

Amir Kalishov · Avishag Zahavi · Amotz Zahavi

Allofeeding in Arabian Babblers (*Turdoides squamiceps*)

Received: 20 September 2004 / Revised: 24 December 2004 / Accepted: 24 December 2004 / Published online: 15 March 2005
© Dt. Ornithologen-Gesellschaft e.V. 2005

Abstract Allofeeding is a common social display among adult Arabian babblers (*Turdoides squamiceps*). The sociology and rates of allofeeding were studied with a tame population of babblers at the Shezaf Nature Reserve in the Rift Valley, Israel. Allofeeding rate varies with the season and food availability. Experimental supplementation to the whole group or to certain individuals greatly increased the rate of allofeeding, but it did not change the social order of the interactions. The interactions were almost always unidirectional: the donor allofed an individual lower in rank. Most of the few exceptions were reciprocal allofeeding among pairs of low-ranking individuals, correlated with a change in dominance between a young male and a young female. Higher-ranking individuals sometimes interfered with allofeedings by lower-ranking ones, and receivers frequently refused to accept the food offered. Allofeeding may therefore be considered as a display of dominance. However, as dominance rank rarely changes, except in very young birds, we suggest that allofeeding interactions display the prestige of the donors, that is, the degree of dominance of one individual over the other.

Keywords Allofeeding · Altruism · Cooperative breeders · Dominance · Prestige

Electronic Supplementary Material Supplementary material is available for this article at <http://dx.doi.org/10.1007/s10336-005-0073-x>.

Communicated by F. Bairlein

A. Kalishov · A. Zahavi · A. Zahavi (✉)
Institute for Nature Conservation Research,
Tel-Aviv University, Tel-Aviv, Israel
E-mail: zahavi@post.tau.ac.il
Tel.: +972-3-5463037
Fax: +972-3-6407304

Introduction

Allofeeding is a common social display among Arabian babblers (*Turdoides squamiceps*). The donor takes a food item in its beak, holds it for a moment, looks around, and flies or walks with a pronounced gait toward another group member, often vocalizing with a special purr (Fig. 1a). It then gives the food to the recipient. There are endless variations in the way the food is offered and accepted. At one end of the scale, the potential recipient may crouch, flutter its wings, gape its beak and utter begging calls like a fledgling (Fig. 1b); at the other end, it may refrain from taking the food altogether (Fig. 1c), or even attack the donor.

Allofeeding among adult individuals that do not breed together occurs mainly in cooperatively living birds. It has been described in Florida scrub jays (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1977), Arabian babblers (Zahavi 1976, 1990; Carlisle and Zahavi 1986), ground hornbills (*Bucorvus leadbeateri*) (Kemp and Kemp 1980), green wood hoopoes (*Phoeniculus purpureus*) (Ligon and Ligon 1983), pied starlings (*Spreo bicolor*) (Craig 1988), and caracaras (*Daptrius americanus*) (Thiollay 1991).

The adaptive significance of allofeeding among adult birds is usually explained in one of the following ways: altruism, or helping the needy; delayed reciprocity (Ligon and Ligon 1983); a mechanism that establishes or reinforces social bonds between individuals (Craig 1988), or contributes to group cohesion (Thiollay 1991); an expression of dominance (Woolfenden and Fitzpatrick 1977; McGraw and Hill 1999); the definition of social status (Kemp and Kemp 1980); or a mechanism for claiming social prestige (Carlisle and Zahavi 1986; Zahavi 1990; Zahavi and Zahavi 1997). In this paper, we use the term “allofeeding” to denote feeding interactions among adults or independent fledglings, and the term “feeding” for the feeding of nestlings or dependant fledglings.

