

American robin nestlings compete by jockeying for position

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Summary. We investigated whether nestling American robins (*Turdus migratorius*) were capable of influencing food distribution in their nests by perceiving that certain sectors of the nest received a relatively high proportion of feedings and positioning themselves accordingly. Feeding observations were obtained from videotape recordings taken at different stages of the nestling period. Parents generally arrived at a predictable location on the nest rim and allocated proportionally more food to nestlings in the central position. The degree of nestling movement was significantly positively correlated with variation in the predictability of parental arrival locations on the nest rim. Furthermore, nestlings moved more in broods suffering brood reduction. This suggests that when competition for food is intense and the location of parental arrival is predictable, nestlings respond by jockeying for access to the most favorable (i.e., central) position in the nest. We conclude that jockeying for position by nestlings can influence the pattern of food allocation by parents, and that hungry nestlings can improve their competitive standing against nestmates by moving to positions where parents are more likely to feed them.

Introduction

In asynchronously hatching birds, size and age differences among nestlings confer advantages on older siblings and facilitate brood reduction when food is limited (Lack 1968; Hahn 1981). The incidences of starvation in passerine nestlings has been well documented (Hussell 1988), but little attention has been paid to the mechanisms by which brood reduction occurs (Mock 1987; Magrath 1990). Hatching asynchrony can be controlled by the parents by incubation scheduling (Magrath 1990). Still, it is unclear to what extent brood reduction is con-

trolled by the parents beyond the point of hatching, and whether nestlings themselves exert some control over the way that parents distribute resources. In this study, we investigate the potential for American robin (*Turdus migratorius*) nestlings to influence the distribution of food delivered by parents by jockeying for the best position in the nest.

By examining the influence that chicks have on the distribution of food in the nest, we seek to document a novel mechanism by which siblings might compete for parental feedings. In egrets and herons, for example, competition between nestlings is manifested in terms of aggression, and commonly escalates to the point of siblicide (Mock 1984; Mock et al. 1987). The extent of sibling aggression appears to be related to the ease with which food delivered by parents can be monopolized by individual chicks. Asynchronously hatching passerine nestlings lack well-developed motor skills and weaponry, and thus are incapable of directly eliminating sibling rivals (but see Alvarez et al. 1976 for an exception).

Passerine nestlings compete for food by more subtle means, resulting in differential survival of nestmates. Several studies have documented the effect of individual begging effort on the adjustment of parental feeding rate both to individual nestlings and to the entire brood (Bengtsson and Rydén 1983; Smith and Montgomerie 1991; Redondo and Castro 1992). Indeed, Smith and Montgomerie (1991) showed that American robin nestlings beg more both when they are hungrier and when their siblings increase their begging. Here, we describe a second mechanism whereby nestlings manipulate parental distribution of food by jockeying for the best positions in the nest.

The relative positions of nestlings in the nests of a few species have been found to affect their chances of receiving food. Rydén and Bengtsson (1980) demonstrated that parent great tits (*Parus major*), European blackbirds (*Turdus merula*) and fieldfares (*T. pilaris*) favored certain positions in the nest when distributing food. Tree swallow (*Tachycineta bicolor*) and pied flycatcher (*Ficedula hypoleuca*) parents also allocate food preferentially to nestlings near the front of the nest box (Stein 1986;

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Gottlander 1987). In cavity nesters, like great tits, tree swallows and pied flycatchers, the parent arrives at a consistent location when delivering food so the location of food sources is highly predictable by nestlings. Food source location might be expected to be more variable in an open-nesting species like the American robin. Hence, our first objective was to determine the extent of variation in the arrival location of parents at the nest.

The potential for nestlings to monopolize food delivered by parents is likely to be enhanced if parents preferentially feed nestlings at particular positions in the nest. Therefore, our second objective was to determine the predictability of food distribution by parents relative to their arrival location.

Given that parental arrival locations and food distribution patterns are predictable to some extent, then there would be some potential for individual nestlings to influence whether they got fed on a given parental visit. Therefore our final objective was to determine the extent to which that potential was realized by the smallest (i.e., last-hatched) nestlings in each nest. We discuss the implications of this form of sibling competition for brood reduction.

