unusual among birds in that females, not males, often nest near their birth site (female-biased natal philopatry; Greenwood 1980, Anderson et al. 1992, Mabry et al. 2013). Some local females may therefore be related, with potential inclusive fitness benefits in social interactions such as brood parasitism (Andersson 1984) and brood merging (Eadie et al. 1988). Recent molecular evidence points to female-biased natal philopatry also in some New World quails (Odontophoridae), opening possibilities for analyses of its causes and of the role of female relatedness in conspecific brood parasitism (CBP), brood merging, and other aspects of sociality.

Waterfowl and quails are members of Anseriformes and Galliformes, respectively, sister groups that together form the ancient clade Galloanserae (Hackett et al. 2008, Winkler et al. 2015). CBP and brood merging may occur in the ancestor of Galloanserae, or even earlier, perhaps in the dinosaur ancestor of birds, given that these traits occur also in ratites (e.g., Bertram 1992, Taylor et al. 2000), sister

group of all other birds (Hackett et al. 2008). Natal philopatry, as far as we know, is female-biased in Anseriformes (Anderson et al. 1992), but its direction varies in Galliformes. Several New World quails have female-biased natal philopatry (discussed below), whereas male bias appears to be the rule in, for example, grouse (e.g., Mabry et al. 2013: fig. 2).

Conspecific brood (nest) parasites lay eggs in nests of other females of the same species: hosts that carry the costs of raising the joint brood. A parasite can benefit by reproducing in situations where it would otherwise not do so (e.g., because of lack or loss of a nest) or by laying extra eggs in addition to those in its own nest, and by avoiding parental care for the parasitic eggs. CBP occurs among many egg-laying animals and particularly in birds; it is frequent in waterfowl and gallinaceous birds that have large clutches and precocial, self-feeding young, both traits that facilitate successful parasitism (Yom-Tov 1980, Andersson 1984, Geffen and Yom-Tov 2001, Lyon and Eadie 2008).

In waterfowl, local females are likely to be related because of their natal philopatry, a crucial part of the hypothesis that kin selection plays a role in CBP and enhances its evolution in this group (Andersson 1984). The hypothesis suggests that indirect fitness gain can partly compensate the host for costs of being parasitized and can sometimes even increase her inclusive fitness. If the parasite has increased reproduction as a consequence of parasitizing a relative, this gain provides an indirect inclusive fitness benefit for the host, in proportion to host–parasite relatedness (Andersson 2017).

Brood merging (amalgamation) is also common in waterfowl, offspring of different pairs being raised together in a mixed brood that is cared for by one or more females or pairs (Eadie et al. 1988, Beauchamp 1997). Female relatedness may also play a role in brood merging (Eadie et al. 1988, Eadie and Savard 2015), for instance in Common Eider (*Somateria mollissima*; Jaatinen et al. 2012).

Male-biased juvenile dispersal and female-biased natal philopatry have been found or suspected in a few other birds (Mabry et al. 2013), among them some New World quails (Odontophoridae; Gullion 1960, Leopold 1977, Calkins et al. 1999, Fies et al. 2002). Philopatry has not been studied with molecular-genetic methods in most New World quails. In species in which it has been studied, the evidence indicates female-biased natal philopatry and local genetic relatedness. This is the case in California Quail (*Callipepla californica*) and Gambel's Quail (*C. gambelii*). Females in those species usually remained in their natal group, but a high proportion of young males dispersed, and genetic distance (F_{ST}) among 5 populations was consistently higher for females than for males (Gee 2003). In Northern Bobwhite (*Colinus virginianus*), genetic analyses of pairwise relatedness (r) vs. distance found male-biased dispersal and female philopatry, with about twice as high relatedness for females as for males at the shortest distances (<1,600 m; Berkman et al. 2013: fig. 6). Studies of additional species are needed to find out how widespread female-biased natal philopatry is in New World quails.