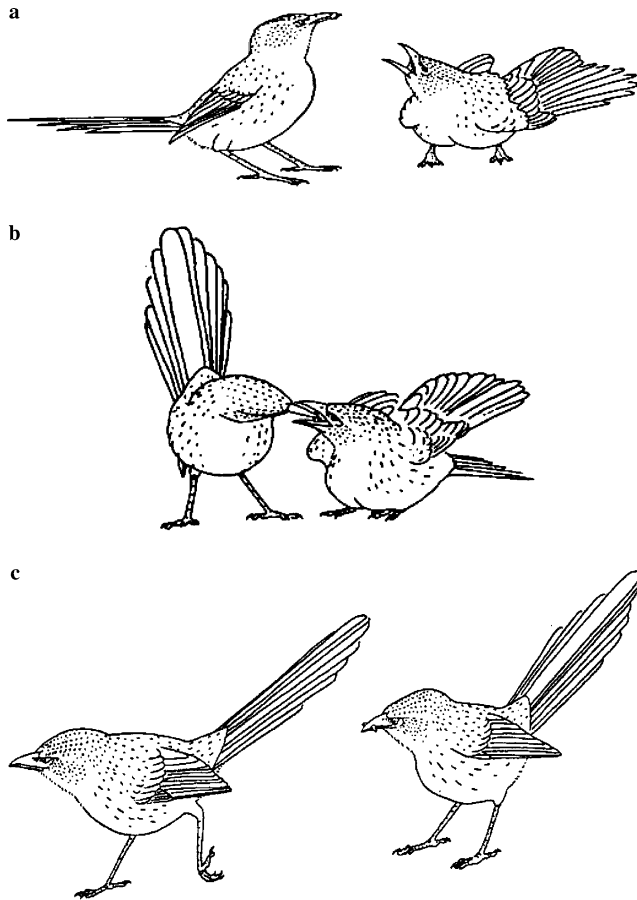


Fig. 1 a The special stance of the donor Arabian babbler (*Turdoides squamiceps*) and a willing receiver. b Allofeeding a willing receiver. c Rejection

The Arabian babbler is a cooperatively breeding bird resident in year-round territories. In our population, most individuals are color-ringed as nestlings and their detailed life history is known from that point on. Male babblers often spend their whole lives in their natal group. Females usually stay in their natal group for about 2 years and then disperse to breed in another group. Within each group, there is a strict dominance hierarchy: older birds dominate younger ones and males dominate females that join the group. Among fledglings, females may dominate males, but by their second or third year of life, young males usually rise in rank above all their female siblings. Birds of the same brood fight each other when they are a few days out of the nest and the winner dominates the loser of the same gender, as long as they stay members of their natal group. Only in a few cases has dominance changed in the first few months of life (Dagai 2002). Breeding females are dominated by all males except their own offspring. Dominance among young babblers can be easily observed in the overt aggression and threats they display at each other. Threats among older males are rare, but, when they occur, the rank order is the same as it was when the same individuals were young (Zahavi 1989, 1990).

In the present paper, we provide data mainly on allofeeding interactions among adult and independent young babblers in relation to their social rank. We also present the rate of allofeedings in different seasons and its dependence on food availability, and the effects of experimental food supplementation. Other aspects of allofeeding interactions will be presented elsewhere.

Methods

The study took place at the Shezaf Nature Reserve, near Hazeva Field Study Center, in the Rift Valley, 30 km south of the Dead Sea, Israel (coordinates: 30°46'N, 35°14'E). The site is an extreme desert, summers are hot and dry. Mean winter rainfall amounts to 35 mm, but it may be as low as a few millimeters in dry years. This babbler population has been studied since 1971 (Zahavi 1989, 1990). Groups are composed of 2–20 individuals. The birds are tame, and observers can make close observations without disturbing them. The detailed life history of most of the individuals is known from the time they were colour-ringed as nestlings.

The data presented in this paper were collected from February 1992 to July 1993 (a total of 1,210 allofeeding interactions in 1,472 h of observations) by Amir Kalishov as part of his MSc thesis (Kalishov 1996). The five groups selected for these observations were very tame and of medium size, 4–9 birds per group, to allow observation of most allofeeding interactions.

Outside the breeding season, each group was observed 3–4 times a month. During the breeding period, the same groups were observed a few times in each of the following breeding stages: courtship (from the time females start picking nesting materials to the end of laying), incubation, feeding of nestlings, and fledglings. Morning observations (3 h) started when the birds descended from their night roost. In the late afternoon, the birds were observed for about 1 h before they ascended to the night roost. In the middle of the day, the babblers are often not very active. The composition of the groups and time spent observing each group in the various reproductive stages is given in Table 1.

