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ORIGINAL ARTICLE

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Snake-directed mobbing in a cooperative breeder: anti-predator behaviour or self-advertisement for the formation of dispersal coalitions?

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Abstract The Arabian babbler (*Turdoides squamiceps*), a cooperatively breeding bird, mobs a wide range of its natural predators, mainly snakes and raptors. The response of babblers to a life-like, gypsum model of the horned viper (*Cerastes gasperettii*) was studied in the Arava valley, Israel. I considered three alternative hypotheses to account for mobbing behaviour: investment in other group members, predator-prey interaction and self-advertisement for the formation of dispersal coalitions. Mobbing response varied with group structure: family groups mobbed more than complex groups in which subordinates were potential breeders. Subordinate group members – potential dispersers – mobbed more than dominant breeders, and females mobbed more than males. Babblers did not increase their mobbing response when vulnerable fledglings were present. The results suggest that babblers may increase their investment in anti-predator behaviour when surrounded by close kin, and that immatures may learn about their potential predators during mobbing. However, snake mobbing by Arabian babblers may also serve functions other than anti-predator defence. It is possible that participation in this risky activity may be an honest signal by which subordinate group members advertise their quality as potential members of dispersal coalitions. However, present data provide only indirect evidence, and more work is needed to assess fitness consequences of advertisement for individual group members.

Keywords Mobbing · Anti-predator · Advertisement · Coalition · Arabian babbler

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Introduction

Animals usually make considerable effort to avoid their predators. However, many species are noted for their tendency to deliberately approach and confront their predators as a group, a behaviour referred to as "mobbing" (Dugatkin and Godin 1992). Mobbing has been described in many species of birds, mammals and fish, and is usually associated with specific vocalisations and conspicuous body postures (Curio 1978; Klump and Shalter 1984).

Dugatkin and Godin (1992) identified five major types of costs associated with approaching a predator: increased risk of mortality to self, increased risk of mortality to relatives, lost opportunity costs, energetic costs and costs of being exploited. For mobbing to be adaptively favoured, whatever benefits accrue from mobbing must outweigh these costs. Dugatkin and Godin (1992) suggested four possible fitness benefits the individual can gain from approaching the predator: acquiring information about the predator, informing others of the potential threat, deterring predator attack and advertising one's quality to mates.

Here I present a study of snake-directed mobbing behaviour by cooperatively breeding Arabian babblers (*Turdoides squamiceps*). The Arabian babbler is a convenient model species to study mobbing due to its complex social system, because costs and benefits may vary with the sex and dominance rank of individuals, and with the group social structure and stage of breeding, which makes it possible to generate predictions for different hypotheses (e.g. Shields 1984; Tamura 1989).

I considered three alternative, but not mutually exclusive, hypotheses to account for the evolution of mobbing behaviour in babblers: (1) investment in other group members through warning off and active prey deterrence; (2) direct benefits through predator-prey interactions by acquiring information about the predator, and predator deterrence by perception advertisement; (3) self-advertisement through displaying the ability to stay in proximity of a predator, as well as the willingness to cooperate with potential coalition members.

Investment strategies in a cooperative breeder can be predicted by kin selection (Hamilton 1964), or a mutualism (e.g. group augmentation or pseudoreciprocity) (Woolfenden and Fitzpatrick 1978; Ligon 1981; Connor 1986, 1995; Brown 1987). Hamilton's rule predicts that babblers are more likely to invest in mobbing when surrounded by close relatives rather than unrelated birds. Thus, simple family groups consisting of parents with offspring are predicted to participate in mobbing more actively than complex groups, which contain unrelated individuals. However, these unrelated birds are often actual or potential subordinate breeders, so that benefits of mate protection may be important (e.g. Sullivan 1985). Also, Arabian babblers usually do not have sufficient information concerning the relatedness within the group (Wright et al. 1999), which is generally very high (Lundy et al. 1998). The data on chick feeding from this population suggest that babblers may gain benefits as a result of pseudoreciprocity or group augmentation (Wright 1997). Therefore, I predict that all group members should invest equally in group mobbing. This prediction is further supported by the fact that Arabian babbler helpers cannot be distinguished from breeders on the basis of their chick feeding effort, and no difference between family and complex groups was found (Wright 1997).

