Ethology

Juvenile Female Aggression in Cooperatively Breeding Pied Babblers: Causes and Contexts

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Received: October 29, 2007
Initial acceptance: December 26, 2007
Final acceptance: January 12, 2008
(J. Schneider)

doi: 10.1111/j.1439-0310.2008.01482.x

Abstract

Sex biases in adult aggression have been well studied and commonly arise when resources which affect survival or lifetime reproductive success are less abundant or more valuable for individuals of one sex. Despite the prevalence of sex biases in adult aggression, evidence for sex biases in juvenile aggression is scant. Here, we present evidence for female-biased juvenile aggression in cooperatively breeding pied babblers (*Turdoides bicolor*). Unlike most cases of non-lethal sibling aggression, juvenile aggression in pied babblers does not seem to be determined by food availability. Instead, we found that juvenile aggression was related to adult dispersal patterns. This study shows that females that were more aggressive as juveniles attempted dispersal earlier than less aggressive females. Potential explanations for the association between juvenile aggression and adult dispersal patterns are discussed.

Introduction

Sex-biased aggression is likely to evolve when resource availability or resource value varies between the sexes (Clutton-Brock 1989). The relationship between sex biases in adult aggression and resource availability/resource value has been well studied (see Searcy & Wingfield 1980; Soma et al. 2000; Boydston et al. 2001; Clutton-Brock et al. 2006); however, there has been much less focus on sex-biased aggression among juveniles. Juvenile aggression is usually related to food competition and the outcome of such competition may result in the death of the losing sibling (reviewed in Drummond 2006). As all individuals should place equal value on survival, sex-biased aggression in siblicidal species is not expected (Drummond et al. 2003). However, non-lethal sibling competition also occurs and commonly results in more aggressive offspring growing faster than less aggressive siblings (reviewed in Drummond 2006). As such, non-lethal juvenile aggression may have important downstream effects on adult phenotype, as juvenile condition has been shown to affect adult condition (Henry & Ulijaszek 1996), sexual attractiveness (Gustafsson et al. 1995) and dispersal ability (Ridley & Raihani 2007).

Juvenile aggression may also have downstream effects which are not mediated through food competition. For example, juvenile spotted hyenas (*Crocuta crocuta*) compete with litter-mates for dominance, which determines adult social rank (Frank et al. 1991). The downstream effects of juvenile competition may have stronger fitness consequences for one sex than the other (see Andersson 1994). Where this occurs, sex differences in juvenile aggression may arise. For example, in spotted hyenas, adult social rank predicts female, but not male, reproductive success (Holekamp et al. 1996; Engh et al. 2002). Thus, female cubs might be expected to compete more aggressively than males for dominance. There is some evidence to support this hypothesis: aggression in all-female litters is higher than aggression in

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mixed-sex litters (Frank et al. 1991); however, conclusive evidence that female pups are more aggressive than male pups is lacking.

Sex biases in juvenile aggression might also arise if juvenile aggression is genetically correlated with adult aggression. For example, in both rainbow trout (*Oncorhynchus masou*) and brown trout (*Salmo trutta*), the sex which competes most aggressively over reproduction as adults are more aggressive as juveniles (Johnsson & Akerman 1998; Johnsson et al. 2001). Other adult life-history traits might also affect juvenile aggressive behaviour. For example, Sih et al. (2004) suggested that the process of dispersal may favour bold, aggressive individuals, perhaps because individuals of the dispersing sex commonly have to fight to immigrate onto another territory (e.g. Holekamp & Smale 1998; Nunes et al. 1998). Evidence from house mice (*Mus domesticus*) and western bluebirds (*Sialia mexicana*) support this hypothesis: in both species, aggression is correlated with propensity to disperse (Rusu & Krackow 2005; Duckworth & Badyaev 2007). A tendency for individuals of the dispersing sex to be aggressive might emerge in infancy, as behavioural tendencies such as boldness and aggressiveness have been shown to emerge early in development (Dingemanse et al. 2002). In addition, individuals might benefit from early dispersal; for example where territories are acquired on a first-come first-served basis (e.g. Drent 1974). Thus, increase'd juvenile aggression might be associated with earlier dispersal: indeed, this has been shown to be the case in western screech owls, *Megascops kennicottii* (Ellsworth & Belthoff 1999).

