

Helping at the nest, allofeeding and social status in immature arabian babblers

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Summary. Arabian babblers, *Turdoides squamiceps*, are cooperatively breeding, group territorial birds, occurring in desert habitats. Non-breeders participate in several types of cooperative behaviour, including care of eggs, nestlings and fledglings, and bringing food to one another (allofeeding). This paper reports on observations of helping with eggs and young, and peer allofeeding, performed by immature babblers, fledged the previous season or earlier in the same season. The birds were from a babbler population studied since 1971 in the Arava valley of eastern Israel. They belonged to groups in which all individuals had been colour-ringed and were accustomed to human observers. Individuals and nests in the territories of these groups could be watched from distances of 1–2 m without causing alarm, so fine details of behaviour could be observed in the field. In most allofeeding interactions observed, a more dominant individual brought food to a subordinate. Sometimes the subordinate bird avoided accepting the proffered food, and was then hit or chased by the bird that had attempted to feed it. Occasionally a subordinate bird attempted to feed a more dominant individual. Dominant birds always refused to take food offered by a subordinate, and hit or chased any subordinate attempting to feed them. Frequencies of visits to nests were correlated with helper rank for those visits where the incoming bird displaced a previous visitor from the nest. Frequencies of visits to unattended nests, however, were not correlated with helper rank. Similarly, frequencies of feeding visits to fledglings were correlated with

helper rank until incubation of the next brood began. After this, the correlation disappeared. Numerous instances of aborted nest visits were observed in which a helper, often carrying food, arrived at the nest-tree but left again without visiting the nest. In many other cases, a helper arrived at the nest-tree but delayed visiting the nest for several minutes. Aborted and delayed visits usually occurred when a more dominant bird was in the vicinity of the nest. This suggests interference between helpers. Direct interference between helpers visiting fledglings was occasionally observed. In such cases, a more dominant helper snatched food from a subordinate approaching fledglings, and then fed this food to the fledglings itself. Interference between helpers, and conflict between profferers and recipients of food during allofeeding, are not easily explained by kin selection or reciprocity. On the other hand, such behaviour is readily explained by a hypothesis which suggests that individuals may increase their social status in the group by performing cooperative behaviour. Babblers that establish status by demonstrating ability to bear the short-term costs of cooperative behaviour, rather than through direct aggression towards rivals, are likely to forge collaborative relationships with other group members. Since babblers must collaborate to establish and defend a territory, such relationships are essential to reproductive success.

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Introduction

The Arabian babbler (*Turdoides squamiceps*, Timalidae) is a group territorial, cooperatively breeding thrush-like bird, occurring in the Arabian and

Sinai deserts, and in the rift-valley between eastern Israel and Jordan. This species resembles many other cooperatively breeding avian species in that non-breeding individuals perform various types of cooperative behaviour, including helping at the nest and with the care of fledglings (Zahavi 1974, 1976; Brown 1975). In addition, adults and immature birds old enough to forage for themselves often feed each other (allofeeding).

In both helping with the care of young and allofeeding, certain individuals appear to behave altruistically towards other members of their social group (cf. Emlen 1981). The occurrence of such behaviour has stimulated a great deal of discussion among behavioural ecologists, and a number of hypotheses exist providing possible evolutionary explanations.

Early discussions of cooperative breeding (e.g., Skutch 1961) considered the social group as the unit of selection, and stressed benefits which cooperative behaviour might bring to the group as a whole. More recently, kin selection (Hamilton 1964) and reciprocity (1971) have been suggested as evolutionary mechanisms for cooperative behaviour such as helping at the nest. In support of the kin selection hypothesis, much evidence indicates that helpers are often close relatives of breeders (e.g., Maynard Smith and Ridpath 1972; Brown 1974; Emlen 1978, 1981). However, this is not always the case (Fry 1972; Brown 1978, Ligon and Ligon 1978). Woolfenden (1975), Ligon and Ligon (1978) and Stallcup and Woolfenden (1979) suggest that non-breeders cooperating with breeders and/or with each other may increase their prospects for survival and future reproduction. A non-breeder helping a breeder, usually a high-ranking individual, might do this by becoming valuable to the breeder and thereby increasing the probability of being allowed to remain and eventually breed on an established territory. A non-breeder helping other non-breeders might form strong bonds, or 'friendships' with these individuals. With their collaboration, it might later establish a new territory. Consequently, non-breeders that behave cooperatively may increase individual fitness through delayed benefits.

In support of reciprocity rather than kin selection, Ligon and Ligon (1978) presented evidence that helping at the nest and other cooperative behaviour in communally nesting birds is not confined to relatives of breeders. Brown (1978), Brown and Brown (1981) and Emlen (1981, 1982), on the other hand, recognizing that individual selection and kin selection are not mutually exclusive, have provided models for the evolution of cooperative

behaviour in which more than one type of evolutionary mechanism may operate.

A fourth hypothesis for the evolution of cooperative behaviour in birds been proposed by Zahavi (1976). Noting that among cooperative breeders, reproductive success for both sexes increases with social rank (e.g., Zahavi 1974, 1976; Woolfenden 1975; Gaston 1977; Woolfenden and Fitzpatrick in press), Zahavi suggested that an individual may increase its expected reproductive success, and therefore its individual fitness, by performing types of behaviour which improve its social status in the group. Cooperative behaviour may function in this way because the extent to which an individual can sustain the short-term cost of cooperative or apparently altruistic acts without coming to serious harm may function as a direct indicator of that individual's quality (Zahavi 1975). Since other members of the group are potentially both rivals and collaborators (Zahavi 1976; Emlen 1978), an individual advertising its quality by performing cooperative behaviour may improve its social status in the group by attracting collaborators and deterring rivals.