In the case of direct benefits to mobbers through predator-prey interactions, individual variation in mobbing response should correlate with alertness or relative escaping ability of the mobber (Hasson 1991). Hence, I predict that dominant, more experienced individuals will participate more actively in anti-predator behaviour. The data on anti-predator sentinel behaviour from this population support this hypothesis (Wright et al. 2001a, b).

Curio et al. (1983) suggested that differential risks taken by individuals during mobbing could potentially have a signalling function (see also Slagsvold 1984; Francis et al. 1989; Moholt and Trost 1989). Zahavi (1995) further suggested that mobbing behaviour in Arabian babblers (along with other activities, including chick feeding, allofeeding and sentinel behaviour) enhance the "social prestige" of the individual (but see Wright 1997, 1999). Recently, Boland et al. (1997) stressed the potential importance of self-advertisement in the formation of the coalitions of dispersers (reviewed in Cockburn 1998; Heinsohn and Legge 1999).

The idea of mobbing as a costly signal looks promising, because by approaching a predator individuals can advertise very specific collaborative abilities (Wright 1999). Indeed, while aggregating around a potentially lethal snake, babblers may demonstrate their current physical condition, agility and speed – information that is useful for a babbler that is "making a decision" of whether to stay longer in its parental group, disperse by itself, or to disperse in coalition with one of its fellow group members. Additionally, the willingness of an individual to participate in a dangerous activity together with others may demonstrate its value as a coalition member.

If babblers mob a snake in order to advertise their quality as dispersal coalition members, I predict the increased involvement of subordinates in this activity, because they are more likely to disperse from their current territory than dominant breeders. Also, females should respond more strongly than males, since females have fewer chances to establish themselves as breeders in their natal territory (Zahavi 1988, 1989, 1990). Additionally, if babblers mob the snake in order to advertise their quality rather than invest in their progeny, then the mobbing response should not be affected by the presence of offspring.

In this study, I evaluated the mobbing response of individual babblers within groups of different social structure by measuring the exact time spent mobbing by every bird during the mobbing session and compared these data with the predictions derived from the "self-advertisement for the formation of dispersal coalitions" hypothesis, as opposed to the "anti-predator behaviour" approach, i.e. investment and predator-prey interaction.

Methods

Study site and population

The study site is situated in central Arava valley, Israel, inside the Syrian-African rift system, between the Dead Sea and Eilat. It extends over 35 km^2 and most of the area falls within the boundaries of the Shezaf Nature Reserve. The fieldwork was conducted in January to October 1997.

The Arabian babbler (*T. squamiceps*) is a medium-sized (65–85 g), long-tailed group-living songbird. It occurs in the Arabian Peninsula and Sinai, extending to the desert areas of Israel. Groups may contain between 2 and 22 individuals and are characterised by an age-based linear dominance hierarchy (for details see Zahavi 1988, 1989, 1990). From one-half to two-thirds of groups are family groups, which consist of the breeding pair and their descendents (Zahavi 1989; Wright et al. 1999). Almost no reproduction of subordinates occurs in family groups (Zahavi 1989, 1990).

The remaining "complex" groups contain more than one breeder of at least one sex (usually males) that compete to reproduce (Lundy et al. 1998; Wright et al. 1999).

Amotz Zahavi established the long-term research project on Arabian babblers in Hazeva in 1971. During the present study, the population consisted of over 30 groups of babblers, each containing between 2 and 16 individuals. All the birds were colour-ringed (usually as nestlings) and most were tame and accustomed to human observers. The groups were monitored on a weekly basis and every change in their composition and breeding cycle was registered. The hierarchy within each group was established according to age or by observing the aggressive interactions between group members in the field.

Babbler dispersal

Most females disperse at 2–4 years old, whilst about 30% of males attain breeding status in their natal group (Zahavi 1989). Dispersal occurs throughout the year, but mostly during the breeding season, which lasts from February to July, and some pairs may breed in autumn and early winter. Babblers usually disperse as adults; however, immatures may disperse when only a few months old, either alone or in coalition with other group members (Zahavi 1989; A.A. Maklakov, personal observation).