Methods

This study was conducted at the Queen's University Biological Station, approximately 45 km north of Kingston, Ontario, Canada, between May and August 1987 and 1988. Adult robins were caught in mist nets and individually color-banded. We visited nests daily and marked eggs as they were laid (Weatherhead et al. 1991) to facilitate the monitoring of hatching order so that relative ages of nestlings could be determined. Other general details of the study area and methods are provided by Weatherhead and McRae (1990).

We videotaped nests using a tripod-mounted camera placed 1–4 m from the nest and left unattended for the duration of the filming episode. This provided a non-intrusive method of observation as the robins appeared oblivious to the camera. Feeding behavior was recorded between 0700 and 1800 hours EDT on different days throughout the 13-day nestling period. Whenever possible, we placed the camera at an angle that allowed the position of all nestlings to be determined. The orientation of the video camera was kept constant for all taping sessions at each nest.

Eight nests were videotaped in 1987, and 12 in 1988. Most of these nests were built either on platforms affixed to tree trunks and buildings or on the buildings themselves (e.g. on window sills). The full range of brood sizes found in this population (two to four) were represented in our sample. Most observations were made in the afternoon, when availability of cameras and favorable lighting conditions most often coincided. To maximize the amount and quality of information obtained, more time was devoted to nests in which filming conditions were optimal.

Taping sessions lasted an average of 63 min (± 14 SE, $n = 193$ sessions) each, with a maximum of two taping sessions per nest per day. Prior to filming, each nestling was marked with a spot of white acrylic paint on an individually distinctive part of the bill. Each nestling was weighed and banded at age 7 days, the 7th day after the first nestling in the brood hatched.

For videotape analysis, we divided each nest into five sectors of equal area that nestlings could occupy: a circular central position and four peripheral positions formed by radially dividing the area outside the central circle (see Bengtsson and Rydén 1981 for a similar method). The nest rim was similarly partitioned into four segments corresponding to the outer edges of the four peripheral nestling positions. These segments were used to assign parental

perch locations during feeding visits. In most nests, one or two of these quadrants were inaccessible to parents due to obstacles.

From the videotapes, we recorded the sex, arrival time, departure time and perch location of the parent, and the size of its food load, each time it visited the nest. Food loads were categorized as small (less than or equivalent to the parent's beak size), medium (from the size of the parent's beak to 4 times that size), or large (greater than 4 times the size of the parent's beak). We also recorded the identity of any nestling(s) fed, each nestling's position in the nest (as defined above) at the time of feeding and the order in which each nestling was fed. For each feeding visit, we estimated the proportion (to the nearest 10%) of the total food load that each nestling received.

For between-nest comparisons of the spatial relationships between nestlings and parents during each parental visit to the nest, we defined the positions of nestlings relative to the parent's perch location. Thus, nestling positions were recorded as "near" (directly beneath the parent's perch on the nest rim), "far" (furthest from the parent on the opposite side of the nest), "side" (left or right sectors on either side of the parent's perch), or "centre" (the central position).

Statistical analyses were conducted either on average values per nest or on the data from each nest separately. When data were analyzed for each nest separately, statistical significance was determined using sequential Bonferroni analysis (Rice 1989). For such analyses, significance is expressed as a tablewise error rate for the number of analyses performed. The sample size of nests varies among analyses because factors such as predation and inclement weather resulted in variation in the extent to which some nests were sampled. To summarize data in some figures, we used box plots in which 10th, 25th, 50th, 75th and 90th percentiles are denoted by horizontal lines and all data points outside the 10th and 90th percentiles are indicated (see Cleveland 1985).

Results

Parent arrival locations

To assess the potential for nestlings to influence food allocation by their parents, we first asked whether the parents at each nest tended to arrive at a particular location on the nest rim. Assuming that both male and female parents appear as equivalent food sources to nestlings, we pooled the data for both parents at each nest to compare the observed distribution of parental perch positions against an expected random distribution, using goodness-of-fit tests. Because we wanted to determine whether parents arrived at locations predictable by the nestlings, we calculated expected values using only those quadrants actually visited by the parents at each nest.