The observations were recorded in writing on cards; when the birds were on the move, observations were recorded on tape and later transferred to cards. Each allofeeding event was recorded for date, time, the individuals concerned, the activity of the group and of the particular interacting individuals before and after the interaction, and the details of the interaction. In the present paper we consider only a few of these parameters.

Two experiments with food supplementation were performed as explained in the following paragraphs.

Table 1 Group composition and duration of observation

Group	Year	Group size	Breeder		Non-breeding adults		Young (6-12 months)		Fledglings (< 6 months)	
			Male	Female	Male	Female	Male	Female	Male	Female
Group composition										
BAR1 ^a	1992	7\5	2	1	0	0	1 ^b	1	1 ^b	1
BAR2 ^a	1993	5	2	1	0	1	0	1	0	0
BMS	1993	6	1	1	3	1	0	0	0	0
MZR1	1992	4	1	1	1	0	1	0	0	0
MZR2 ^a	1993	6\5	3	3 ^b	0	0	0	0	0	0
ZEH	1992	4	1	1	0	0	1	1	0	0
ZVA1 ^a	1992	8\9	2 ^b	1	0	0	4	1	1	1
ZVA2	1993	9	1	1	4	1	1	1	0	0

Group	By period				Total
	Non-breeding	Courtship	Incubation	Feeding of brood	
Observation time (h)					
BAR1 ^a	107	20	5	55	188
BAR2 ^a	35	45	18	–	98
BMS	49	22	–	–	72
MZR1	130	8	10	–	148
MZR2 ^a	–	16	–	–	16
ZEH	117	19	–	–	136
ZVA1 ^a	47	33	20	51	151
ZVA2	21	12	6	6	45

^aComplex groups with more than one male or female breeder

^bOne bird ousted or disappeared during the study

Experiment 1

We supplemented food to the whole group for 1 h, in order to study the effect of food abundance on allofeeding rate. This experiment was conducted with three groups, three mornings each outside the breeding season and three mornings each during the courtship stage (a total of 18 sessions). In the first hour of the day the babblers were offered bread ad libitum; when they stopped taking bread they were fed with crickets. We recorded the allofeeding separately for that first hour when food was supplemented (Table 2) and for each of the two following hours (not shown).

Experiment 2

We supplemented only the second male in the hierarchy. The aim of this experiment was to study the competition over allofeeding between the two top males. For 3 h in the morning, food (bread) was delivered to the second male when the rest of the group could not see it. At the end of the three experimental hours, the whole group was supplemented with breadcrumbs, in order to reduce artificial differences in satiation. In two of the groups, the second male was a potential breeder; in the third, he could not breed because he was the son of the breeding female (Zahavi 1989). In two groups, this experiment, like the previous one, was repeated three mornings in the courtship stage and three mornings outside the breeding

season. However, in the third group (ZVA1), it was carried out only in the non-breeding stage, because M2, who received the food supplementation, was chased from the group a few days after the termination of the first part of the experiment (see below).

In most tables the data are presented as the rate of allofeeding interactions per 10 h of observations (figures are rounded to the nearest 0.1). Individuals are named according to their ring combination (one metal and three coloured rings). The groups are arranged according to alphabetical order. Within each group the birds are arranged according to rank.

Results

Rates of allofeeding (the number of allofeeding interactions per group or individual per an hour of observation)

The allofeeding rate per group is up to 2 orders of magnitude lower than the rate of feedings of nestlings and dependent fledglings: up to 20 feedings per hour of nestlings at the nest, as compared with an average of about 1 allofeeding interaction per hour of observation of a group. The size of the items fed is also smaller. Sometimes the display is done with a non-food item, or with no item at all. Allofeeding occurs throughout the

Table 2 Rates of allofeeding (interactions per 10 h; figures rounded to nearest 0.1) by donors with and without food supplementation, outside the breeding season (*a*) and during courtship (*b*), and average rates received (both periods)

