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Parental aggression against dependent young results in task partitioning in a cooperatively breeding bird

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In cooperatively breeding species, helpers can alleviate reproductive constraints by assuming the role of primary carers to first-born young, liberating breeders to invest in subsequent broods. However, evidence on how first-born young are transferred to helpers is currently lacking. We propose that breeder–offspring aggression might facilitate inter-brood division and test this idea using data from a wild population of cooperatively breeding pied babblers (*Turdoides bicolor*). After second-brood young hatch, breeders become increasingly aggressive to first-brood fledglings and attack them when they beg for food. After an attack, fledglings reduce begging. Helpers are much less aggressive to begging fledglings and fledglings subsequently tend to target helpers, rather than breeders, when begging for food. In this way, first-born dependent young are transferred to helpers, resulting in a partitioning of tasks among breeders and helpers. Task partitioning in eusocial insects is thought to be determined by the morphological or physiological characteristics of individuals. This complementary study suggests that flexible behavioural strategies may also result in specialized roles in cooperatively breeding vertebrates.

Keywords: parental aggression; task partitioning; brood division; pied babbler; cooperative; division of labour

1. INTRODUCTION

In cooperatively breeding pied babblers (*Turdoides bicolor*), non-reproductive helpers alleviate the trade-off between current and future reproduction (cf. Lessells 1991), by assuming the responsibility for feeding first-born young (Ridley & Raihani in review). Breeders can then reduce investment in first-borns and divert investment to subsequent breeding attempts (Ridley & Raihani in review). Such inter-brood division (*sensu* Ridley & Raihani in review) may be relatively common in cooperatively breeding species (Langen & Vehrencamp 1999; Langen 2000), and is comparable to intra-brood division in biparental species (e.g. Slagsvold 1997), in that different subsets of young are cared for by different adults. The mechanisms underlying intra-brood division have been well studied (see Slagsvold 1997; Leedman & Magrath 2003); however, it is not yet known how inter-brood division in cooperative species is achieved and maintained.

A possible mechanism is breeder aggression to first-borns. Although parental aggression often precipitates the nutritional independence of offspring (e.g. spotted flycatchers *Muscicapa striata*: Davies 1976; moorhens *Gallinula chloropus*: Leonard *et al.* 1988; black-capped chickadees *Parus atricapillus*: Leonard *et al.* 1991; domestic dogs *Canis lupus familiaris*: Malm & Jensen 1997; naked mole rats *Heterocephalus glaber*: Stankowich & Sherman 2002), an alternative function for parental aggression might be to maintain brood division. For example, Horsfall (1984) showed that European coot (*Fulica atra*) parents are more likely to aggressively 'tousle' chicks when they are not the primary feeders of the chick in question. This then deters the tousled chick from approaching the aggressive adult. In cooperative species, breeder–offspring aggression might facilitate inter-brood division in a similar way, by encouraging first-born young to target helpers rather than breeders when begging for food.

We investigated this possibility using data from a wild population of pied babblers. Groups comprise a dominant breeding pair, plus non-reproductive helpers that contribute to feeding offspring produced by the dominant pair (Ridley & Raihani 2007). Previous work has shown that brood overlap is relatively common, such that adults may be provisioning a brood of fledglings and a younger brood of nestlings at the same time (Ridley & Raihani in review). Under these circumstances, helpers assume responsibility for the older brood of fledglings (first-borns), while breeders direct investment to the new brood (Ridley & Raihani in review). We hypothesized that if breeder–offspring aggression served to transfer first-borns to helpers, then (i) breeder aggression to first-borns should increase after second-brood young hatch (while helper aggression should not increase) and (ii) first-borns should subsequently target helpers more often than breeders when begging for food.

2. MATERIAL AND METHODS

Data were collected from September 2003 to December 2006 in a total of 13 pied babbler groups at the Kuruman River Reserve in the southern Kalahari, near Van Zyl's Rus (25°8′ S, 20°49′ E; see Raihani & Ridley (2007) for a detailed site description). We investigated the terms adult fledging aggression. The total time that each adult was targeted by a begging fledgling and the number of times each adult attacked a fledgling were both summed across two consecutive observation periods: 10–35 and 36–60 days post-fledging. The first observation period began at 10 days post-fledging as young were poorly mobile and did not follow foraging adults before this time (N. Raihani 2003–2007, unpublished data). Fledglings were defined as young during the former and old during the latter observation period. For each period, the total number of attacks by each adult was divided by the total time (min) that the adult was targeted by begging fledglings to obtain a rate of aggression per begging minute for each adult. Adult aggression rates were arcsine square-root transformed to achieve normality and set as the response term in a linear mixed model (LMM). Adult sex, status (breeder/helper) and mean weight (g) during the observation period, together with fledgling age (young/old), adult : offspring ratio, rainfall (low/medium/high) and the number of nutritionally dependent broods (1/2), were all included as potential explanatory terms in the model. Data come from 73