At 14 of 20 nests the distribution of parental visits was significantly different from random (G -test, $G = 8.2$ – 272.5 , tablewise $P < 0.05$, $n = 14$ nests), with one or two quadrants used most often at each nest. On average, over all nests 67% of visits were to the most-visited quadrant (Fig. 1). Thus parental arrival locations were potentially predictable by their nestlings, though to a varying degree from nest to nest.

Distribution of food loads

Robin parents occasionally removed food from a nestling's gape immediately after introducing it. For nests at

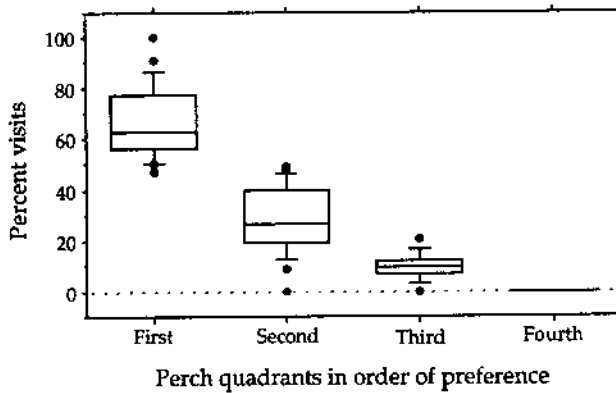


Fig. 1. Percentage of visits by both parents in which the most-preferred (*first*), as well as *second*, *third*- and *fourth*-most-preferred perch quadrants were used. Each *box plot* summarizes data for 20 nests. Only those quadrants accessible to the parents were tallied at each nest

which we observed at least 20 feeding visits, an average of 6% of those visits per nest resulted in food being taken away from a nestling after it had been offered one or more times (range 0–19%, $n = 15$ nests with 22–202 feeding visits each). In the following analyses of food load distribution, we considered only those “feedings” in which food was actually left in the nestling’s mouth.

For the 17 nests in which the identity of all nestlings could be determined on the videotapes, an average of 55% of the feeding visits (range 15–75%, based on 8–114 feeding visits per nest) resulted in a single nestling receiving the entire food load. Thus, for more than half of the feeding visits, there was no division of food loads among nestlings. When food was distributed between two or more nestlings during a feeding visit, the mean percentage of the load allocated to the first nestling (51%, range = 38–63%) was significantly greater than the mean percentage given to each subsequently fed nestling (40%, range = 31–50%; Wilcoxon test, $T = 12$, $P < 0.005$, $n = 15$ pairs of nest means based on 5–44 divided food loads per nest). There were no differences in the mean proportions of the food load received by first-fed nestlings in broods of different sizes (Kruskal-Wallis $H = 3.78$, $P > 0.10$, $df = 2$, $n = 3$, 5 and 7 broods of 2, 3 and 4 nestlings respectively). Since the first nestling fed received most or

all of the food load on each visit, we considered only the first-fed nestling when comparing the success of nestlings in obtaining food.

To determine whether nestlings in certain positions were more likely to be fed, we analyzed the distributions of first feedings relative to positions actually occupied on each feeding visit. Each nest was analyzed individually. For each parental visit to the nest, we recorded which positions were occupied by nestlings. We then recorded whether the nestling occupying it received food first. For each nest, we tabulated the proportion of first feedings that went to each position and expressed these as percentages. This procedure allowed us to compare nests with different brood sizes. There was significant variation in the proportion of feedings given to each position (Kruskal-Wallis $H = 14.1$, $P < 0.01$, $df = 3$), and the centre position received the highest proportion (Fig. 2).

Jockeying for position

In this section we ask whether the predictability of food delivery was related to the degree of nestling movement by comparing variation in both of these factors among nests. We first recorded the position of each nestling during each parental visit to determine whether some positions were occupied more often than others. For the 15 nests with more than 10 feeding visits in which all nestling positions were recorded, the central position was not occupied significantly more often than the other positions (Kruskal-Wallis $H = 2.1$, $P = 0.55$, $df = 3$; Fig. 3). However, 40.4% of all first feedings went to that position. In comparison only 1.7–16.1% (medians, overall range 0–39%) of first feedings at these nests went to each of the other positions. Thus, there was a clear advantage to chicks occupying the central position. Given that the central position is superior, the predictability of parental arrival location would seem unimportant since the central position remains the same regardless of where the parents arrive on the nest rim. However, the central position is only advantageous when the nestling is facing in the right direction (i.e. toward the parent). Thus nestlings should jockey more to get into the central position when they can predict where the parents will arrive on the nest rim.