There is also evidence of frequent CBP or “dump nests” in New World quails (Klimstra and Roseberry 1975, Johnsgard 1988, Brown et al. 1998, Calkins et al. 1999). CBP was recently estimated with microsatellite analyses to occur in 19% of nests of Northern Bobwhites in Florida (Faircloth 2008) and in 21% of nests in Oklahoma (Orange 2015). Merging of broods during the breeding season is also frequent, several paired adults with young forming communal groups (Brown et al. 1998, Lott and Mastrup 1999, Faircloth et al. 2005, Calkins 2007). All 11 merged broods observed in California Quails by Lott and Mastrup (1999) involved nearest-neighbor adults.

Are female neighbors, host–parasite pairs, and brood-merging parents in quails often genetic relatives, as in

waterfowl, with potential inclusive fitness consequences (see references in Eadie and Lyon 2011, Andersson 2017)? Neighbor relatedness in quails has not been studied directly, but adults in family groups of California Quails during the breeding season in 1 of 3 yr were more related to one another than to other adults in the population (Calkins 2007; see also Gee 2003). Quails form social groups (“coveys”) during the nonbreeding season, and mean relatedness within such groups of Northern Bobwhites was also higher than background levels (Faircloth 2008).

It has not been fully recognized, in the context of CBP and brood merging, that some New World quails are probably female-philopatric. They therefore offer possibilities to test, in another group, the kin-based and other hypotheses on brood parasitism, brood merging, and other aspects of sociality suggested for female-philopatric waterfowl (Andersson 1984, 2017, Eadie et al. 1988, McKinnon et al. 2006, Roy Nielsen et al. 2006, Tiedemann et al. 2011, Jaatinen et al. 2012). I predict that brood-merging females, as well as hosts and parasites, in female-philopatric quails are more closely related than other females in the population, with potential for indirect inclusive fitness benefits in CBP and brood merging. High relatedness can arise without kin recognition, simply because neighbors under strong natal philopatry often happen to be close kin, as in Common Moorhen (*Gallinula chloropus*; McRae and Burke 1996). But hosts and parasites can be more closely related than neighbors if there is kin recognition and discrimination against unrelated females (Waldeck et al. 2008, Andersson et al. 2015).

Because there are other important differences between waterfowl and New World quails, which have less extreme sex differences in natal philopatry, are smaller and have lower survival, these predictions may fail for several reasons, which will then be of interest to clarify. For example, life expectancy is low in these quails, with few exceeding 4 yr of age (Brown et al. 1998, Calkins et al. 1999). Maximum age is several decades in waterfowl, well over 30 yr in eiders, and some females were older than 15 yr in the study by Tiedemann et al. (2011). The presence of relatives, with potential for beneficial kin interactions, seems to increase with female age (e.g., Tiedemann et al. 2011, Jaatinen et al. 2012), perhaps making such interactions more frequent in waterfowl.

The generality of the hypotheses suggested for female-philopatric waterfowl can be tested by molecular-genetic studies of relatedness among nesting neighbors and other females in quail populations (and among males, given that quails have biparental care), of hosts and parasites in CBP, and of adults with merged broods. Combining such genetic analyses with video recording of behavioral interactions between marked individuals at nests and elsewhere can

further clarify their relationships and reproductive tactics (Andersson et al. 2015). By comparison with other galliform birds, it may also be possible to analyze causes and consequences of female-biased vs. male-biased natal philopatry, which are incompletely understood (Dobson 2013, Mabry et al. 2013). In Northern Bobwhite, Berkman et al. (2013) suggested that male-biased dispersal to access females may yield higher fitness than staying and defending a territory with resources that are likely to fluctuate. A suitable group for comparison may be partridges in the genus *Alectoris*, such as Red-legged Partridge (*A. rufa*) and Chukar (*A. chukar*), which seem to have male-biased natal philopatry, frequent CBP, and brood merging (Green 1983, Casas et al. 2009, Alkon 2015).

The results reviewed above suggest that molecular-genetic and behavioral studies of CBP and brood merging in relation to kinship in New World quails are likely to shed light on the importance of female-biased natal philopatry and relatedness for these traits. Comparison with male-philopatric species in Galliformes may also help explain the evolution of female-biased natal philopatry.

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