This hypothesis is distinct from those discussed by previously cited authors, although it is similar to the reciprocity hypothesis in that the evolutionary mechanism proposed operates through direct but delayed benefits to individuals. However, an individual that advertises its quality through cooperative behaviour increases its fitness whether group members that are helped reciprocate or not. Therefore cheating cannot occur, and it is unnecessary to postulate the coevolution of mechanisms for detecting and discriminating against cheats. This is not the case with reciprocity. Zahavi's hypothesis is therefore at least as parsimonious as existing alternatives attempting to explain the evolution of cooperative and apparently altruistic behaviour in communally breeding birds. However, it should be recognized clearly that just as reciprocity does not exclude kin selection, Zahavi's advertising hypothesis does not exclude either reciprocity or kin selection. The three mechanisms may complement one another, each contributing to the evolution of cooperative behaviour.

The purpose of this paper is to provide evidence from a field study of helping at the nest and allofeeding in Arabian babblers that in this species the advertising mechanism proposed by Zahavi has played an important role in the evolution of these behaviours. We contend that several features of the behaviour patterns we observed in babblers are easily explained by the advertising hypothesis, but are not easily explained by reciprocity or kin selec-

tion. This would imply that helping at the nest and allofeeding in babblers have probably evolved at least partly because they are effective methods of advertising quality to gain status, whether or not reciprocity and/or kin selection have also played a role.

Methods

The study area consists of 25 square kilometers of desert habitat at Hatzeva, located about 30 km south of the Dead Sea in the Arava rift valley of eastern Israel. The Arava valley extends between the Dead Sea in the north and the Red Sea in the South. The average yearly rainfall in the vicinity of Hatzeva is only 50 mm. However, near-surface sediments in this area, which was once a lake basin, consist of alternating layers of sandy deposits and clays. Rainfall is prevented from draining away from the surface, so vegetation in this area is denser than in other parts of the Arava valley. This vegetation, which includes trees and bushes, supports a food supply (insects, small reptiles, seeds, berries, etc.) and provides shelter from predators for a comparatively dense babbler population. In other parts of the Arava valley trees and bushes occur only sporadically, in dry river valleys, and the babbler population is correspondingly sparse.

About 20 babbler groups in the Hatzeva area have been studied continuously, since 1971, by a team from Tel Aviv University led by A. Zahavi. All babblers belonging to these groups are colour-ringed in the nest to facilitate individual identification. In another 40–50 groups, occupying surrounding territories from which immigration might occur, birds are ringed whenever possible. At the time this study was conducted, about 85% of such birds were ringed.

Birds in the study area are occasionally fed by observers, usually with small pieces of bread. Birds in these groups are therefore seldom alarmed by the presence of human observers, and it is usually possible to approach nests closely, and to monitor them from a distance of 1–2 m. This facilitates the observation of fine details of behaviour in the field.

The present study uses data collected between April 1981 and June 1982 from 12 babbler groups, ranging in size from 6–16 individuals excluding nestlings and fledglings. We chose to collect data from immature babblers, fledged either earlier in the season or the previous year. There were two reasons for this.

First, aggressive interactions involving yearlings and younger birds are commonplace under natural conditions, and are also easily induced by human manipulation. It is therefore comparatively easy to establish the relative social ranks of immature babblers belonging to a particular group. By contrast, overt, spontaneous aggression between adults is rarely observed, and it is much more difficult, sometimes impossible, to induce aggression between adults (cf. Gaston 1977).

Secondly, it was common for several immature birds of similar ages and comparable social positions to be present in the same group. During the 1981 breeding season, for example, following unusually heavy rains and an exceptionally productive breeding season in 1980, one of our babbler groups contained 10 yearlings. Adults, on the other hand, were fewer in number, and generally occupied unique and less easily defined social positions in their groups, delineated in part by age, sex, relationships with other adults, and group size. Thus we felt that general predictions could be tested more easily by observing variation in the behaviour of immature birds.

Several types of aggression were observed between imma-

ture babblers in our study population. From the outcomes of these interactions, observers could infer the relative ranks of the pairs of birds involved.

Intense fights occur between members of the same brood during their first month out of the nest. After the first month, however, aggressive encounters between babblers become increasingly brief, subtle and ritualized. Nevertheless, the identities of the winners and losers of such encounters are always obvious. Three main categories of aggressive interaction were observed for older fledglings and yearlings: (1) The aggressor makes a stabbing motion of the beak towards another bird, without actually making contact. The other bird withdraws. (2) The aggressor stabs or hits another bird with its beak, often lightly but sometimes repeatedly. The other bird withdraws. (3) The aggressor chases another bird. The aggressor may or may not also hit the other bird before chasing it or after catching up with it. The chase sometimes emits distress calls.

Many of the aggressive interactions observed occurred spontaneously, often apparently precipitated by competition for naturally occurring food items. Others were induced by throwing small food items, usually tidbits of bread, onto the ground between two individuals whose relative ranks the observer wished to determine, or by handfeeding one bird in the presence of a rival.

For each group studied, identities of individuals involved, and outcomes of aggressive encounters, were recorded until sufficient data were accumulated to determine the relative ranks of all fledglings and yearlings. Wherever possible we attempted to obtain repeat observations of interactions between each pair of closely ranked individuals. However, it was sometimes difficult to induce fights between lower ranking members of the same brood, particularly if they were female. Occasionally, therefore, our estimates of relative rank depend on single observations.