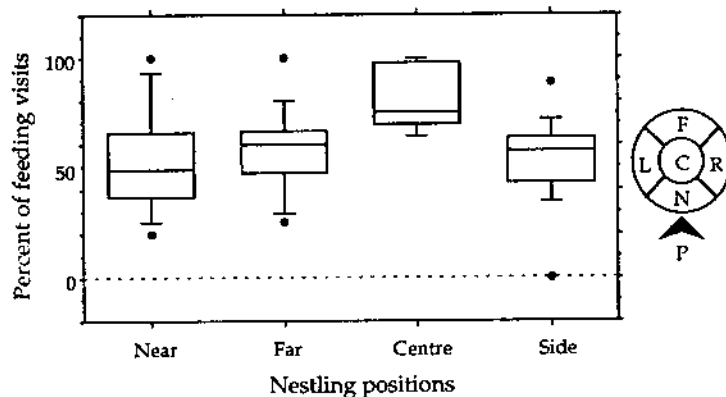


Fig. 2. Percentage of parental feeding visits for which each nestling was fed in relation to the position that it occupied. Nestling positions (Centre; Near; Far; Right; Left) and the parent perch location on the nest rim (P) are indicated in the *diagram*. Data from left and right sides are pooled. *Box plots* summarize data for 50 chicks from 15 different nests with 11–184 feedings each ($\bar{x} = 81.3$ feedings per nest)

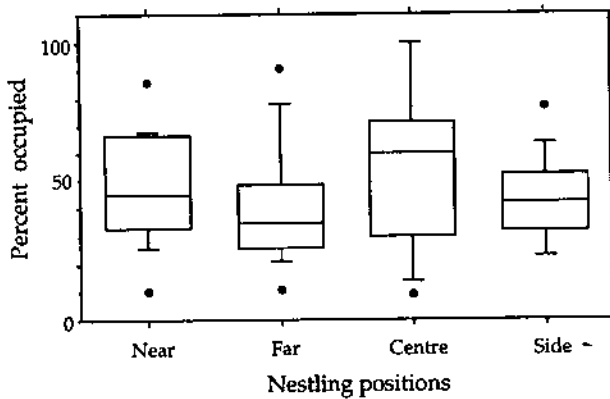


Fig. 3. Percentage of times that nestlings occupied the different positions in the nest relative to the parent's perch on the nest rim. Each box plot summarizes data from 15 nests

To test this prediction, we calculated the amount of nestling movement relative to the predictability of parental arrival location on the nest rim. For every feeding visit, we determined whether each nestling was in the same or a different position from the one it was in during the previous visit. The total number of position changes by nestlings was summed for the entire brood and divided by the brood size to give an average number of position changes per nestling. We then divided this total by the number of feeding visits observed to give a mean rate of position change per feeding visit. When parental perch location was more predictable (i.e., the percent of parental visits to the most frequently used perch quadrant was higher), nestlings changed position more often (Spearman rank correlation $r_s = 0.71$, $P = 0.01$, $n = 13$ nests; Fig. 4a) and, moreover, a greater proportion of those movements were specifically into the central position ($r_s = 0.73$, $P = 0.01$, $n = 13$ nests; Fig. 4b).

Consequences of jockeying for position

To evaluate whether nestmates received approximately the same amount of food overall, we estimated the size of food loads brought by parents and the proportion of each load given to different nestlings. Based on our load size criteria (see Methods), we estimate that large loads were twice the size of medium loads, and medium loads twice the size of small loads. Using data on the proportion of a food load fed to each nestling, we calculated the average amount of food received by each member of the brood relative to one another during observation periods. To minimize bias due to variation in load sizes brought to different nests, we compared the rank sums of these scores for nestlings (rather than actual estimates) using Kruskal-Wallis tests on data from each of 20 nests with 9–111 food loads per nest. There was only one nest in which there was significant variation in the amount of food received by each brood member ($H = 19.5$, $n = 1$ nest with 3 nestlings obtaining 57 feedings; for other 19 nests, tablewide $P > 0.05$). This suggests that, in general, food was equitably distributed among nestlings.