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Table 1. LMM analysis of the terms affecting adult aggression to begging fledglings. (χ^2 is the Wald statistic. Effect sizes for significant explanatory terms (in italics) are presented.)

model term	χ^2	p	effect ± s.e.
constant			0.014 ± 0.009
fledgling age	11.4	< 0.001	
young			0.00 ± 0.00
old			0.03 ± 0.01
dependent broods × adult status	10.1	0.001	see figure 1
dependent broods	6.72	0.01	
1 brood			0.00 ± 0.00
2 broods			0.08 ± 0.02
adult status	4.21	0.04	
breeder			0.00 ± 0.00
helper			0.03 ± 0.02
adult sex	1.62	0.20	
rainfall	2.77	0.25	
adult weight	1.33	0.25	
adult : offspring ratio	0.26	0.61	

adults and 34 fledgling broods from 12 groups (10 broods had an overlapping younger brood, 24 did not have a younger brood present).

We then determined the effect of adult aggression on fledgling begging behaviour by investigating (i) whether fledglings reduced begging immediately after an attack and (ii) whether begging fledglings targeted aggressive adults less often. We conducted 20 min focal watches (Altmann 1974) on fledglings, recording the time (s) each fledgling spent begging to an adult per focal watch and the occurrence of adult attacks on the focal fledgling. To determine whether attacks affected begging levels, we used paired data from 63 focal watches on 25 fledglings. The time spent actively begging in the 60 s immediately before and after an attack were both summed. Mean 'before' and 'after' values for each fledgling were calculated and analysed using a paired *t*-test. Based on the prediction that breeders would be more aggressive to begging fledglings after a second-brood had hatched, we asked whether begging fledglings targeted breeders less after a younger brood had hatched. The total time (min) that each adult was targeted by begging fledglings (per observation period) was divided by the total begging time for that group (during the same period) to obtain the proportion of total begging time each adult received. This was arcsine square-root transformed and set as the response term in an LMM. The sex, status and mean weight of each adult, adult: offspring ratio, fledgling age, rainfall and the number of dependent broods were included as potential explanatory terms in the model. Data came from 73 adults and 34 fledgling broods from 12 groups. See electronic supplementary material for further methodological details.

3. RESULTS

Adults attacked fledglings on average 2.5 ± 0.4 times for every hour that they were targeted by begging fledglings. Most adult aggression (816/864 attacks, mean per group = 95.6 ± 0.0%) resulted in the fledgling moving away from the adult, without receiving any food. However, on 48 out of 864 occasions (mean per group = 4.37 ± 0.0%) the adult attacked the fledgling immediately after a feeding event. This always occurred after a persistent bout of begging from the fledgling for the food item in question. Fledglings substantially reduced begging after an attack: the mean time spent begging in the minute before an attack was 21.2 ± 3.3 s, compared with 10.7 ± 1.6 s in the minute following an attack (paired *t*-test: $t_{24} = 2.72$, $p = 0.01$). When groups were simultaneously feeding nestlings and fledglings, breeders were more aggressive than helpers to fledglings (table 1; figure 1), after controlling for the significant effect of fledgling age (table 1). First-born fledglings directed more of their total begging effort to helpers, rather than breeders under these circumstances (table 2; figure 2). This result was significant after controlling for the fact that in groups with high adult to offspring ratios, begging fledglings had more adults to target, resulting in a reduction in the proportion of begging directed at each adult (table 2).

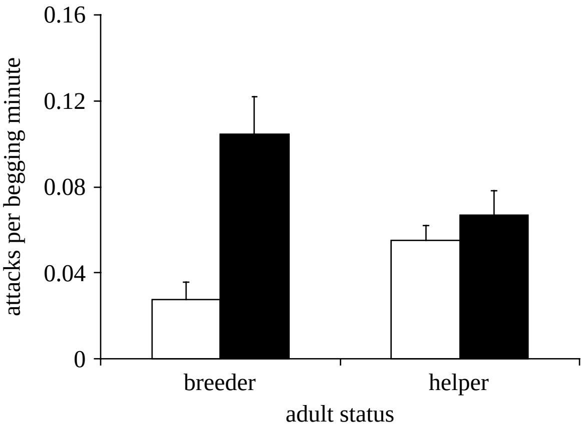

Figure 1. The effect of interaction between adult status (breeder/helper) and the number of dependent broods (1/2) on adult aggression. Means and standard errors were generated from predicted means of the LMM presented in table 1 (white, 1 brood; black, 2 broods).