Data collection

Each group was followed for at least 30 min in order to make sure that all individuals were present and that no natural mobbings had

occurred immediately prior to the experiment. If something extraordinary happened (e.g. predator attack, inter-group fight or the chasing of an intruder), I let another 30 min elapse before recording. Sometimes the group was very dispersed throughout its territory and the individuals were located hundreds of metres apart. Under these circumstances, I waited for the birds to regroup.

A trial began when all birds of the experimental group were present and the distance from the dummy snake to the group centre was less than 10 m, while no bird was more than 25 m away from the model. The group centre was defined as the mean of all distances between the dummy and the group members. This allowed a fast gathering of group members around the dummy, upon the discovery of dummy's location by one or more individuals. The snake model was placed in the direction of group movement on the ground near a bush, in the vicinity of a rodent burrow, partially covered by sand, which mimics the natural location of the viper.

The whole mobbing session was videotaped with a Sony 8 mm Hi-Fi camcorder, using the external directional microphone from a distance of 5 m, while the observer was sitting on the ground. Every change in the mobbing scene (e.g. birds moving in and out, becoming sentinels, preening, foraging) was recorded with the microphone. The films were analysed on a Sony 8 mm Hi-Fi recorder and with a Sony Trinitron colour monitor on normal speed and frame-by-frame motion.

The trial ended when 2 min had elapsed since the last individual stopped mobbing (see Definitions) or after the group moved further than 25 m away from the dummy. The trial was cancelled if the mobbing session was interrupted by some unusual event (e.g. predator attack, intrusion of the neighbouring group, passing vehicle).

I used a gypsum, coloured model of the adult horned viper (*Cerastes gasperettii*) to induce mobbing. It is one of the most common snake species in the study area, as well as the one most often mobbed by babblers (A.A. Maklakov, personal observation). It is an ambush hunter, which preys mainly on small rodents, up to and above the size of an adult babbler. When mobbed it usually lies still until the mobbing ceases and the birds move away. Sometimes it may react by head movements, coiling or attacking if the birds come too close. On rare occasions, snakes were seen escaping to the nearby hole, but this is likely to be a reaction to the disturbance caused by a human observer rather than by mobbing babblers. Carmeli (1988) reported no difference in mobbing duration, wing-lifting or vocal performance by babbler groups mobbing a live snake and a gypsum dummy. Although a moving snake elicits greater reaction, most of the natural mobbings occur when the viper is lying in ambush or resting, making it an ideal subject for the study without using a live snake.

Definitions

The bird classes were alpha males (dominant breeders), alpha females (dominant breeders), subordinate males and subordinate females (adults, at least 1 year old), fledglings (young of the year, less than 2 months old) and immatures (young of the year, at least 3 months old).

The experiments were performed at three stages of the breeding cycle: (1) before the onset of breeding (BBS), i.e. at least 2 weeks prior to first nest-building attempt; (2) groups with fledglings (FLD), and (3) groups with immatures (IMM).

A bird was considered mobbing when it performed at least one of the characteristic mobbing postures (neck-stretch, tail-spread, wing-lifting, wing-flicking) as described in Carmeli (1988), moved in circles around the dummy or emitted a special snake-mobbing call (Cramp and Perrins 1993). The bird was considered as "stop mobbing" if it was observed performing any other activity (e.g. foraging, preening, sentinel) for longer than 30 s, even if it stayed in the proximity of the dummy, or if it moved more than 2 m away, and did not perform mobbing postures or calls. Such definitions were very useful because babblers usually leave and rejoin the mobbing several times during the session. Sometimes they could fly away up to 50 m, but return shortly thereafter, while on other occasions they could stay close to the dummy without actually mobbing it.

The individual mobbing response was measured as the total time spent mobbing by a bird (i.e. sum of all mobbing episodes during one trial). The group mobbing response was measured as group mobbing duration, which is the time when the last individual stopped mobbing minus the time when it was started by the first bird.