Group/Year	Donor			Interactions per 10 h in period						Rate received (a + b)
	Name	Month hatched	Rank ^a	Control, no supplement		Supplement to group		Supplement to M2		
				a	b	a	b	a	b	
BAR1/1992	ACLT ^b	3/1989	M1	1.2	5.0	–	23.3	–	–	0.11
	STVL ^b	9/1990	M2	1.6	9.4	–	43.3	–	–	0.21
	LAHT ^b	3/1986	F1	2.1	2.5	–	13.3	–	–	2.82
	ZTLA	5/1991	YF	0.8	3.0	–	10.0	–	–	1.76
	VLTM	5/1991	YM	0.3	5.5	–	23.3	–	–	2.39
	HCTA	5/1992	GF	0	0	–	–	–	–	0.64
	CTLV	5/1992	GM	0	0	–	–	–	–	0.85
BAR2/1993	ACLT ^b	3/1989	M1	2.0	5.6	16.7	–	–	–	0.10
	STVL ^b	9/1990	M2	1.7	11.6	23.3	–	14.1	23.4	0.10
	LAHT ^b	3/1986	F1	2.1	1.8	10.0	–	–	–	6.20
	ZTLA	5/1991	F2	3.0	2.7	3.3	–	–	–	1.54
	HCTA	5/1992	YF	0	0.2	0	–	–	–	6.22
BMS/1993	VTMZ ^b	6/1986	M1	1.0	2.3	–	–	–	–	1.25
	LTLL ^b	4/1986	F1	2.6	4.5	–	–	–	–	0.28
	ZCTC	6/1990	M2	2.2	6.3	–	–	9.9	26.0	0.83
	VSST	6/1990	M3	0.2	3.2	–	–	–	–	2.08
	HLHT	5/1991	M4	1.2	7.7	–	–	–	–	3.47
	LTAL	5/1991	F2	0.4	4.5	–	–	–	–	6.11
MZR/1992	VTVM ^b	3/1986	M1	2.5	9.2	23.3	66.7	–	–	0.54
	LVTT ^b	4/1986	F1	1.8	1.2	30.0	16.7	–	–	0.68
	LTCZ	5/1989	M2	2.4	9.2	13.3	16.7	–	–	1.82
ZEH/1992	MLTA	1/1991	YM	1.1	0	6.7	3.3	–	–	5.34
	TTZL ^b	4/1986	M1	2.7	11.9	33.3	56.7	–	–	0.07
	VTLL ^b	9/1986	F1	1.5	9.7	20.0	26.7	–	–	3.31
ZVA1/1992	AHZT	5/1991	YM	4.4	17.3	6.7	46.7	–	–	3.24
	CTCV	5/1991	YF	1.2	3.2	3.3	6.7	–	–	7.50
	HZMT ^b	> 1/1989	M1	2.2	5.8	–	–	–	–	0.33
	HHZT ^b	4/1989	M2	1.0	2.7	–	–	9.36	–	1.06
	SLTV ^b	> 10/1990	F1	1.8	3.9	–	–	–	–	1.26
	CTLA	4/1991	YM1	1.2	0.6	–	–	–	–	0.86
	VTVL	4/1991	YM2	1.2	0.6	–	–	–	–	0.60
	AMTA	4/1991	YM3	0.8	0.6	–	–	–	–	0.60
	CMTM	6/1991	YF	0.7	1.2	–	–	–	–	1.32
	MTZL	6/1991	YM4	0	0	–	–	–	–	3.25
ZVA2/1993	ZZTC	5/1992	GM	0	–	–	–	–	–	3.19
	TTSS	5/1992	GF	0	–	–	–	–	–	0.87
	HZMT ^b	> 1/1989	M1	3.8	6.3	–	–	–	–	0.66
	SLTV ^b	> 10/1990	F1	2.4	4.5	–	–	–	–	0.89
	CTLA	4/1991	M2	4.8	5.4	–	–	–	–	0.22
	VTVL	4/1991	M3	3.4	3.7	–	–	–	–	1.11
	AMTA	4/1991	M4	2.9	2.7	–	–	–	–	1.11
	CMTM	6/1991	F2	3.4	9.6	–	–	–	–	2.89
	MTZL	6/1991	M5	1.0	7.2	–	–	–	–	2.44
	ZZTC	5/1992	YM	0.5	4.5	–	–	–	–	6.67
	TTSS	5/1992	YF	0	1.8	–	–	–	–	8.44