In this study, we investigated variation in juvenile aggression in cooperatively breeding pied babblers (*Turdoides bicolor*). In this species, offspring are nutritionally dependent on adults for an extended period post-fledging (Ridley & Raihani 2007) and interact aggressively with each other during this time. Groups typically comprise a dominant breeding pair, plus non-breeding helpers that are typically the retained offspring of breeders. Dispersal is female-biased and immigration is usually contingent on dispersing females overthrowing resident breeding females when they arrive on non-natal territories (N. Raihani, pers. obs.). In contrast, males are philopatric and typically attain dominant status by inheriting breeding vacancies (N. Raihani, pers. obs.). Here, we first established whether juvenile aggression was sex-biased. We then asked why sex biases in juvenile aggression may arise, using three alternative, but not mutually exclusive, hypotheses. First, we asked whether juvenile aggression arose as a result of immediate competition for food. Second, we asked whether there were any downstream effects of juvenile competition on adult phenotype. Previous work on this species has shown that juvenile weight is positively correlated with adult dispersal success (Ridley & Raihani 2007), raising the possibility that females compete for food in infancy in order successfully disperse. Finally, we asked whether juvenile aggression was linked to adult life-history traits. In this species, the female route to dominance favours aggressive individuals (N. Raihani, pers. obs.), such that correlations between juvenile aggression and adult propensity to disperse might be expected.

Methods

Study Site and Species

Data were collected from Oct.2003 to May 2007 on a population of wild pied babblers located at the Kuruman River Reserve, situated in the southern Kalahari, near Van Zyl's Rus (26°58′S; 20°49′E) (see Raihani & Ridley 2007a for a detailed site description). This population has been habituated to the close presence (< 2 m) of human observers, enabling detailed behavioural data to be collected. All babblers were individually identifiable by a unique colour-ring combination and were sexed using a DNA test (see Radford & Ridley 2006). Groups were observed for three consecutive hours at least once per week, either from first light, or in the afternoon before they went to roost. Data come from a total of 77 fledglings from 26 broods from nine groups, although not all data were available for all analyses.

Aggression

Aggression was defined as any physical attack (pecking/clawing/aggressor jumping onto recipient or holding recipient down). All aggressive interactions between fledglings were recorded *ad libitum* (Altmann 1974) on handheld data loggers, noting the aggressor and recipient identities. We excluded interactions where it was unclear who initiated the attack.

Fledgling aggression was measured from day 10 post-fledging until the end of the period that young were dependent on adults for food (mean: 58.9 ± 1.9 days post-fledging; see Ridley & Raihani 2007 for definition of nutritional independence). The period before day 10 was excluded as newly fledged young are poorly mobile (Raihani & Ridley

2007b) and sit passively in trees, without interacting with one another (N. Raihani, pers. obs.). The number of times that a fledgling physically attacked a broodmate was summed and divided by the total observation time for that fledgling to obtain aggression per hour per fledgling. To investigate general patterns of fledgling aggression, this value was log-transformed and set as the response term in a linear mixed model (LMM) with a normal distribution of errors and an identity-link function, using the programme GENSTAT 8.1 (Lawes Agricultural Trust, Rothamstead UK). Linear mixed models allow repeated measures, such as group identity, to be included as random terms, thereby controlling for their effect on the distribution of the data (Schall 1991). All explanatory terms were added to the model, and then sequentially dropped; retaining only those whose removal resulted in a significant loss of the model's explanatory power. *P* values and Wald statistics for non-significant terms were obtained by adding these terms individually to the minimal model. All two-way interactions were tested but are only presented when significant.

