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Favouritism or intrabrood competition? Access to food and the benefits of philopatry for red-cockaded woodpeckers

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In species showing delayed natal dispersal, broodmates vary in natal dispersal timing and strategy, where some choose to disperse early while others delay. In the cooperatively breeding red-cockaded woodpecker, *Picoides borealis*, typically only one juvenile male per brood delays dispersal despite the lifetime fitness benefits associated with delayed dispersal. We sought to determine whether adult favouritism or intrabrood competition over the distribution of natal food resources provides a mechanism for the persistence of individual variation in natal dispersal strategies. We show that fledgling red-cockaded woodpeckers form male-biased, linear dominance hierarchies as a result of frequent aggressive conflicts. For males, high nestling condition relative to male broodmates was a strong predictor of future dominance, and this condition–rank relationship persisted after individuals reached nutritional independence. Adults were never observed interfering with broodmate conflicts, and were only rarely aggressive towards fledglings. Adults showed no overt favouritism towards offspring when targeting individual fledglings during provisioning early in the postfledging period. However, conflict rates increased with decreasing targeted-feeding rates, suggesting that access to resources is an important function of dominance hierarchies. After fledglings were developmentally able to compete for positions near foraging adults, first- and second-ranking males were fed more often than subordinate females. Of the juvenile males surviving to spring, subordinates were more likely to disperse during their first year than were their dominant broodmates. Together, our findings suggest that for young red-cockaded woodpeckers, intrabrood social rank provides a mechanism for prioritized access to natal resources and variation in natal dispersal strategy.

The social environment within family groups is an important but often overlooked factor in the evolution and maintenance of dispersal strategies (Ekman et al. 2002). Tolerance of current offspring by parents and retained offspring from previous broods is a critical step for the development of delayed dispersal behaviour (Ekman & Griesser 2002). Nepotistic behaviour directed towards offspring may create a natal safe haven for birds waiting for reproductive opportunities (Kokko & Ekman 2002; Griesser & Ekman 2004, 2005; Eikenaar et al. 2007). Theory predicts that parents should allocate resources evenly among their brood (Fisher 1930), but extended parental care may provide an opportunity for weaker individuals to gain access to resources if at least one parent directs increased feeding effort towards late-hatched, or otherwise competitively disadvantaged, young (Gottlander 1987; Ploger & Medeiros 2004). Parents may directly benefit from extended parental care if the offspring they tolerate are better able to attain higher-quality breeding territories or have higher first-year survival (Ekman et al. 1999; Griesser et al. 2006). Alternatively, social interactions with adults on the natal territory may lower the relative benefits of philopatry. In times of food shortage, adults could limit access to resources to all offspring or to a selected subset of offspring, and thereby indirectly encourage early dispersal behaviour (Ekman & Griesser 2002). In situations where increased group size is costly to future reproduction, resident adults would benefit from evicting surplus offspring (Eikenaar et al. 2007).

Social interactions with broodmates may also influence dispersal strategies. Allocation of resources on the natal territory may be determined in part by nestling competition (Mock & Parker 1997). Direct physical aggression (interference competition) or scramble competition for food brought by adults or preferred positions within the nest can result in a biased distribution of resources in both siblicidal (see review in Drummond 2006) and nonsiblicidal species (Gottlander 1987; McRae et al. 1993; Ostreiher 1997; Tanner et al. 2008). In grey jays, *Perisoreus canadensis*, socially dominant siblings expel subordinates and thereby gain full access to stored food on the natal territory and increased winter survival (Strickland 1991).

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The cooperatively breeding red-cockaded woodpecker, *Picoides borealis*, presents a unique case where typically only one juvenile male per brood delays dispersal and remains home as a helper, while all other male and female juveniles disperse to search for independent breeding opportunities by their first spring (J. R. Walters, personal observation). Female helpers are uncommon, but their frequency differs between populations (Koenig & Walters 1999). As estimated by a demographic model, young males adopting the delayed dispersal strategy have equal or slightly higher first-year survival than males that disperse within their first year (Walters et al. 1992b). The probability that early dispersers will obtain a breeding vacancy and become a breeder is very low, and young breeders have poor reproductive success (Walters et al. 1992b). These combined factors lead to greater lifetime reproductive success for young males choosing to delay dispersal and remain on the natal territory during their first year, and thus explain the occurrence of this tactic in this system (Walters et al. 1992b). Since delayed dispersal has beneficial fitness consequences for juvenile males, and only one sibling per brood remains home as a helper, there is the opportunity for competition among broodmates over dispersal strategy. Natal dispersal strategy has been linked to nestling size at banding (age 5–10 days), where male nestlings with lower body mass relative to their brothers are more likely to disperse during their first year (LaBranche 1992; Pasinelli & Walters 2002). Also, males from broods with more male fledglings are more likely to disperse early, suggesting the importance of intrabrood social interactions on dispersal behaviour (Pasinelli & Walters 2002). However, the mechanisms explaining how size differences between broodmates during the nestling and fledgling stages can influence individual dispersal choices remains unknown. The combined roles of adult allocation of resources and intrabrood competition have yet to be applied as possible mechanisms regulating first-year natal dispersal in this system.

