Group provisioning limits sharing conflict among nestlings in joint-nesting Taiwan yuhinas

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Offspring often compete over limited available resources. Such sibling competition may be detrimental to parents both because it entails wasted expenditure and because it allows stronger offspring to obtain a disproportionate share of resources. We studied nestling conflict over food and its resolution in a joint-nesting species of bird, the Taiwan yuhina (*Yuhina brunneiceps*). We show that adult yuhinas coordinate their feeding visits, and that this coordination limits competition among nestlings, leading to a 'fairer' division of resources. Transponder identification and video-recording systems were used to observe adult feeding and nestling begging behaviours. We found that: (i) yuhinas feed nestlings more often in large parties than in small parties; (ii) feeding events occurred non-randomly in bouts of very short intervals; and (iii) food distribution among nestlings was more evenly distributed, and fewer nestlings begged, during large-party feeding bouts compared with small-party feeding bouts. To our knowledge, this is the first study in a cooperative breeding species showing that adults can influence food allocation and competition among nestlings by coordinating their feeding visits. Our results confirm the hypothesis that the monopolizability of food affects the intensity of sibling competition, and highlight the importance of understanding the temporal strategies of food delivery.

Keywords: sibling competition; cooperative breeding; conflict resolution

1. INTRODUCTION

Conflict is an inherent part of social life. An important target of conflict in cooperative groups is the allocation of group resources. This conflict over resource-sharing often causes costly competition between group members and thus lowers the fitness of cooperating group members (Mock & Parker 1997; Reeve *et al.* 1998). Sibling competition has been an important focus of studies of conflict resolution. When food supplies are limited, offspring will

often compete over available resources. Such sibling competition may be detrimental to parents, both because it entails wasted expenditure and because it allows stronger offspring to obtain a disproportionate share of resources (Godfray & Parker 1991; Mock & Parker 1997).

Mock (1985) argued that the intensity of sibling competition was linked to the monopolizability of food by individual nestlings. This prey-size hypothesis states that parents can manipulate the size of provisioned prey items to reduce the competition for food between nestlings. For example, it has been shown that large prey items in ardeids (Mock 1985) and a large number of small food parcels in parrots (Krebs 2002) are more difficult for nestlings to monopolize. A relatively unexplored aspect of parental provisioning strategies is control of the temporal distribution of food (Drummond 2002; Royle *et al.* 2006). In bi-parental care systems, the feeding interval is usually considered to be inversely correlated with the total amount of food provided. Therefore, short feeding intervals lead to lower nestling competition because more total food is provided (Mock & Parker 1997). However, little is known about whether male and female parents can coordinate and use a contingent feeding pattern (given that the total amount of food provided is fixed) as a strategy to influence nestling competition.

Here, we examine how conflict over food distribution to nestlings is resolved in a cooperatively breeding, joint-nesting species, the Taiwan yuhina (*Yuhina brunneiceps*). Breeding groups of yuhinas typically comprise two to three unrelated monogamous pairs and sometimes one non-breeding helper (Yuan *et al.* 2004). Female group members lay eggs in the same nest and all group members share the parental care duties (Yuan *et al.* 2005). Yuhinas are especially suitable for studying the resolution of conflicts over food distribution among nestlings because 'battlegrounds' exist not only among the nestlings and between nestlings and parents, as in standard animal families (Godfray & Parker 1991), but also among unrelated adult group members.

We test whether adult yuhinas coordinate their feeding visits and use non-random group provisioning to manipulate the temporal distribution of food as a strategy to limit the competition among nestlings. A transponder identification mechanism, nest-mounted video-recording system and focal observations at nests were used to study adult feeding and nestling begging behaviours. If coordinated group provisioning is a parental strategy influencing the allocation of food among nestlings, we should find that: (i) yuhinas feed nestlings more often in large parties (defined as more than half of the group members visiting the nest together to feed the nestlings) than in small parties; (ii) feeding events should occur non-randomly in bouts of very short intervals; and (iii) food distribution among nestlings should be more evenly distributed and fewer nestlings should beg during large-party feeding bouts compared with small-party feeding bouts.