Analysis

The data for all group members of each class were pooled to obtain the mean values of time spent mobbing by that class in given group type and at a particular stage of breeding season. The data were tested for normal distribution with the Kolmogorov-Smirnov one-sample test using Lilliefors probability (two-tailed). Data were normalised using cubed log-transformation [$\log (\text{data}+1)^3$]. I applied a mixed model using a REML procedure (SAS System for Windows V8) with rank (dominant or subordinate), sex (male or female), group structure (family or complex), group reproductive stage (before breeding season, groups with fledglings and groups with immatures) and group size as fixed effects. Group identity and individual babbler indentity were included as random effects. I also included potentially important interactions: rank by sex, group structure by rank, group structure by group reproductive stage, group structure by sex and sex by group reproductive stage. Non-significant interactions ($P>0.1$) were removed and I present the output for the reduced model in the results section. I used the REML procedure to compare the mobbing response of immature babblers to that of adults, with group structure, group size and individual age class (adult or immature) as fixed effects and group identity as random effect and group structure by age class interaction. Group mobbing response was also analysed using REML, with group structure, reproductive stage and group size as fixed effects and group identity as random effect. The original data were normalised using log transformation. Two-tailed *P*-values are given throughout.

Results

Individual mobbing response

The outcome of the fixed effects is presented in Table 1. There were significant effects of babbler rank, sex and group reproductive stage on the mobbing response of an individual babbler (Fig. 1; Table 1). There was no effect of group size on mobbing response. Additionally, three interactions – group structure by rank, group structure by group reproductive stage and sex by rank – significantly

Table 1 The effect of group structure, rank, sex, group size and reproductive stage on time spent mobbing by an individual babbler. Results are presented as numerator and denominator degrees of freedom; *F* values and P values from REML model. Non-significant interactions were removed. See text for details

Effect	Num *df*	Den *df*	*F* value	P
Group structure	1	72	0.7	0.4
Rank	1	72	32.7	<0.001
Sex	1	72	10.4	<0.01
Group size	1	72	1.7	0.18
Reproductive stage	2	72	8.9	<0.001
Group structure*Rank	1	72	9.1	<0.01
Group structure*Reproductive stage	2	72	7.4	0.01
Sex*Rank	1	72	4.3	0.041

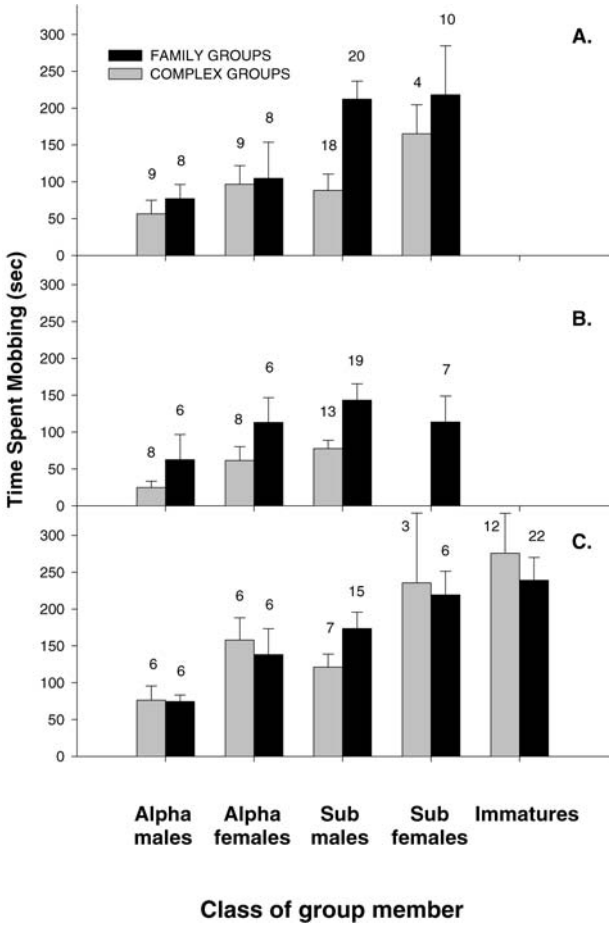

Fig. 1 Time spent mobbing (mean+SE) by five classes of group member (alpha males, alpha females, subordinate males, subordinate females, immatures) during the three stages of the breeding cycle: before the onset of breeding (**A**), groups with fledglings (**B**), and groups with immature babblers (**C**). The *number* of birds is shown above the *error bars*. Both sex and rank of individual group member showed a significant effect on the time spent mobbing (see text for details)