The relative ranks of immature birds in each group studied were also rechecked as frequently as possible, so that any changes in dominance hierarchy could be tracked. Hierarchical changes were expected for this age-group: Although there is no overall tendency for either sex to dominate the other among newly fledged babblers, yearling males tend to rank higher than yearling females. Changes in rank often coincide approximately with the emergence of a sexual dimorphism in the appearance of the eye (Zahavi, unpublished data).

As with aggression, our data-set for allofeeding among immature babblers contains many instances in which the behaviour occurred spontaneously, but even more in which it was induced by human observers. Allofeeding was induced in exactly the same manner as aggression. In fact, it was impossible to predict on a general basis whether an attempt to induce an interaction would precipitate aggression or allofeeding, or would fail to elicit a response. Allofeeding data were therefore collected concurrently with information on dominance hierarchies.

For each instance of allofeeding observed, the identities and roles (feeder or recipient) of the individuals involved in the interaction were recorded. During allofeeding, the individual bringing food typically adopts a tall posture and trills. At the same time, the bird receiving food usually crouches with its head raised and its beak gaping towards the feeder, often flutters its wings, and sometimes utters loud 'begging' calls. However, begging calls are rare in birds more than a few months old.

These postures, gestures and vocalizations form a mutual display which is of essentially similar form for all allofeeding among Arabian babblers, whether the interaction is between adult and fledgling or between two peers. Nevertheless, the details of this display and the manner in which individuals

react to each other during allofeeding are highly variable. Therefore, each particular interaction observed was described for our records in as much detail as possible.

Most breeding in our study population occurs in spring and summer, approximately from February to July, but occasionally in other months as well, depending on the extent, timing and pattern of winter rain (Zahavi, unpublished data). During the 1981 and 1982 breeding seasons we monitored nests and broods of newly fledged juveniles, recording identities and frequencies of visits for helpers participating in the care of eggs, nestlings or fledglings. We also recorded behavioural details such as the activity performed (e.g., feeding or shading nestlings, or cleaning the nest), the duration of the visit, and the type of vocalization, if any, associated with the visit. Finally, we recorded details of interactions between two or more helpers visiting the same nest or fledgling brood at the same time.

Results

Social rank

Our observations on the frequencies of aggressive interactions between immature babblers in the groups studied are summarized in Table 1. To determine dominance hierarchies, we attempted to minimize the number of scores appearing above the upper-left to lower-right diagonal for each sub-table. Hence, the hierarchies that we consider most probable for the time periods indicated appear, in order of decreasing social rank, from left to right and from top to bottom of each sub-table.

Table 1. Frequencies of aggressive interactions observed between immature babblers fledged for at least one month. Observations are presented by territorial group and by date. Individuals are distinguished by an identifying numeral and letter. A Roman numeral indicates that the bird in question was fledged in 1980, and Arabic numeral that it was fledged in 1981, and an underscored Arabic numeral that it was fledged in 1982. Birds of the first brood in a particular season are given the numeral one, those of the second the numeral two etc. Individuals within broods are distinguished from each other by letters. Columns in each table are headed by the identities of aggressors. The identities of recipients of aggressive acts are shown to the left of each row. The sex of each individual, if known, is also shown to the left of each row. Asterisks indicate individuals that apparently exchanged rank

Group 1:

July – September 1980

	IA	IB	IC	ID
♂ IA				
♀ IB	1			
♀ IC	3	3		
♀ ID	2	3	3	

May 1981

	IA	IB	IC	ID	1A	1B	1C	1D
♂ IA								
♀ IB								
♀ IC								
♀ ID								
♂ 1A								
♂ 1B						2		
♂ 1C	1					3	1	
♀ 1D								

Juli–September 1981

	IA	IB	IC	ID	1B*	1A*	1C	1D
♂ IA								
♀ IB	7							
♀ IC	4	1						
♀ ID	1					1		
♂ 1B*	5	2						
♂ 1A*	1	2				13		
♂ 1C	4					23	5	
♀ 1D	1			1		13	2	1

Group 2

September 1980–April 1981

	IA	IB	IC
♂ IA			
♂ IB	10		
♀ IC	2	4	

April 1981

	1A	1B	1C
♂ 1A			
♀ 1B	1		
♂ 1C	1	1	

August – November 1981

	1A	1B	1C	2A	2B	2C	2D	3A	3B
♂ 1A									
♀ 1B	3								
♂ 1C	3								
♀ 2A	4								
♀ 2B	6	1	5	4					
♀ 2C	5	1	1	3	2				
♂ 2D	1		1	4	1	1			
♀ 3A	3	4				2	2		
♂ 3B	2					7	7	7	

Table 1 (continued)

Group 2 (continued)

January–February 1982

	1A	1B	1C	2A	2C*	2D*	2B*	3A	3B
♂ 1A									
♀ 1B	3								
♂ 1C	2	5							
♀ 2A	1	2	1						
♀ 2C*	2	1	2	1		1	2		
♂ 2D*		1		3	3		2		
♀ 2B*	1	1		2	4	16			
♀ 3A	1		1	1		7			
♂ 3B	1			1	7	3		8	

March – April 1982

	1A	1B	1C
1A			
1B	5		
1C	2	3	

Group 3:

April–May 1981

	IIA	IA	IIB	1A	1B	1C	2A	2B	2C
♂ IIA									
♀ IA	3								
♀ IIB	3	2							
♂ 1A			1						
♀ 1B		1		4					
♂ 1C				4	3				
2A			1						
2B							10		
2C							5	5	

Group 4:

July–August 1981

	3A	3B	3C	3D
♀ 3A				
♀ 3B	2			
♂ 3C	3	2		
♀ 3D	3	3	1	

Table 1 (continued)

Group 4 (continued)

November 1981–January 1982

	1A	1B	1C	1D	2A	2B	3A	3C*	3B*	3D
♂ 1A										
♂ 1B	6									
♂ 1C	4	2								
♀ 1D	6	2	3							
♀ 2A								3		
♂ 2B	3				2					
♀ 3A	2	1	1	1		1				
♂ 3C*			1			2	2			
♀ 3B*	4			1			1	2		
♀ 3D							3	3	1	

February 1982

	1A	1B	1C	1D	2B*	3C*	2A*	3A	3B	3D
♂ 1A										
♂ 1B	1									
♂ 1C	4									
♀ 1D			2							
♂ 2B*			1							
♂ 3C*					2					
♀ 2A*						2				
♀ 3A	1						2			
♀ 3B			1							
♀ 3D			1			2		1	3	

Group 5:

September 1981–February 1982

	1A	1B	1C	1D
♂ 1A				
♂ 1B	6		1	
♀ 1C	11	6		1
♀ 1D	9	5	9	

Group 6:

October 1981–March 1982

	1A	2A	1B	2B	2C
♂ 1A					
♂ 2A	28				
♀ 1B	8	3			
♂ 2B	30	2	1		
♂ 2C	24	6	2	1	

Table 1 (continued)

Group 7:

December 1981–February 1982

	1A	1B	1C	2A	2B	2C
♂ 1A						
♀ 1B	3					
♂ 1C	6	2				
♂ 2A		2	4			
♂ 2B	2	1		4		
♀ 2C	3		3	3	2	

Group 8:

December 1981–February 1982

	1A	1B	2A	1C	1D	2B	2C	2D
♂ 1A								
♂ 1B	5							
♂ 2A	6	13						
♀ 1C	7	5	4					
♀ 1D	2	7	2					
♂ 2B	4	4	23	4	1			
♀ 2C	1	1	16	3		4		
♀ 2D	4	1	12	3		3	2	

Group 9:

January–March 1982

	1A	1B	1C
♀ 1A			
♀ 1B	4		
♀ 1C	1	3	

Group 10:

January–March 1982

	1A	1B	2A	2B	2C
♂ 1A					
♂ 1B	4				
♂ 2A		12			
♂ 2B	2	3	6		
♀ 2C		2	6	8	

Group 11:

January–February 1982

	1A	1B	1C	2A	2B	2C
♂ 1A						
♂ 1B	2					
♀ 1C		1				
♀ 2A	2	2	1			
♂ 2B	5			2		
♀ 2C	1				2	

Group 12:

January–February 1982

	1A	1B	1C
♂ 1A			
♂ 1B	5		
♀ 1C		3	

Allofeeding

During July 1981–March 1982 we observed 94 instances of allofeeding among immature siblings aged between four and thirteen months. In 86 cases a dominant individual brought food to a more subordinate sibling. In the remaining eight cases, the converse occurred.

During the same period we observed 438 aggressive acts between immature siblings belonging to groups in which we also saw allofeeding. In only 11 instances did a bird behave aggressively towards a sibling which we judged to be of higher rank on the basis of previous and subsequent observations of aggressive interactions.

Observed frequencies for aggressive acts and allofeeding between peers, according to the sexes of participants, are given in Table 2. Expected frequencies were calculated according to the null-hypothesis that the ratio in which the two types of act occur is independent of the sexes of the individuals involved. This hypothesis was rejected ($G_3 = 12.24$, $P < 0.01$). In particular, males showed a greater ratio of attacks to feeding acts towards peers of either sex than females ($G_1 = 8.63$, $P < 0.001$), with males more likely to attack and less likely to feed than females. On the other hand, there was no significant difference between the sexes regarding the ratio of allofeeding to aggressive acts received ($G_1 = 0.39$, $P < 0.5$). Nor did a significant difference emerge when interactions be-

Table 2. Frequencies of aggression and allofeeding between peers for babblers fledged for four to thirteen months

	Interaction		
	Aggression	Allofeeding	Aggression/ feeding
♂ performer	316	53	5.96
♀ performer	122	41	2.98
♂ recipient	190	44	4.32
♀ recipient	248	50	4.96
Participants of same sex	214	39	5.49
Participants differently sexed	224	55	4.07

tween siblings of the same sex were compared to those involving siblings of different sexes ($G_1 = 2.56$, $P > 0.5$).

We observed 14 cases in which a subordinate yearling approached a more dominant sibling which was carrying food, and solicited allofeeding by adopting the 'begging' posture of a recipient. Allofeeding followed in 11 instances. In the majority of our observations (65 out of 94), however, we observed that the recipient adopted the begging posture only after its sib had approached with food and trilled. We also observed 16 cases in which the recipient refused to take most of the food offered, only swallowing a little bit, and 9 cases in which food was completely refused.

In 7 of our observations of partial or complete refusals in which the bird bringing food was the more dominant, the food-bearer followed up its feeding attempt by hitting and/or chasing its sibling. In three cases the subordinate individual tried to run away before it was hit, and gave distress calls. Conversely, in all 6 cases in which we observed a bird refusing food from a subordinate sibling, the proposed recipient hit the bird offering food. In our most extreme example, a 10 month-old female, refusing to accept food presented by her subordinate 8 month-old sister, did not adopt a begging posture, but instead raised herself up, matching her height to her sister's. She then snatched the bread from her sister's beak and thrust it down her sister's throat, appearing at the same time to force her into the begging posture. When the subordinate bird had swallowed the food, the dominant sister hit her repeatedly with her beak until she ran away. Immediately afterwards, the subordinate sister fetched another piece of bread and went to allofeed her even lower-rank-

ing 8 month-old brother, who was foraging about 10 m away.