^aRank: *M* Male, *F* Female, *Y* Young 6–12 months old, *G* Fledgling < 6 months old

^bPotential breeder

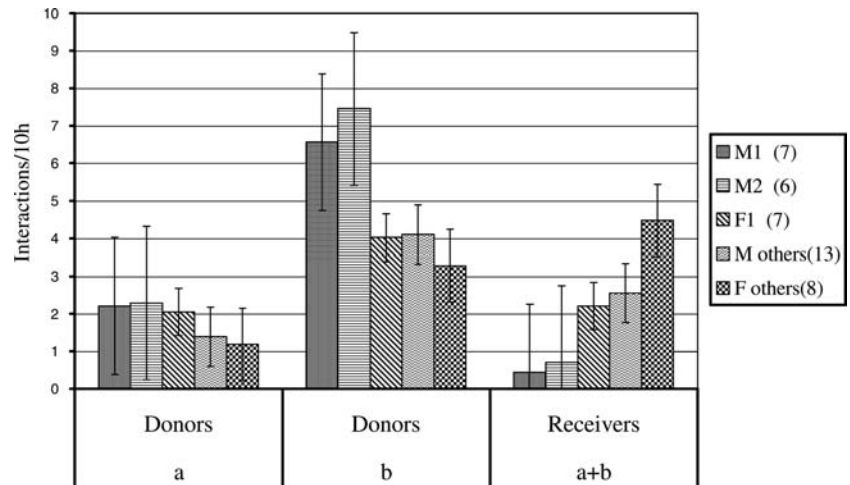
year and among all group members. Its rate depends on the season and on availability of food. It varies among groups mainly according to the social composition of the group and of food availability to the group.

The average rate of allofeeding interactions outside the breeding season was 0.98 per hour of observation of a group. During the courtship stage the rate more than doubled to 2.7 interactions per hour. At the start of incubation the rate fell drastically to 1.67 interactions per hour. During the presence of nestlings and fledglings the rate was minimal: 0.65 interactions per hour. In all groups the difference between the courtship stage and all

other stages was highly significant: $P=0.001$. (ANOVA repeated measurements; Feldman et al. 1987)

The rates of allofeedings per individual according to rank category is presented in Fig. 2. In Table 2 we present data on rates of allofeeding by individual donors: interactions per 10 hour by donors without food supplementation and during the experimental food supplementation. These data are given separately for the period outside the breeding season (*a*) and during courtship stage (*b*). We also present data on rates of allofeedings received by the same individuals (averaged for both periods combined).

Fig. 2 Rates of allofeeding interactions (interactions/10 h + SE) **a** By donors in the non-breeding period. **b** By donors during the courtship stage. **a + b** By receivers in both periods



It is evident from Fig. 2 and Table 2 that, although in general higher-ranking individuals tended to allofeed more than lower-ranking ones, this was not always the case (see below). Both breeders and non-breeders increased their rate of allofeeding during the courtship stage. Supplementing food to the whole group markedly increased allofeeding interactions both outside and during the courtship stage. This suggests that the availability of food affects allofeeding rate. At the same time, even when food was supplemented, there were significantly more allofeeding interactions during courtship than there were outside the breeding season, even though food was supplemented ad libitum during both periods.

The dependence of the rate of allofeedings on food availability was demonstrated following a burst of a water pipe in the ZVA territory, changing for a while the ecology of their desert habitat. As a consequence of the increase in food availability the rate of allofeeding interactions increased greatly in ZVA2 as compared with that of ZVA1 (Table 2).

Activity of the recipient before the interaction

In 52% of 1,100 interactions the recipient of allofeeding was actively searching for food; in about 4% it was eating food found by itself. In 7% of the cases the recipient initiated the interaction without the donor showing any intention to allofeed; in these latter cases the transfer of the food was often unceremonial. In 25% of the interactions the recipient had been acting as a sentinel, it was replaced by the feeder in 75% of these cases. Other interactions happened when the recipient had been resting, playing or preening itself.