2. MATERIAL AND METHODS

The data analysed in this study were collected in the 2006 and 2007 breeding seasons, in which 14 and 19 breeding groups, respectively,

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Figure 1. (a) The percentage of feeding trips in large parties (greater than 50% of group members) and in small parties (less than or equal to 50%). (b) The evenness of food allocation among nestlings, estimated by the feeding skew index, in large-party feeding trips (greater than 50%) and in small-party feeding trips (less than or equal to 50%). Feeding skew index = 0 means equal feedings to all nestlings and 1 represents feeding completely monopolized by one nestling.

were closely monitored. The study site is located at the National Taiwan University Highlands Experiment Farm at MeiFeng in central Taiwan (Yuan *et al.* 2004). For more details about the study site see electronic supplementary material A.

To observe provisioning behaviours of yuhinas, we implanted RFID transponders (ID100A, Trovan) under the skin between the upper thigh and body of adult birds for remote monitoring of individual nest visits. Antennae for reading transponders and bullet cameras (1/3" B/W IR, Yaba) for recording the adult and nestling behaviours were installed around the nests in the evening to reduce risks of nest abandonment and avoid disturbance of daytime activities. Nestlings were marked with non-toxic acrylic paint on their bills and/or heads for individual identification. Teams of three to four researchers performed focal observations together, observing from different angles, to record the exact number of adults coming to the nests. This combined procedure was used because some adults approached the nest without entering to feed nestlings and thus could not be recorded by the camera. We obtained a total of 122 h of adult provisioning data, which include 1393 feeding trips from 11 and 6 nests in 2006 and 2007, respectively. We did not obtain provisioning data from every group we monitored. The group size of provision-monitored nests ranged from three to six adults.

To analyse whether yuhinas were more likely to provision nestlings in larger parties, we counted the number of adults visiting the nest together by focal observations and later confirmed this number with the recording and transponder data. A 'feeding trip' was defined as any number of adults flying simultaneously to the nest with food for nestlings. (The dominant male gives flight calls to coordinate simultaneous departure of group members from the foraging area.) We classified trips into two feeding types: 'large-party provisioning' when more than 50 per cent of group members visited the nest together, and 'small-party provisioning' when 50 per cent or fewer of group members visited the nest. The numbers of feeding trips by large and small parties observed in each nest were then compared using a paired *t*-test (see electronic supplementary material B). To quantify the distribution of food among nestlings during large- and small-party provisioning trips, we summed the total number of food items each nestling obtained for trips of each feeding type. A feeding skew index was calculated from these individual food counts based on the skew index *S* (Pamilo & Crozier 1996), $0 \leq S \leq 1$, where 0 indicates equal sharing and 1 indicates that food is completely monopolized by one nestling. For more details about our procedure for estimating feeding skew see electronic supplementary material B. We used a mixed linear model to analyse variation in (i) time interval between feeding events (defined as a single food item delivered to a nestling) and (ii) percentage of non-begging nestlings in each feeding trip, including group identity as a random factor to account for a possible correlation of behaviours between individuals of the same group. Neither year (2006 or 2007) nor Julian date (from 188 to 251) affected the covariance structure of the data. All figures are presented as mean $\pm$ s.e.

3. RESULTS

We found that adult yuhinas were much more likely to feed nestlings in groups than to visit the nest alone. Only 10.5 per cent of the 1393 feeding trips were solo visits. In addition, adult yuhinas were more likely to provision together with a majority of group members (large-party provisioning, 66.9 per cent of trips) than with fewer group members (small-party provisioning, 33.1 per cent) (figure 1a; paired *t*-test: $t_{2,17} = -2.622$, $p = 0.019$). The observed percentage of large-party provisioning is also much greater than expected by chance. If each adult visited the nest randomly, the probability of large-party provisioning in a four-adult group would range from only 8.4 per cent to 14.4 per cent, based on simulation results with the most appropriate parameter values (see electronic supplementary material C). Gender and dominance rank did not affect an adult's likelihood of participating in large- or small-party provisioning (rank: Kruskal–Wallis test; $H_{2,1042} = 0.380$, $p = 0.827$; gender: Mann–Whitney *U* test, $U_{1,1042} = 88\,348$, $p = 0.127$). We also found that large-party provisioning resulted in more even food distribution among nestlings than small-party provisioning (figure 1b; paired *t*-test: $t_{2,11} = 2.671$, $p = 0.023$).