Table 2. LMM analysis of the terms affecting the proportion of total begging time directed towards each adult.

model term	χ^2	p	effect ± s.e.
constant			0.46 ± 0.04
adult: offspring ratio	11.42	< 0.001	−0.03 ± 0.009
dependent broods × adult status	6.05	0.014	see figure 2
adult sex	2.72	0.099	
dependent broods	1.33	0.249	
1 brood			0.00 ± 0.00
2 broods			−0.15 ± 0.05
rainfall	4.54	0.103	
adult status	0.31	0.577	
breeder			0.00 ± 0.00
helper			−0.02 ± 0.06
adult weight	0.1	0.748	
fledgling age	0.02	0.896	

4. DISCUSSION

Previous work on pied babblers has shown that when two broods are simultaneously dependent, helpers primarily feed first-borns, whereas breeders divert investment to the new brood (Ridley & Raihani in review). However, the mechanism by which inter-brood division occurred was not known. In this study, we tested the hypothesis that breeder aggression serves to transfer first-borns to helpers, by deterring them from targeting breeders when begging for food. In accordance with our prediction, breeders became more aggressive to dependent first-borns after a younger brood had hatched, whereas helper aggression did not significantly increase. The possibility that

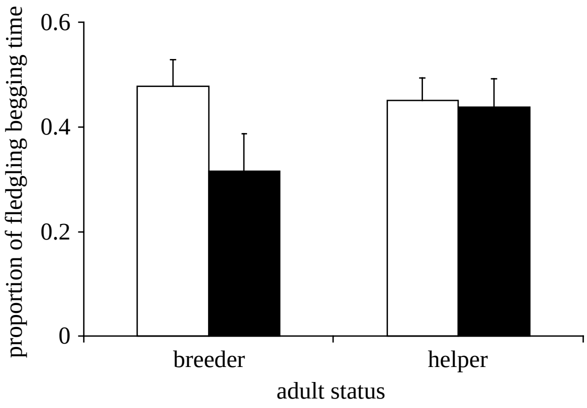

Figure 2. The effect of interaction between adult status (breeder/helper) and the number of dependent broods (1/2) on the proportion of the total begging time fledglings directed to adults. Means and standard errors were generated from predicted means of the LMM presented in table 2 (white, 1 brood; black, 2 broods).

breeder aggression arose from an increased number of mouths to feed (rather than inter-brood division) seems unlikely, as we found no effect of adult : offspring ratio on aggression. Furthermore, if adult aggression varies with offspring number, then we would expect both helpers and breeders to become more aggressive to first-borns after a second-brood hatch. Our data do not show this. Instead, our findings are consistent with the idea that breeder aggression is used to transfer dependent first-born offspring to helpers. Aggression deterred offspring from begging and begging fledglings targeted helpers more often than breeders in response to breeder aggression.

Although sibling competition determines how food is distributed among offspring in some species, parental control is likely to be important when offspring vary in size and competitive ability (Slagsvold 1997). For example, in budgerigars (*Melopsittacus undulatus*), hatching is asynchronous and mothers preferentially feed the smallest chicks in the brood (Stamps *et al.* 1985). Similarly, Leonard *et al.* (1991) proposed that moorhen mothers attack larger chicks to prevent them from monopolizing access to food. Brood overlap in cooperatively breeding species can be considered as an extreme case of hatching asynchrony, in that dependent young vary markedly in age, size and competitive ability. When broods overlap, parents might therefore be expected to control food allocation, by reprimanding older offspring, in order to ensure that younger, inferior competitors also receive their share of food.

Since adults are presumably free to choose which subset of offspring to provision, why do breeders not ignore begging fledglings, rather than attacking them. The observations of adults attacking fledglings immediately after donating food items suggest that fledgling begging might occasionally manipulate adults into feeding against their preferences, which may help to explain why breeders use an aggressive, rather than passive, strategy to transfer first-borns to helpers. In future work, playback experiments will be necessary to determine whether increased levels of fledgling begging alter adult provisioning strategies away from a preferred optimum. Alternatively, parental aggression might optimize fledgling begging: since begging may be costly both in terms of energy expenditure (Leech & Leonard 1996) and increased predation risk (Haskell 1994), fledglings might benefit from begging only to those individuals that are likely to feed them.

Parental aggression often occurs at weaning and signals the end of care for offspring (Leonard *et al.* 1988, 1991; Malm & Jensen 1997; Stankowich & Sherman 2002). In some cooperative species, however, aggression might signal the end of care from specific subsets of adults. The capacity for concurrent operations, mediated through specialized worker roles, has been invoked to explain the extremely high productivity seen in many eusocial insect societies (Wilson 1971; Bourke & Franks 1995). In most social insect societies, worker roles are determined by morphological or physiological characters (Wheeler 1986); however, this study demonstrates how flexible behavioural strategies might also result in the partitioning of tasks among individuals within a group.

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