Refusals

In many cases the apparently-intended recipient refused to accept the food offered. It was not always possible to ascertain whether or not the food was accepted, therefore the number of refusals presented includes only those

interactions where this could be observed with certainty. When sentinels were being allofed, the food was refused in 31% of 252 interactions as compared with 19% refusing in 462 cases where the recipients had been searching for food before the interaction; this difference was highly significant ($X^2 = 12.77$; $df = 1$; $P = 0.0004$). A high degree of refusal was also evident in the many cases of reciprocal allofeedings presented in Tables 5 and 6.

Who feeds whom?

Allofeedings were never random. In most cases it was apparent that the feedings were deliberate: the donor went towards a particular individual with a special gait (Fig. 1a), sometimes around a bush or other obstacles, or up a tree towards a sentinel. Along the way, the donor often ignored other individuals who begged for the food. The recipient was often aware of the donor's intentions. Recipients' reactions varied greatly: at one end of the spectrum, the receiver might run or climb down towards the donor, sometimes crouching, flapping its wings and vocalizing like a begging fledgling (Fig. 1b). At other times food might be accepted without any ritual—or, at the other end of the spectrum, refused altogether (Fig. 1c). There are endless patterns of allofeeding interactions. We believe that they are affected by, and represent, the relationships between the individuals involved; details of these will be presented elsewhere.

With very few exceptions (see below), allofeeding interactions went from a dominant to an individual lower than it in rank. In fact, when we exclude the allofeedings by M1, who, by being the highest-ranking individual, can allofeed only those lower in rank, and those of the lowest ranking individual in each group, who, by being lowest, can only allofeed individuals ranking higher than itself, we find that in 97.9% of all allofeedings the donor was ranking higher than the recipient. However, the rates of allofeedings within each group by each donor was not always closely correlated with its rank. M2 fed on average at a higher rate than

M1 (Fig. 2), and in several groups lower ranking individuals fed more than both dominant males (see BAR2, BMS, ZEH and ZVA2 groups in Table 2).

In experiments 1 and 2, food supplementation greatly increased the rate of allofeeding, but supplementation did not change the social order of the interactions: only in a single case a bird that was not allofed by a certain individual without supplementation was allofed by it during the supplementation—a fledgling who was fed by its father. Once food supplementation ceased, the number of allofeeding interactions immediately went back to its normal levels outside the breeding season, but during the courtship stage the rate of allofeeding remained higher than normal for the following 2 h (not shown).

When only the second males were supplemented with food (Experiment 2), they increased their rate of allofeeding (Table 2). In two groups thus supplemented, most other group members reduced somewhat their former allofeeding rate, but the reduction was not statistically significant. However, in the BAR group, although the first male reduced its general rate of allofeeding, it actually increased its allofeedings of M2 while the latter was being supplemented with food. In the ZVA group, allofeeding interactions among other group members stopped altogether. In the BAR group, the only one in which both the first and second experiments were conducted, the allofeeding rate by M2 was lower when it alone was supplemented (Experiment 2) than when the whole group was supplemented (Experiment 1—see Table 2) (for the tables that illustrate the effect of the dominance hierarchy on allofeeding interactions with and without food supplementation see electronic supplementary material).

In Experiment 2, food was offered to the second males when the rest of the group could not see them. In 79 out of 282 cases the second males refused to accept the food offered to them, rather than use it to feed other group members. This suggests that the adaptive significance of allofeeding was not to provide food for hungry group members; we could assess the hunger of other group members by their eagerness to accept the food provided following the experiment.

Interference by the dominants

Dominant individuals (mainly M1 and M2) often interfered with allofeedings by other individuals. In 27 cases, the appearance of the dominant disrupted the interaction. In 19 other instances the dominants acted aggressively towards the donors following the interaction. The first males also sometimes interfered with allofeeding by the second males (M2) (Table 3). Without food supplementation, such interference was seen in the present study only in the BAR2 group (in about 10% of the interactions). However, when the second male alone was supplemented, interference by M1 with the allofeedings of M2 was observed in all groups. In the ZVA group, M1 was observed interfering with M2's attempts

to allofeed the female when M2 was supplemented with food, following which M2 refused to take the food offered to it by the experimenter. A few days later M2 was chased from the group. We speculate that the expulsion could have been the result of the increase in M2's allofeeding activity when supplemented with food.