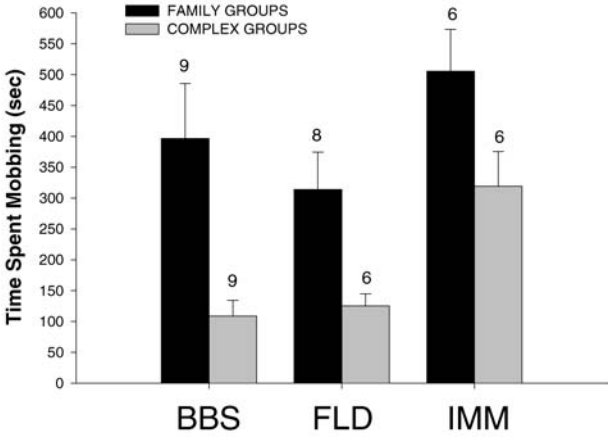

Fig. 2 The effect of group structure on mobbing duration at the three stages of the breeding cycle (*BBS* before the onset of breeding; *FLD* groups with fledglings; *IMM* groups with immatures). The *number* of groups is shown above the *error bars*. There was a difference in mobbing activity between family and complex groups when the group size was taken into account (see text for details)

Table 2 The effect of group structure, group size and individual age class (adult or immature) on individual time spent mobbing. Results are presented as numerator and denominator degrees of freedom; *F* values and *P* values from REML. Non-significant interaction (group structure by age class) was removed. See text for details

Effect	Num *df*	Den *df*	*F* value	*P*
Group structure	1	76	0.3	0.57
Group size	1	76	0.1	0.8
Age class	2	76	37.8	<0.001

Table 3 The effect of group structure, group size and reproductive stage on group time spent mobbing. Results are presented as numerator and denominator degrees of freedom; *F* values and *P* values from REML. Non-significant interactions were removed. See text for details

Effect	Num *df*	Den *df*	*F* value	*P*
Group structure	1	12	13.1	0.003
Group size	1	12	0.1	0.74
Reproductive stage	2	12	3.9	0.046

influenced time spent mobbing by an individual babbler (Table 1). The interaction between group structure and babbler rank reflected the increased response by subordinate birds versus dominants in family groups compared with that in complex groups (Fig. 1, especially A). The interaction between group structure and group reproductive stage resulted from a relatively large increase in time spent mobbing by babblers in complex groups towards the end of the reproductive season (compare Fig. 1C vs A and B). Finally, the sex by rank interaction was due to a consistently stronger response of alpha females versus alpha males, as compared with a less consistent sex difference among subordinates (Fig. 1). Babblers decreased their individual mobbing response when they had fledglings (FLD), in comparison to the period before the onset of the breeding season (BBS) (see Fig. 1). The mobbing response increased when adult babblers were joined by immature birds (IMM) (Fig. 1).

Mobbing by immature babblers

Immatures participated actively in mobbing behaviour irrespective of group structure (Fig. 1C). They mobbed longer than adults both in family and complex groups, whilst there was no difference in time spent mobbing by immatures between the two group types (Table 2).

Group mobbing response

The outcome of the fixed effects is presented in Table 3. There were significant effects of group structure and group reproductive stage on the mobbing response of a group (Fig. 2; Table 3). There was no effect of group size

on mobbing response and no significant interactions. Family groups mobbed longer than complex groups (Fig. 2). The presence of immature birds resulted in increased group mobbing response (Fig. 2), whilst there was no difference between the first two reproductive stages.

Discussion

The results show that snake-directed mobbing behaviour in Arabian babblers varies with sex and rank of individual birds, as well as with reproductive stage of the group. Subordinate group members mobbed longer than dominants and females mobbed longer than males. Babblers decreased their time spent mobbing during the period when they had dependent fledglings and increased it when immatures were present.