The following explanatory terms were included in the model: fledgling sex, mean group size, mean adult:offspring ratio, mean brood size, mean fledgling weight, total rainfall during the dependent period and the year that the fledgling was born. Mean values for brood size, group size, adult:offspring ratio and fledgling weight were calculated over the period that fledgling aggressiveness was measured. Group size was defined as the mean number of adults (all individuals over 12 mo old) present during the observation period. Total rainfall (mm) during the observation period and 60 d prior to the start of the observation period was measured and included as a proxy for food availability, as there is commonly a protracted period between rainfall and increased insect abundance (Cumming & Bernard 1997). A mean weight for each fledgling was calculated by weighing individuals at the start of each morning observation session (before daily foraging had begun) using mealworms as an incentive to jump onto a top-pan balance. A minimum of three weights per fledgling were used to calculate mean weight. Data come from 62 fledglings (25 broods; 9 groups) that survived to 60 d post-fledging. Group and brood identities were set as random terms in the model.

Paired analyses were used to compare whether aggressive and non-aggressive broodmates received different amounts of food, or were likely to differ in condition. We termed fledglings 'aggressive' if they initiated more attacks (per hour) than the upper quartile of the population average, and all others 'non-aggressive'. To ensure that there were significant differences in aggression between the two types, we conducted a paired t-test, comparing aggressive fledglings with non-aggressive broodmates: aggressive fledglings initiated 0.47 ± 0.1 attacks (per hour) compared with 0.04 ± 0.0 attacks (per hour) by non-aggressive young (paired t-test: $t_{13} = 6.61$, $p < 0.001$). Data come from 14 broods. For all analyses comparing aggressive and non-aggressive fledglings, if broods contained more than one fledgling in each category (e.g. two aggressive fledglings), mean values were calculated.

Fledgling aggression might increase as a consequence of food deprivation (Drummond 2001). To investigate this possibility, we used two separate analyses. First, we asked whether the early provisioning rate (biomass provisioned per hour to fledglings in the first 10 d post-fledging) affected subsequent fledgling aggressiveness. Biomass provisioned was calculated as follows: all food items fed to fledglings were categorized into one of five size categories and each category was assigned an average wet biomass value (g) derived from weighing 50 items representative of that category (see Raihani & Ridley 2007a for category values). Biomass provisioned was the number of items in each category multiplied by the category value. We restricted this analysis to the first 10 d post-fledging because at this point fledglings were entirely nutritionally dependent on adults (Ridley & Raihani 2007), thus allowing the total biomass ingested by fledglings to be calculated. Furthermore, fledgling aggression was extremely rare prior to 10 d post-fledging, thus allowing the causal relationship between food intake and aggression to be examined. We used paired data from 12 broods to compare the early provisioning rates to aggressive and non-aggressive broodmates. Secondly, we asked whether fledglings that initiated fights had received less food than their broodmates in the 10 min prior to the fight. Data were restricted to two-chick broods and to fights where the initiator was known. We summed the biomass fed to both the aggressor and the aggressor's broodmate in the 10 min prior to the fight and used a paired t-test to ask whether aggressors had received less food than broodmates prior to initiating a fight. Analysis was conducted on 13 pairs of chicks; where data for more than one fight were available for each dyad, mean biomass values were calculated.

Next, we investigated whether fledglings used aggression to secure more food from adults. We used a paired t-test to compare the biomass received (g/h) by aggressive and non-aggressive fledglings from 14 broods from day 10 until the end of the dependent period. Finally, we investigated whether there were any long-term effects of fledgling aggression, by using a paired t-test to compare the mean morning weights of aggressive and non-aggressive fledglings from six broods during the 60 d following nutritional independence.