Helping at the nest and care of fledglings

Our data on the frequencies of visits to nests and fledglings by immature Arabian babbler helpers are presented in Table 3. It should be noted that since there were different numbers of helpers for each group, and sometimes for each brood within a group, and since nests and fledgling broods were not watched for a standard length of time or at a standard time of day, the data from different nests and broods could not be pooled for the purpose of fitting overall regression lines. Regression analysis was therefore carried out on each nest or brood separately, and joint probabilities were calculated for all F -values. Their separate degrees of freedom, approximate probabilities, and associated regression coefficients are given in Table 4. Figure 1 provides a visual summary of our findings on relationships between brood-rearing activity and rank.

For yearlings visiting nests and displacing another bird sitting on the nest, we found a significant tendency for visiting rate to decline with decreasing social status ($P < 0.05$, see Table 4 for F -values). This trend was irrespective of helper sex ($F_{1,14} = 1.67$, $P > 0.1$). For yearlings visiting unattended nests we found no tendency for visiting rate to be related to rank, nor did one sex of helper visit at a significantly higher rate than the other ($F_{1,17} = 3.55$, $0.1 > P > 0.05$).

A breeding Arabian babbler female may lay several clutches per season, if conditions are favourable, with incubation of a new clutch beginning before fledglings from the previous brood can forage independently. For yearlings and juveniles feeding fledglings, we found that prior to the start of incubation of the new clutch, the rate at which fledglings were fed declined with decreasing helper status ($P < 0.001$, see Table 4 for F -values), and that females fed fledglings at a higher rate than males ($F_{1,28} = 4.97$, $P < 0.05$). The latter difference was significant despite an overall tendency for yearling females to be subordinate to their brothers. Both relationships disappeared for fledgling-feeding occurring concurrently with incubation and care of new eggs and nestlings. For male versus female feeding rates, $F_{1,19} = 1.63$, $P > 0.1$.

Another set of our observations concerned delayed nest-visits, where incoming helpers did not go straight to the nest but waited perched in the nest-tree for several seconds to minutes before going to the nest, and abortive nest-visits in which

Table 4. Statistical data from linear regression of frequencies of nest-visits and fledgling-feeding on helper social rank. The columns provide the following information: F is the ratio of variance explained by the regression to unexplained variance; b is the regression coefficient; df gives degrees of freedom for the denominator of F (the numerator always has one degree of freedom); P gives probabilities for obtaining the same or higher values of F in comparable repeat tests. These probabilities were similar to corresponding two-tailed probabilities that the regression coefficients are significantly different from zero. The four groups into which the data are separated correspond to the following situations: A – visits by helpers to nests attended by a previous visitor. B – visits by helpers to unattended nests. C – fledgling-feeding by helpers before the start of incubation at the next nest. D – fledgling-feeding by helpers after the start of incubation at the next nest. For groups A and C joint probabilities for all the F -values were found by calculating the value of $2 \ln P$, which is distributed as X^2

	F	b	df	P
A	4.96	-2.69	1	<0.4
	3.34	-0.65	7	<0.2
	11.30	-1.14	6	<0.02
B	26.47	1.50	1	>0.25
	0.0008	-0.05	7	>0.9
	0.001	-0.21	5	>0.9
	0.03	0.16	4	>0.9
C	191.04	-8.00	1	<0.05
	7.26	-3.41	4	<0.1
	6.47	-1.85	9	<0.05
	3.61	-1.40	7	<0.1
	55.05	-2.13	8	<0.001
	42.39	-2.32	6	<0.001
	14.91	-5.69	4	<0.025
	18.44	-2.33	7	<0.005
	4.18	-2.53	8	<0.1
	0.04	0.90	3	~1.0
D	0.01	-0.24	7	>0.9
	1.56	0.54	8	>0.25

helpers flew to the nest-tree, sometimes began a closer approach to the nest, but then flew away again without visiting the nest. 68 delayed nest-visits were observed, and could be placed into four main categories.

In the first category (24 observations), the incoming helper was subordinate to a helper already at the nest. The subordinate bird waited at least a meter from the nest for between one to twelve minutes. In 18 cases the subordinate helper approached closer to the nest only after the dominant bird had left. In the remaining 6 cases the subordinate bird approached the nest cautiously, and with many hesitations, until the dominant bird left the nest vacant.

In the second category (12 observations), the incoming bird was dominant to another helper already at the nest. In 8 cases the subordinate bird

left the nest making chirruping calls when the dominant finally approached. In the remaining 4 instances the subordinate was cleaning the nest. When the dominant arrived at the nest the subordinate crouched, gaped its beak towards the dominant bird, and then continued to clean the nest while the dominant fed the nestlings. Birds at the nest were significantly more likely to leave without delay if their replacement was of higher rank than if it was a subordinate ($t_{\infty} = 2.87$, $P < 0.005$).

In the third category (30 observations), the bird that waited was subordinate to another visitor arriving in the nest-tree within a few seconds of its own arrival. The subordinate bird always waited for the dominant to go to the nest first, and in all but two cases only approached the nest itself after the dominant had left. On 6 occasions we observed 'queues' of three or five helpers who arrived at the nest-tree within seconds of each other and visited the nest not in the order of their arrival, but in strict order of decreasing rank.