There was no significant effect of group structure (family or complex) on individual mobbing response, which is consistent with the previously reported data on this species. Thus, no effect of group structure on chick feeding (Wright 1997) or sentinel activity (Wright et al. 2001a, b) was found. However, there was a significant interaction between group structure and babbler rank, reflecting the increased mobbing by subordinates in family groups. Increased mobbing by subordinates translated into increased group mobbing response by family groups. Increased mobbing by family groups is consistent with predictions derived from Hamilton's rule (Hamilton 1964), which supports the hypothesis that mobbing is an anti-predator behaviour that benefits other group members and that individual birds adjust their effort accordingly. However, it is less clear why dominant group members mob less than subordinates. Increased mobbing by subordinates in family groups supports the "dispersal coalitions" hypothesis. This is because in complex groups there is a potential for subordinates to reproduce, as opposed to family groups, in which no reproduction of subordinates occurs due to an "incest taboo" (Zahavi 1989). Therefore, subordinates in family groups may be more motivated to disperse.

The above results resemble those reported for vigilance behaviour of dwarf mongooses (Rasa 1987), in that subordinate group members carry out the majority of anti-predator behaviour. However, in mongooses, mainly sub-adult males perform the vigilance behaviour. Rasa (1987) suggested that such a pattern might be explained either by: (1) males signalling their status to other males in the group, or (2) males advertising their potential quality to the alpha female. However, in babblers, both sexes participate in mobbing, and when there is a difference, it is females that are more active. Additionally, alpha females appear to perform a great deal of mobbing. Family groups were shown to spend more time mobbing than complex groups. Given that subordinate females in family groups have very low chances of reproducing within their natal group (Zahavi 1989) and there is no reason to expect that status signalling should be more important for females than for males, these explanations (status or mate-quality signalling) seem unlikely. In addition, I did not observe any interference among group members that could be associated specifically with mobbing. Aggressive events were extremely rare, and were observed only between individuals that expressed aggression towards one another prior to a mobbing session.

Female-biased mobbing by subordinates, however, supports the idea of mobbing as self-advertisement for the formation of dispersal coalitions. This is because the females are more likely to disperse than the males (Zahavi 1990), since the females have few chances of inheriting the breeding position in their natal group (Zahavi 1989, 1990). Also, alpha females may have to disperse together with their daughters upon the death of the alpha male, whereas the death of the alpha female is followed by the arrival of new females (Zahavi 1988, 1989). Consequently, alpha females may be more motivated to advertise their quality as potential coalition members than alpha males. Indeed, the mobbing response of alpha females versus alpha males was consistently greater than that of subordinate females versus subordinate males, as indicated by the significant sex by rank interaction.

Babblers decreased their time spent mobbing when they had dependent fledglings, probably due to the increased pressure of food provisioning on their time budget. They increased their mobbing response beyond the initial level (before the onset of the breeding season) when immatures started to join the group activities. Immatures mobbed longer than any other bird class and contributed to the increased group mobbing duration at this stage. Immature birds may be learning about different types of predators, which may explain their increased mobbing reaction. Similarly, increased mobbing response by adult babblers when immatures are present may facilitate the transmission of predator recognition. Cultural transmission of predator recognition has been experimentally shown in birds (Curio et al. 1978a, b).

There was significant interaction between group structure and group reproductive stage in individual babbler mobbing response. It reflects a relatively greater increase in mobbing response by complex groups during the stage with immatures. Increased mobbing by complex groups later in the breeding season is consistent with the "self-advertisement for dispersal coalitions" hypothesis. This is because, as already stated, in complex groups there is a potential for subordinates to reproduce, as opposed to family groups, in which no reproduction of subordinates occurs due to the "incest taboo" (Zahavi 1989). Subordinates in family groups may be more motivated to disperse before the start of the breeding season than subordinates in complex groups, which is supported by a significant rank by group structure interaction, indicating that subordinates in family groups mob longer than subordinates in complex groups. Later in the season, complex groups include immatures which carry out much of the group mobbing. As immature babblers will not reproduce with members of their natal group, irre-

spective of their real relatedness (Zahavi 1990), they have the same incentive to disperse as immature babblers from family groups.