We then investigated whether fledgling aggressiveness or conditions experienced during the dependent fledgling phase were correlated with the age at which individuals first attempted to disperse (days post-fledging) (*sensu* Rusu & Krackow 2005). Dispersal attempts were recorded when individuals voluntarily left the natal territory alone and were subsequently seen interacting with individuals in other groups: such interactions were typically aggressive and often involved the intruder being chased away by resident individuals (N. Raihani, pers. obs.). Data for this analysis were restricted to females as dispersal is female-biased in this species (N. Raihani, pers. obs.). Dispersal attempts could usually be reliably predicted, as females tended to gain weight before leaving their natal group (N. Raihani, pers. obs.). For this model we had a restricted sample size relative to the number of potential explanatory terms, which ruled out the possibility of using LMM analysis. Instead, we used Akaike's information criteria corrected for small sample sizes (AICc) (Burnham & Anderson 2002), using maximum likelihood estimation in the program MLWIN (Centre for Multi-Level Modelling, University of Bristol, Bristol, UK). Using AICc, a series of models are tested, with each model representing a biological hypothesis. A series of models, each investigating the effect of a single term on the earliest dispersal age were tested. First, we tested a basic model, including just the constant, the random term and the residual variance. In subsequent models, we used a conservative approach of adding one explanatory term at a time to the basic model. Akaike weights (w_i) were calculated for each model. Akaike weights sum to 1: models which have Akaike weights approaching 1 receive the most support relative to other models (Johnson & Omland 2004). Aggressiveness (aggressive/non-aggressive), mean fledgling weight (g), brood size, group size, rainfall and adult to offspring ratio were all sequentially investigated. As none of these terms were significantly correlated with another, if more than one term received considerable support, another model investigating the terms together was generated. Data come from 17 females from seven groups. Group identity was set as a random term in the model.

Results

Female fledglings were more aggressive than male fledglings (Fig. 1; Table 1). There was a non-significant tendency for aggression to increase when rainfall was low (LMM: $\chi^2 = 3.62$, $p = 0.06$; Table 1), suggesting that aggression may be affected by food availability. However, further analyses suggested that food availability was not the sole predictor of aggression. We found no difference in the amount of food received by aggressive (2.23 ± 0.2 g/h) vs. non-aggressive broodmates (2.12 ± 0.2 g/h) (paired t-test: $t_{13} = 0.99$, $p = 0.34$). Furthermore, there was

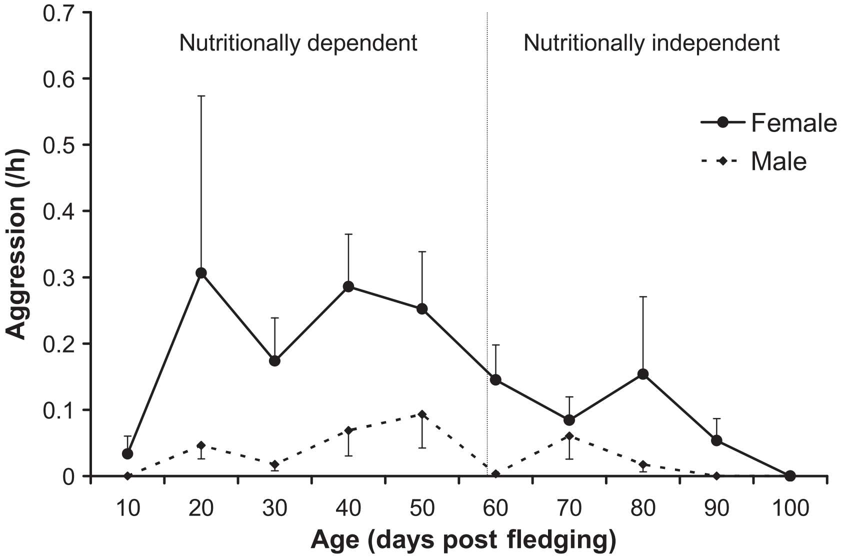

Fig. 1: Raw data on mean (±SEM) number of aggressive interactions initiated per hour by 77 fledglings from 26 broods from nine groups, as a function of fledgling age. The solid line represents females (n = 42): the dashed line represents males (n = 35). The mean age at which fledglings become nutritionally independent is indicated. Age (days post-fledging) was split into 10 d categories.