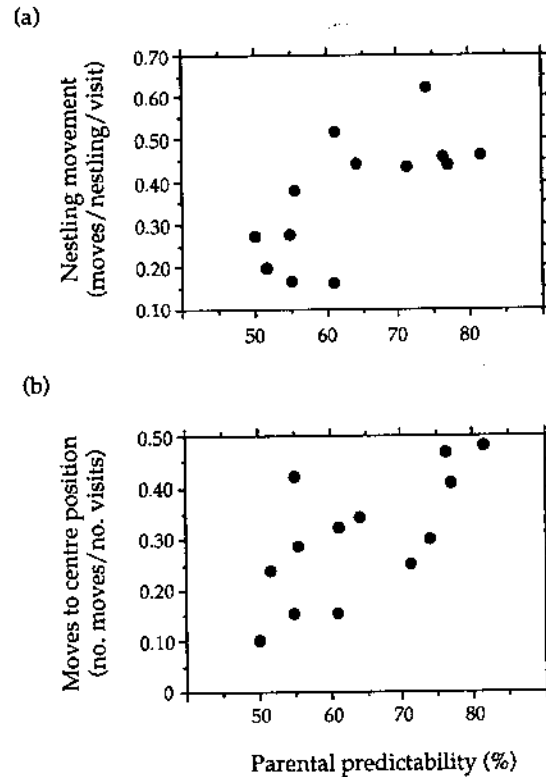


Fig. 4a, b. Relation between nestling movement and the predictability of parental perch locations when: a the overall degree of nestling movement is estimated as the mean number of position changes per nestling per feeding visit, and b the number of moves by individual nestlings into the centre position is expressed as a proportion of the total visits. Parental predictability is the percentage of parental visits to the most-visited quadrant on the nest rim. Each data point represents a nest, with 23–141 ($\bar{x} = 67.5$) feeding visits per nest

Although food appeared to be equitably distributed among nestlings, the last-hatched nestling starved to death in 5 of the 11 nests that successfully fledged young and had initial brood size of 3 or 4. Thus, the approximately equal distribution of food among nestlings was not always sufficient to prevent some nestlings from starving. Brood reduction occurred within the first 6–7 days after hatching. The victims of brood reduction appeared weakened and received few or no feedings in their last day of life. However, this would not necessarily have affected the overall feeding score calculated over the entire filming period for each brood size at each nest.

We compared the degree of nestling movement between nests with and without brood reduction. In brood-reduced nests, the degree of nestling movement before the last-hatched nestling died (median = 0.46, range 0.20–0.62 moves per nestling per parental visit) was not significantly different from the degree of nestling movement in the same nests after the last-hatched nestling died (median = 0.55, range 0.48–0.60 moves per nestling per visit; Mann-Whitney $U = 5$, $P = 0.11$). However, broods that were reduced had higher degrees of nestling movement both before and after the loss of the last-hatched nestling than broods that were not reduced (median = 0.28, range 0.16–0.44 moves per nestling per visit), and the difference is significant (“before” com-

parison: Mann-Whitney $U=4$, $P=0.045$; "After" comparison: $U=0$, $P=0.02$; $n=5$ reduced, 6 intact broods). This suggests that nestling competition was generally more intense in nests where one nestling eventually died, presumably because of poor provisioning by parents. Even brood reduction was not sufficient to significantly reduce competition among nestlings in those nests.

Discussion

Robin nestlings receive a higher proportion of feedings when occupying the central position in the nest. By gaining access to this position, a nestling increases its chances of being fed. Since the location of parental arrival is generally predictable at any given nest, and the observed degree of nestling movement is correlated with that predictability, we argue that nestlings compete with one another by jockeying for the best position to receive the next feeding.