Large-party provisioning caused multiple feeding events to occur in a bout, with short time intervals averaging 48.6 s (figure 2a; $F_{1,4} = 151.13$, $p < 0.001$). Figure 2a also shows that feeding trips were, on average, about 7 min apart. The mixed model analysis revealed that nestlings were more likely to beg during solo provisioning trips and during early feeding events of multiple-feed trips (figure 2b; $F_{1,4} = 9.178$, $p < 0.001$). Moreover, the percentage of begging nestlings increased as breeding group size decreased ($F_{1,3} = 24.246$, $p < 0.001$) and as brood size decreased ($F_{1,3} = 11.064$, $p = 0.003$). A similar analysis showed that shorter feeding event intervals significantly reduced the percentage of begging nestlings. However, because of the collinearity between provisioning trip type and feeding event interval (Pearson correlation

Figure 2. (a) Feeding event intervals for different provisioning trip types and for feeding events within sequences. (b) The percentage of non-begging nestlings for different provisioning trip types and feeding events within sequences. Here, 'solo' refers to feeding trips by a single individual, and 'group' refers to trips by more than one individual. First represents the first adult to feed a nestling during a feeding trip and so on. The feeding interval for a solo provisioning event is the interval since the last time any nestling at that nest was fed. Numbers above each bar indicate sample sizes.

$r = -0.451$, $n = 1461$, $p < 0.001$), only the analysis of the provisioning trip type is presented.

4. DISCUSSION

All three of our key predictions were supported, suggesting that large-party provisioning is a strategy that adult yuhinas use to influence food allocation and competition among nestlings. Our study also shows that by large-party provisioning, food was delivered to nests in short time intervals (less than a minute, figure 2a), which resulted in a more even distribution of food and less competition among nestlings. This occurred because when food was provided in a bout, those individuals who had already obtained food were less likely to beg again, presumably because they were still processing the food they had already received (S.-F. Shen and H.-W. Yuan 2004–2007, unpublished data). Note that the way we calculate the food distribution is to sum the total amount of food each nestling obtained in cases of large-party provisioning and small-party provisioning during the total sampling period. Thus, the difference between large- and small-party provisioning is the provisioning interval, not the total amount of food brought to the nest by adults. It has been shown that degree of sibling competition is associated with a limited supply of resources in many studies (Drummond & Chavelas 1989; Mock & Parker 1997). Our study further shows that manipulating temporal distribution of food can also decrease nestling competition.

To our knowledge, this is the first study in a cooperatively breeding species showing that adult group members coordinate feeding visits and thereby influence food allocation and competition among nestlings. Large-party provisioning can be viewed as a cooperative strategy because it results in a more even distribution of food among nestlings and less nestling begging, which presumably decreases the energetic costs that nestlings would otherwise incur

in competing for food. However, it is still largely unknown how commonly this coordinated group provisioning strategy is used even in bi-parental care species. For example, in zebra finch (*Taeniopygia guttata*), parents raising young together do not coordinate their feeding bouts, causing greater nestling competition than in broods reared by single parents (Royle *et al.* 2006). It is not clear what the potential explanations are for the variation in coordinated provisioning among different species. Coordinated provisioning could be less efficient because of the costs of coordination; for instance, if one individual finds food faster, he or she would have to wait until the other individual(s) also obtained food. However, coordinated provisioning could be beneficial if a 'more eyes' effect reduced predation risk on adults and enhanced feeding efficiency (Pulliam 1973). Clearly, more studies are needed to determine the costs and benefits of coordinated provisioning.

Our results also confirm the general idea that the monopolizability of food by individual nestlings is important in affecting the intensity of sibling competition (Mock & Parker 1997; Drummond 2002). This study highlights the importance of understanding how temporal strategies of food delivery influence the resolution of competition among offspring, which has received relatively little attention in studies of family conflict.

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