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Table 1: Output of linear mixed model investigating the terms affecting fledgling aggressiveness

Model term	χ^2	p	Effect ± SE
Constant			0.069 ± 0.0
Fledgling sex	9.62	0.002	
Female			0.00 ± 0.0
Male			−0.05 ± 0.0
Rainfall	3.62	0.057	
Year of birth	5.87	0.118	
Mean fledgling weight	1.29	0.256	
Brood size	0.58	0.562	
Adult:offspring ratio	0.16	0.691	
Group size	0.10	0.746	

χ^2 is the Wald statistic associated with each term. Data come from 62 fledglings (33 females; 29 males). Brood (n = 25) and group (n = 9) identities were included as random terms in the model.

no difference in their mean weights at nutritional independence: aggressive (69.6 ± 0.9 g) vs. non-aggressive (70.9 ± 0.9 g) broodmates (paired t-test: $t_5 = 1.39$, p = 0.22), suggesting that aggressive fledglings did not gain an unequal share of the food delivered by adults. It was unlikely that fledglings became aggressive as a result of being fed less than broodmates early in life: we found no difference in the biomass received by aggressive (2.05 ± 0.4 g/h) and non-aggressive (2.60 ± 0.6 g/h) broodmates during the early provisioning period (paired t-test: $t_{11} = 1.13$, p = 0.28). Nor was fledgling aggression precipitated by short-term food deprivation: fledglings that initiated fights had not received less food than broodmates in the 10 min prior to the fight (initiator: 0.72 ± 0.1 g; recipient: 0.54 ± 0.1 g; paired t-test: $t_{12} = 1.17$, p = 0.26). Instead, our data revealed that female aggressiveness during the fledgling phase was strongly correlated with the age at which they first attempted dispersal (Table 2). Females first attempted dispersal from 102 to 777 (mean: 370 ± 42) days post-fledging and aggressive females attempted dispersal earlier than non-aggressive females (aggressive females: 280 ± 36 days post-fledging; non-aggressive females: 536 ± 50 days post-fledging).

Discussion

Fledgling aggression is strongly female-biased in pied babblers. Treatments of non-lethal sibling aggression have typically shown that siblings compete over food and that aggression increases when food is scarce (e.g. blue-footed booby, *Sula nebouxii*, Drummond & Garcia Chavelas 1989). In pied babblers, this potential explanation for juvenile aggression seems unlikely.

Table 2: Model selection for parameters affecting age at earliest dispersal attempt (days post-fledging)

Model	*D*	*K*	AICc	ΔAICc	w_i	Effect	SE
Constant	222.1	3	230.0	9.76	0.005	370.5	40.3
Aggressiveness							
Aggressive	208.9	4	220.2	0	0.633	−256.0	57.2
Non-aggressive						0.00	0.00
Aggressiveness + mean fledgling weight	206.2	5	221.6	1.45	0.307	−197.9	62.9
						11.2	6.56
Mean fledgling weight	214.0	4	225.3	5.13	0.049	22.4	6.93
Rainfall							
Low	218.8	4	230.2	9.98	0.002	0.00	0.00
Medium						189.1	100.7
High						163.5	110.3
Group size							
Small	219.9	4	231.3	11.1	0.001	0.00	0.00
Medium						−133.9	94.4
Large						−117.4	94.4
Brood size							
2	220.0	4	231.4	11.2	0.002	0.00	0.00
3						−108.8	81.0
4						−131.1	125.5
Adult:offspring ratio	221.8	4	233.1	12.9	0.001	29.5	51.6

The table lists all candidate models. *D* represents the deviance (−2LogLikelihood) output for each model. *K* is the number of parameters. The basic model included the constant, the random term (group identity) and residual variance (σ^2) (*K* = 3). Akaike weights (w_i) indicate the support for each model, relative to the other models tested. AICc is Akaike's information criteria adjusted for small sample sizes; ΔAICc is the difference between the AICc value for that model and the model which received the most relative support (highlighted). Data come from 17 females. Group identity (*N* = 7) was included as a random term in the model.