The results of snake-mobbing experiments in Arabian babblers are still more interesting when compared to the available data from other bird studies. The only three studies that investigated mobbing in cooperatively breeding birds other than babblers are snake mobbing by Florida scrub jays (*Aphelocoma c. coerulescens*) (Francis et al. 1989), nest defence in noisy miners (*Manorina melanocephala*) (Arnold 2000a, b) and response to cuckoos by splendid wrens (*Malurus splendens*) (Payne et al. 1985). In splendid wrens, the breeding female usually spent more time in contact with the cuckoo than any other bird in the group and was usually also the first to discover and attack it, while all other group members participated equally in mobbing. The stuffed cuckoo was placed near the nest, which probably elicited the relatively greater response of the breeding female. There was no effect of group structure (i.e. groups with non-breeding auxiliaries and single pairs) on mobbing response.

The data on Florida scrub jays is of special interest, since the researchers used a live snake in order to elicit mobbing. The mobbing behaviour demonstrated by the members of jay groups was directly the opposite of what I found in Arabian babblers. The breeding male was the most active mobber; the breeding female and subordinates responded about equally, while fledglings mobbed less than the adults.

Why is the pattern of mobbing behaviour so different in two cooperatively breeding species? The answer may lie in the different degree of danger that snakes represent for jays and babblers. Snakes are among the main predators of scrub-jay nestlings and fledglings. Hence, we may expect that dominant breeders will invest in mobbing if it helps to protect their young. In this way, snake mobbing in jays is more like raptor mobbing in babblers (see below). However, the snake species that is most often mobbed by babblers, the horned viper *Cerastes gasperettii*, cannot climb trees to reach nests and is dangerous to adults or fledglings only when overlooked on the ground. Indeed, once discovered, the viper presents no danger for foraging babblers. The horned viper is an ambush hunter and does not actively chase foraging babblers. It would be useful for the birds if they could drive the snake away from their territory, but I never saw this happening. Thus, it seems that the prolonged, active mobbing of *C. gasperettii* has no fitness consequences for the babblers, besides the supposed self-advertisement.

In noisy miners, many group members participate only in nest defence, whilst not contributing in any other way to the care of the brood (Arnold 2000a, b). The mobbing behaviour of noisy miners can probably be explained in terms of self-defence or pseudoreciprocity (Arnold 2000a), or it may be that some group members are "specialists" focusing on a different form of helping (Arnold 2000b). Arnold (2000a) also suggested that mobbing behaviour by noisy miners might also have a signalling function used to identify future mates, although why exactly the good mobbers would become good mating partners is unclear.

Most remarkably, the pattern of raptor mobbing in Arabian babblers (Anava 1992) differs principally from what we see in snake mobbing, suggesting that different selective forces may underlie these behavioural activities. Dominant breeders are among the most active mobbers while facing a raptor, as would be predicted by many models that emphasise the defensive function of mobbing. It is possible that mobbing behaviour originated as an anti-predator tactic but, in cooperatively breeding species, has been adapted to fulfil additional functions.

Avian mobbing, being a widespread behaviour, has attracted many theories (Curio 1978) and is often regarded as multifunctional (see, for example, Frankenberg 1981; Curio et al. 1985; Regelmann and Curio 1986; Carmeli 1988; Flasskamp 1994). Although mobbing has been extensively studied for many years, surprisingly little is known about this behaviour in cooperatively breeding species. The anti-predator component of snake-directed mobbing by babblers is apparent as a sensible warning system in the stable, kin-structured groups. This study suggests that subordinate babblers mob longer when surrounded by close kin, which implies that babblers can adjust their investment based on within-group relatedness. Active participation by immatures also suggests that offspring may learn about their predators during mobbing. The present study provides insight into yet another possible function of this behaviour and the evolutionary forces that drive it. The prolonged active mobbing that is mainly performed by adult subordinates rather than dominants, and by females rather than males, is difficult to explain within the framework of the classical anti-predator behaviour models. It is possible that the participation in this risky activity may be used as an honest signal by which group members advertise their quality as potential members of dispersal coalitions. The next obvious step would be to test if the best mobbers are actually more likely to create a dispersing coalition, and if mobbing activity increases prior to dispersal events.

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