Aims and Predictions

In the present study, we sought to explore how social interactions with resident adults and broodmates, particularly during resource allocation, may provide a causal mechanism for individual variation in first-year natal dispersal strategies among broodmates. We present our research in four parts. In Part 1, we formally describe social conflicts experienced by red-cockaded woodpecker fledglings during the postfledging dependent period. We predicted that, within broods, fledglings would form male-biased dominance hierarchies, given that social dominance of males over females is a species-wide pattern in adults (Jackson 1994). We also predicted that intrabrood conflict would increase with decreasing social distance, since closely matched individuals would have to dispute more frequently to establish and maintain rank. As such, fledgling males should engage in aggressive conflicts more frequently with closely ranked broodmates than with distantly ranked broodmates and adults. These basic behavioural descriptions have not been previously published, yet they are a critical first step in our understanding of how intrabrood social dynamics shape individual life history strategies.

In Part 2, we first explore the link between fledgling social rank during the postfledging dependent period with relative competitive ability as a nestling. We predicted that, within sexes, nestling condition relative to that of broodmates (resource holding power; Parker 1974), would be positively associated with intrabrood social dominance as a fledgling. Second, we assess the permanence of this size–rank relationship by comparing the sizes of male broodmates with known social rank after they were nutritionally independent but still remained with their family on the natal territory.

In Part 3, we address the main question of interest for this paper: how intragroup social interactions contribute to the allocation of food resources among broodmates during the postfledging dependent period. To do this, we examine three nonmutually exclusive hypotheses. First, broodmates control the allocation of food as fledglings through intrabrood competition. Support for this hypothesis includes frequent conflict among broodmates and little or no conflict between adults and fledglings. If broodmates, rather than adults, control allocation of food, then parents should distribute food evenly among fledglings regardless of social rank or sex early in the postfledging period, when adults control food distribution by targeting sedentary young. However, fledgling food allocation should shift, favouring socially dominant individuals later in the postfledging period after fledglings become developmentally capable of scramble competition near foraging adults. If broodmates use competition to gain access to limited resources, then intrabrood aggression should increase as food availability decreases. The second hypothesis is that adults control distribution of natal resources, favouring low-ranking fledglings as a compensating form of extended parental care. Here, we expect frequent aggression by adults towards fledglings directed primarily at high-condition fledglings, and we expect infrequent aggression among broodmates. If parents favour low-condition young during provisioning, then we expect feeding rates for the lowest-ranking fledglings to be higher than that of their dominant broodmates regardless of the degree of fledgling mobility. Third, adults control the distribution of natal resources postfledging, favouring high-ranking fledglings over their low-ranking broodmates. Under this hypothesis, adult–fledgling aggression would be common and targeted towards subordinate young, and intrabrood conflicts would be rare. Parents would favour dominant fledglings when making feeding decisions and this bias would persist regardless of the degree of fledgling mobility.

Lastly, in Part 4, we extend the three hypotheses introduced in Part 3 by considering how postfledging survival and natal dispersal patterns of fledglings differ according to intrabrood social rank. Here we focus on juvenile males primarily, since only males regularly adopt both the ‘stay and help’ and the ‘depart and search’ strategies. In line with our first hypothesis that intrabrood competition controls access to resources on the natal territory, we predicted that socially dominant fledglings would be more likely to survive through their first winter. Surviving dominant fledglings would then choose to remain on the natal territory as helpers during their first spring, since this is the life history strategy with greater lifetime fitness benefit in this species. Alternatively, subordinates would be less likely to survive the winter and more likely to disperse by their first spring. Under our second hypothesis that parents control resources and favour subordinate fledglings, we predicted that subordinates would not show reduced overwinter survival as a result of the benefits provided through extended parental care. Also, subordinates surviving the winter should be just as likely, or more likely to remain on the natal territory as their dominant broodmates. The predictions for postfledging survival and dispersal under our third hypothesis match the first; if parents control access to resources and favour dominant fledglings, then we would expect overwinter survival of dominants to be higher than that of subordinates, and subordinates would be more dispersive than dominants.

GENERAL METHODS

Study Population and Species Biology

The study population consists of over 220 individually banded family groups located in the Sandhills region of southcentral North