In the remaining category (2 observations), the incoming bird seemed to be alone, but still paused for as long as five minutes at least a meter away from the nest before going to the unattended nest. It is possible that these birds were aware of nearby group-members concealed from our vision.

Abortive nest-visits could similarly be grouped into three categories: Out of a total of 44 observations of aborted visits, 27 involved helpers arriving in the nest-tree while a higher-ranking bird was on the nest. In 26 of these instances the dominant bird did nothing, and continued to sit on the nest. In the single exceptional case, the dominant bird gave a loud, sharp cry from the nest while continuing to sit. This cry was similar to loud 'shouts', audible for many meters, often given by birds approaching the nest.

In the second category (5 observations), a higher-ranking bird arrived at the nest-tree while a subordinate was making a hesitant approach to the nest. Upon the dominant's arrival the subordinate halted its approach and flew away, either immediately or after a few second's pause.

The final category (12 observations) involved birds that arrived in the nest-tree while a subordinate was on the nest. In these cases the dominant flew off immediately after the subordinate occupant had 'chirruped' ($n=5$), had 'chirruped' and stood up in the nest ($n=5$), or had 'chirruped', stood up and left the nest ($n=2$).

We also found that abortive visits were more likely to be accompanied by a 'shout' on the part of the approaching helper than successful nest-visits, regardless of whether the incoming bird