Although juvenile aggression was highest when young were nutritionally dependent, we found no evidence to suggest that aggressive young were food deprived. The biomass provisioned to newly fledged young did not affect their propensity to become aggressive later in development. Furthermore, if aggression emerged in response to food deprivation, we would have expected initiators of fights to have received less food than broodmates prior to the fight. However, our analyses revealed no difference in the biomass received by initiators and recipients prior to a fight. This analysis may not have fully controlled for fledgling hunger, as food intake from self-foraging was not recorded. In future, it would be interesting to conduct short-term food-deprivation experiments, in order to quantitatively establish the effect of immediate hunger on fledgling aggression. Nonetheless, together, these analyses suggest that hunger is unlikely to be the sole determinant of fledgling aggression.

Previous studies have shown that aggressive young are able to monopolize access to food delivery and may grow faster than non-aggressive siblings (Drummond 2006). Thus, pied babbler fledglings may aggressively compete for food in order to maintain or improve body condition. This may also have positive downstream effects, as previous work has shown that weight at nutritional independence is positively correlated with adult weight (Ridley & Raihani 2007). However, in this species, aggressive fledglings were not fed more than their less aggressive broodmates; nor were aggressive fledglings heavier at independence, indicating that fledgling aggression is unlikely to be a mechanism for securing increased access to food in this species.

Further investigation revealed that fledgling aggression was linked to dispersal: females that were highly aggressive as fledglings attempted dispersal earlier than less aggressive females. This is reminiscent of observations of western screech owls, where socially dominant juveniles disperse before their siblings, despite no apparent effects of social dominance on juvenile condition (Ellsworth & Belthoff 1999). In pied babblers, immigration is typically contingent on a female's ability to forcefully remove resident dominant females (N. Raihani, pers. obs.), indicating that the process of dispersal may favour aggressive individuals. At this stage, however, we do not know whether juvenile aggression influences a female's chance of successful dispersal, or, if so, the mechanism by which this would occur. One possibility is possible that females fight with broodmates in order to hone their fighting skills (e.g. Nunes et al. 2005), although evidence for the motor skills hypothesis is currently equivocal (Sharpe 2005). Alternatively, juvenile female aggression might simply arise as a consequence of the need for aggression later in life (e.g. Sih et al. 2004). Similar correlations between patterns of juvenile and adult aggression have also been reported in two species of trout (Johnsson & Akerman 1998; Johnsson et al. 2001) and in lobsters (*Homarus americanus*, Peeke et al. 1998).

In order to determine whether juvenile aggression positively influences dispersal success or has another adaptive function further investigation will be needed. However, our findings support the idea that early behaviour may be correlated with life-history tactics, such as dispersal. Such correlations can arise when variation in life-history and behaviour are governed by underlying genetic or hormonal mechanisms (reviewed in Sih et al. 2004). Although research has traditionally focussed on either adult *or* juvenile behaviour, we propose that studies that consider the selection pressures faced by adults may reveal interesting and novel perspectives on juvenile behaviour.

Acknowledgements

We thank Tim Clutton-Brock for supervising this study and all members of the Kalahari Meerkat Project for support and assistance at the field site. Thanks to Sinead English, Sarah Hodge, Alex Thornton and Andy Young for useful discussion. The Northern Cape Conservation Authority permitted work on pied babblers and the Kotzes and the de Bruins kindly allowed us access to babbler groups on their land. Krystyna Golabek, Jenny Oates and Andy Radford all contributed to the habituation of the babbler groups at this study site. Thanks also to two anonymous reviewers and Jutta Schneider for comments on the manuscript.

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