Two lines of evidence suggest that most passerine nestlings do some jockeying for the best feeding position in the nest. First, there are anecdotal reports of nestling movement in a wide variety of species (e.g., Skutch 1976; Reed 1981; Nolan 1978; Greig-Smith 1985). Second, many parents show a strong preference to arrive at and feed nestlings from specific regions of the nest rim (Nolan 1978; Rydén and Bengtsson 1980; this study). Even in open-nesting birds like field sparrows (*Spizella pusilla*, Best 1977) and prairie warblers (*Dendroica discolor*, Nolan 1978) where parents could potentially land anywhere on the nest, there are strong tendencies for parents to arrive at particular locations on the nest rim. Thus there is the potential for nestlings to predict the location of their food source with some accuracy.

Altricial and semi-altricial young of a variety of avian species have specialized means of attracting parental attention and soliciting feedings. For example, nestling herring gulls (*Larus argentatus*) peck a spot on their parent's bill to solicit regurgitation by the parent (Tinbergen and Perdeck 1950), and in pelican and sulid chicks, convulsions are rewarded by parental feedings (Drummond 1987). Evidence that passerine nestlings exert some control over parental distribution of food is two fold. First, it has been shown that parents adjust their feeding rate in relation to their chicks' begging intensity (Bengtsson and Rydén 1983; Smith and Montgomerie 1991; Redondo and Castro 1992). Second, nestlings change positions in the nest and by doing so alter the proportion of feedings they receive (Rydén and Bengtsson 1980; this study).

Stamps et al. (1985, 1989) reported that female budgerigars (*Melopsittacus undulatus*) favored their youngest nestlings when distributing food. They argued that parents will always have ultimate control over apportionment of food, regardless of strategies used by nestlings to increase their relative share. However, their study was conducted in a controlled environment where food was superabundant. In our study, where food was not superabundant, asynchronously-hatched broods that suffered brood reduction exhibited relatively more movement in

the nest. This result suggests that nestlings are moving in the nest in order to compete for food.

There is actually little evidence that parent birds have ultimate control over the way in which resources are divided among their offspring (McGillivray and Levenson 1986). For parents to be able to "overrule" the influence of sibling competition on distribution of food, they would need to be able to recognize individual offspring. It has yet to be shown convincingly, however, that parents are capable of distinguishing their own nestlings from those of others (Beecher 1988), let alone recognizing individual nestlings. The inability of parents to recognize individual offspring has been demonstrated through experiments in which nestlings were transplanted, or cross-fostered from one nest to another (McGillivray and Levenson 1986; Wright and Cuthill 1989, 1990; Medvin et al. 1992; Teather 1992). Since passerine nestlings are sedentary (i.e., confined to the nest), they would derive little advantage from having signature begging calls prior to fledging. The intensity of begging should provide a sufficient signal to the parent of the nutritional need of the individual in question. An entirely nestling-mediated food distribution system would be effective even in cavity nesters where dim lighting may impair the parent's ability to see the nestlings clearly. Thus we argue that a *laissez-faire* parental strategy in terms of the distribution of food amongst brood members is entirely conceivable.

Growth rate and survival of last-hatched nestlings are affected by variation in food abundance (Magrath 1989) and parental provisioning ability (Quinney et al. 1986). We suggest that jockeying for position is a form of interference competition. By this mechanism, offspring can achieve essentially equal shares of food despite the parents' tendency to favour one (central) location in the nest. In our study population, hatching asynchrony was common, but brood reduction occurred only at nests where the degree of jockeying for position was high. Movement in the nest may thus be determined by the hunger level of the smallest (hungeriest) nestling, but only when that nestling is unable to get sufficient food by its movement will brood reduction occur. Because jockeying for position will involve some energetic cost, the hungry nestling may actually accelerate its own demise when jockeying fails to result in more food.

Parents are expected to allocate investment such that the number of surviving young is maximized (Trivers 1974). However, when brood reduction occurs, the benefit in fledging condition accrued by each surviving chick may outweigh any gain in inclusive fitness to that chick had the brood not been reduced. Consequently, parents and older nestlings are expected to disagree about whether brood reduction should occur, at least when food is plentiful (O'Connor 1978; Parker and Mock 1987; Godfray and Harper 1990; Clutton-Brock 1991). Our finding that the extent of jockeying for position is correlated with the occurrence of brood reduction is consistent with the idea that sibling competition affects the outcome of this conflict of interests.

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