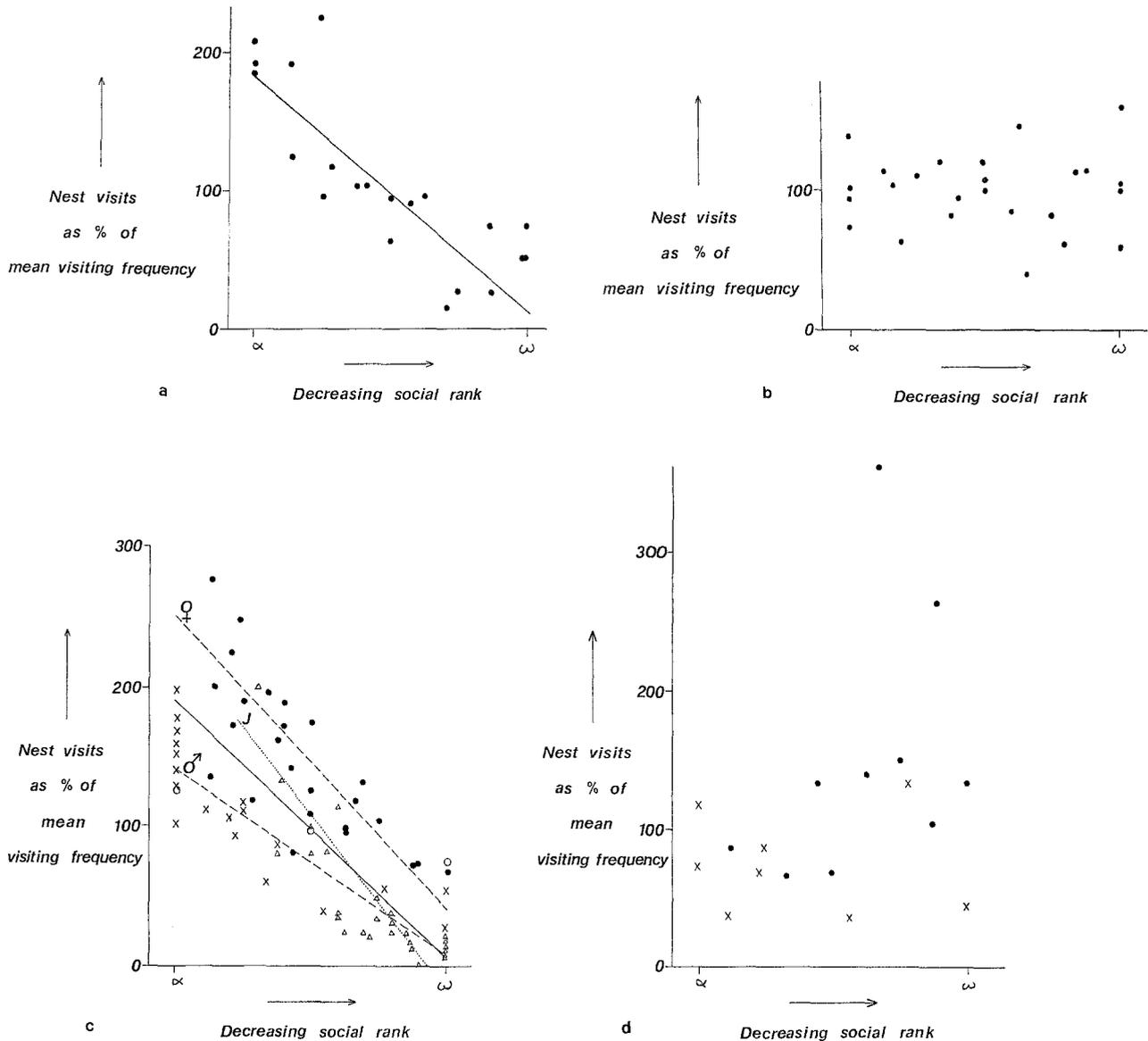


Fig. 1 a-d. Relationships of nest-visiting and fledgling-feeding rates to dominance for immature helpers. Visits by individual helpers are plotted as % of the sample mean for each set of yearling and juvenile helpers visiting a particular nest or group of fledglings. The points for each set of helpers are uniformly distributed along the abscissa between, for the most dominant bird, and, for the most subordinate. The various sets of points on any one graph are not directly comparable in a statistical sense. Lines plotted on the graphs are therefore not true regression lines, but are intended merely to emphasize trends which were confirmed by statistical analysis (see text). **a** Visits to attended nests. This graph summarizes 187 observations from 3 nests visited by 3-9 yearling helpers. In all observations the incoming helper replaced another bird on the nest. The solid line indicates that rate of nest-visits declined with decreasing social rank of the helper. **b** Visits to unattended nests. This graph summarizes 598 observations from 4 nests visited by 3-9 yearling helpers. Incoming helpers came to nests which were not attended by another bird in their group. There was no apparent relationship between rate of nest-visits and the helper's rank. **c** Feeding visits to fledglings before incubation of the next clutch. This graph summarizes 1106 observations from 10 broods of fledglings visited by 3-11 yearling and juvenile helpers. Data points for female yearling helpers are represented by open circles if there were no male yearling helpers in the same group, and by closed circles otherwise. Data points for male yearling helpers are represented by crosses, and for juvenile helpers by triangles. The solid line indicates an overall decline in rate of visits with decreasing helper rank. The dashed lines indicate that females feed fledglings at a higher rate than males. The dotted line indicates that feeding rate also declines with decreasing rank for juvenile helpers. **d** Feeding visits to fledglings after the start of incubation of the next clutch. This graph summarizes 408 observations from 2 broods of fledglings visited by 9 and 10 yearling helpers. Circles and crosses have the same significance as in **c**. There was no apparent relationship between feeding rate and helper rank or sex.

ranked higher or lower than the bird already on the nest ($G_1 = 23.17$, $P < 0.001$).

Although we were aware of the possibility that an incoming helper might aggressively chase a subordinate off the nest, we never observed this. However, we did observe yearlings (twice) and juveniles (three times) chasing and hitting subordinate siblings which had either just fed fledglings or were approaching fledglings, carrying food in their beaks. Twice a higher-ranking juvenile snatched food from a sibling's beak, then fed the fledgling itself.

Discussion

Our primary purpose here is to determine whether Zahavi's advertising hypothesis provides a parsimonious explanation for the evolution of two types of cooperative behaviour in Arabian babblers, namely peer allofeeding and helping with care of eggs, nestlings and fledglings. We shall therefore discuss several aspects of our observations which we believe are readily explained by Zahavi's hypothesis, but are not always consistent with the predictions of kin selection and reciprocal altruism.

First, we have reported a number of instances in which young birds resist being fed by their peers. We have also reported observations of higher-ranking individuals punishing subordinate siblings that had resisted allofeeding, and of subordinates punished by dominants they had attempted to feed. This type of behaviour is expected under Zahavi's hypothesis because a bird that feeds a rival should gain status, while conversely, a bird receiving food from a rival should lose status. Hence we should expect to see birds resisting attempts by other similarly ranked individuals to feed them, and to see more dominant birds attempt to quash resistance in subordinates they attempt to feed. Kin selection and reciprocal altruism, on the other hand, both predict a mutual benefit to the proferer and the recipient of food during allofeeding, the former in terms of increased inclusive fitness and the latter in terms of increased individual fitnesses. Therefore conflict between feeder and fed is not easily explained by either kin selection or reciprocal altruism.

Secondly, we have observed many instances in which helpers draw attention to their acts by uttering piercing cries while approaching the nest. Clearly this behaviour might have the undesirable consequence of alerting predators to the whereabouts of the nest, and since inclusive fitness for helpers related to the breeders would thereby be

reduced, such behaviour is unlikely to have evolved through kin-selection. On the other hand, 'shouting' while approaching the nest is entirely consistent with Zahavi's hypothesis. Under this hypothesis, the welfare of eggs and nestlings should be an incidental byproduct of the helper's bid for status, so that the cost to the helper of revealing the location of the nest to predators should be small. At the same time, if a helper is indeed advertising its quality when it goes to the nest, shouting would increase the impact of the advertisement. However, bearing in mind that the breeders in the group as well as the nest's occupants stand to benefit from helpers' nest visits, it may be argued that drawing attention to nest visits is also consistent with reciprocal altruism. A helper that does not ensure that dominant breeders are aware of its usefulness may risk being driven from the group.

Several lines of evidence point to the existence of interference between helpers. Most strikingly we found that although individual babblers do not defend personal space around themselves, high-ranking yearlings and juveniles sometimes attacked siblings bringing food to fledglings. 'Queuing' to go to the nest also indicated interference. Here there was no overt aggression, but if lower-ranking birds did not fear reprisals from their superiors they should not delay visiting the nest. Lost foraging time increases the cost of nest visits.

Similarly, we propose that the simplest explanation for bringing food to the nest-tree, but leaving without visiting the nest when a higher-ranking bird is there, is that the lower-ranking bird fears punishment. The evidence for interference is even more direct during incubation, where we found that birds often delayed or refused completely to move off the nest after a replacement had arrived.

Interference can be explained by Zahavi's hypothesis because if helping is an effective means of advertising quality and gaining status, an individual whose status is threatened may benefit from suppressing similar advertising by rivals. On the other hand, interference is not generally predicted by either kin selection or reciprocal altruism. Under kin selection, if a third party helps an individual's relative, then so much the better for that individual's inclusive fitness (Carlisle 1981; Zahavi 1981). The only conceivable circumstance in which this would not be true is if the third party is a very young relative for which the activity concerned (e.g., guarding nestlings from predators) might be unduly dangerous. Certainly in cases where helpers are siblings of the same age-class, it should be counterproductive to interfere.

Similarly, under reciprocal altruism, invest-

ment in young as possibly future collaborators yields just the same benefits if made by a third party. Moreover, breeders might be more likely to drive away a non-breeder that prevents other non-breeders from helping. Rather than punishing subordinate helpers, higher-ranking individuals would do better to reprimand subordinates that do not help, thereby avoiding costs associated with investments that they would otherwise have to make themselves.

Under Zahavi's hypothesis, correlations between nest-visiting frequency and rank might be explained as a consequence of interference between helpers. However, they are also consistent with both kin selection and reciprocity, because the fitness cost of helping to a high-ranking individual should be less than to a low-ranking individual: Dominants have more to give (West-Eberhard 1975; Carlisle 1981). On the other hand, neither kin selection nor reciprocity can easily explain why these correlations sometimes disappear.

Zahavi's hypothesis is able to do so: If correlations between nest-visiting frequency and rank are indeed a consequence of helper interference, such correlations should only be in evidence in situations where opportunities for interference are reasonably high. Opportunities for interference are high where helpers attempt to visit nests still attended by the previous visitor, and low where helpers come to unattended nests. Opportunities for interference are also initially high during fledgling-feeding, since fledgling mobility enables helpers to forage close to the group of fledglings, whereas they roam far from the nest while provisioning nestlings. However, interference opportunities drop to a low level when incubation at the next nest starts, because the new nest distracts the attention of the more dominant helpers away from the fledglings. In support of this argument, we found a clear relationship between frequency of helper visits and rank in the two cases where opportunity for interference was high, but no relationship was detected in the two cases where it was low.

The fact that aggression and allofeeding among immature Arabian babblers can be induced in the same way and occur spontaneously under the same conditions suggests that these two types of behaviour may represent alternative means to the same end. Under Zahavi's hypothesis, this end would be improved social status. The higher ratio of aggressive to allofeeding events observed for males than for females further suggests that females may have a tendency to allofeed peers under circumstances in which males are more likely to hit or chase. Helping behaviour also seems to differ slightly between the sexes, since females feed new

fledglings at a higher rate than males. Zahavi's hypothesis could explain both these sex-related differences if, for some reason, feeding other members of the group is a more effective method of advertising quality for a female than for a male, and if the converse holds for aggressive behaviour.

Among Arabian babblers, the most effective way to advertise 'quality' may be to perform behaviour which explicitly demonstrates to peers the bird's value as a potential future collaborator. The most valuable male collaborator would probably be a superior fighter because such an individual would be effective in attempts to establish and defend a territory. Female babblers also participate in territorial defence, but usually fight other females, not the physically stronger males. The fighting prowess of a female collaborator may not therefore be as crucial to the success of the group as that of a male. A breeding female, on the other hand, must be able to produce and incubate eggs, and her ability to do so may depend on her skill at foraging. While an immature bird may advertise ability to fight through aggressive interactions with peers, foraging skill may be demonstrated more effectively by bringing food to other members of the group.

Under kin selection, the primary function of feeding a fledgling or a peer would not be display, but direct investment in a relative. Possibly the cost to a male babbler of feeding others is greater than to a female, because male fitness may be more closely correlated with size and strength, and therefore with amount of food consumed. A greater tendency for females than males to feed peers and fledglings may therefore also be explained through kin selection. On the other hand, kin selection does not explain why allofeeding occurs almost exclusively under conditions in which aggression is commonly observed.

Under the reciprocation hypothesis, peer allofeeding would represent direct investment in a future collaborator, as opposed to display directed towards future collaborators. However, as with some other communally breeding species (e.g., the acorn Woodpecker, MacRoberts and MacRoberts 1976), young adult babblers usually disperse from their natal territories in company with siblings of the same sex. Therefore sub-adults should feed siblings of the same sex, who may become future collaborators, more often than siblings of the opposite sex, who will almost certainly disperse to different groups. At the same time, aggression towards peers of the same sex should be reduced.

We failed to detect any difference in the ratio of allofeeding to aggression between immature babblers of the same sex and of different sexes.

Therefore this prediction is not supported. Zahavi's hypothesis does not generate a similar prediction because a bird that feeds or hits another is not only showing off to the recipient of its act, but also to other group members who may be watching. These spectators include potential future collaborators.

Reciprocity, like kin selection, could explain why females bring food to fledglings at a higher frequency than males, on the basis that the cost of feeding fledglings may be lower for females than for males. On the other hand, neither reciprocity nor kin selection can explain why females do not feed fledglings more than males once incubation of the next brood has started, or why females do not feed nestlings at a greater frequency than males. Under Zahavi's hypothesis, differences between the rates at which males and females feed fledglings would disappear in situations where helpers do not have a good audience. They would not have a good audience after the main focus of attention has switched from fledglings to a new clutch of eggs. The absence of a significant tendency for female helpers to visit nests more frequently than males, however, is more difficult to understand. A possible explanation is that competition to visit nests may be more intense than it is to feed fledglings. Males may therefore interfere more with the helping efforts of their generally lower ranking female rivals in the context of nest visiting than of fledgling feeding.

Conclusion

In a communally-breeding, group-territorial species, survival and reproductive success for the individual may ultimately depend on its ability to cooperate with others. In such species, attempting to establish dominance solely through aggression may be counterproductive because it may be difficult for a highly aggressive individual to find collaborators. Alternative means to establish status should therefore evolve. The evidence presented here strongly suggests that in the Arabian babbler, behaviour such as helping at the nest and allofeeding are used for this purpose.

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