Aggression among partners to the allofeeding interactions

In 32 cases the receivers acted aggressively towards the donors. In 20 of these cases the donor tried to allofeed an individual of a higher rank than itself. In other 70 cases donors acted aggressively towards the receivers, who invariably were of a lower rank. In 27 of these cases the aggression followed the refusal by the receiver to accept the food offered.

Allofeeding among breeders

The occurrences of allofeeding among breeders in different breeding stages are presented in Table 4.

There were more allofeeding interactions during the courtship stage than during any other time (Table 4). Allofeeding of breeding females by males declined during the incubation period that followed the courtship stage. In groups where M2 was the son of the breeding female, that male never fed its mother. In the MZR group the breeding female (the mother of M2) was chased from the group by a coalition of three alien females during the courtship season (the group thus becoming MZR2, see Table 1). Following this change, M2 could compete with its father over breeding. This was manifested on the one hand by the allofeeding of the females by M2 (Table 4), and on the other hand by the enormous increase in the rate of allofeeding of M2 by M1 following the arrival of the new females: before the females arrived M1 allofed M2 at the rate of 2.6 interactions per 10 h during the courtship season (not shown). After their arrival the rate almost doubled to 4.4 allofeeding interactions per 10 h. In the present observations M2 were never seen allofeeding M1.

Reciprocal allofeeding

Among individuals at the bottom of the hierarchy, between dyads of young, low ranking individuals, reciprocal allofeeding was found in most of the groups studied. These involved a male and a female sibling, in which the lower ranking individual (usually a male) allofed an individual one rank higher than itself (usually a female) and was itself fed at a particularly high rate by that higher ranking individual. These interactions were sometimes so intense that the rate of allofeedings by one or both individuals surpassed that of the dominants of their group. The rates of allofeeding interactions and the type of interaction of such dyads are presented in Ta-

Table 3 Interference of M1 in allofeedings by M2 with and without food supplementation

Group	Period ^a	No supplementation			Supplementation to M2		
		Allofeedings by M2	Interference by M1	Percentage of interference	Allofeedings by M2	Interference by M1	Percentage of interference
BAR2	a	65	6	9.2	59	11	18.6
BAR2	b	48	5	10.4	40	4	10
BMS	a	12	0	0	14	3	21.4
BMS	b	14	0	0	44	2	4.5
ZVA	a,c,d	22	0	0	13	3	23.1

^aPeriod: *a* Non-breeding, *b* Courtship, *c* Incubation, *d* Feeding of brood

ble 5. These interactions often occur when the dominance relationship between two individuals is challenged. In the first year of their lives, females often dominate their male sibs of the same brood (Dagai 2002). However, as they grow older, most males dominate all their female sibs and all females that join the group (as distinct from females who were already breeders in their group when they hatched). Young females often seem reluctant to give up their dominance, and this is manifested in the many displays of reciprocal allofeeding between male and female sibs that coincide with a change of rank. In many of these interactions the food was rejected (Table 5). The changes of dominance was usually demonstrated by threats or by overt aggression. Such changes in dominance is well manifested in the ZVA group. In 1992 (ZVA1) the young female CMTM was dominant over MTZL, a brother of the same brood. In the following year, 1993 (ZVA2), she lost her dominance over MTZL and was challenged by ZZCT, a male one year younger.

Exceptional allofeedings

The very rare cases, in which non-breeding babblers offered food to their dominants other than those presented in Table 5, are presented in Table 6.

In six cases young, non-breeding females offered food to their dominants; in only two of those cases was the food accepted.

Three males tried to feed individuals dominant over them. In BAR group, VLTM once tried to feed his mother, who refused the offer. In ZVA group, AMTA, the lowest in hierarchy among three male sibs of the same brood, offered food to his more dominant sibs four times; his offerings were refused in three of them. Eventually AMTA and one of his more dominant sibs founded a new group (SHR); the dominant sib was later chased from the group by AMTA, who remained the sole breeding male in the new group. The case of MLTA in MZR1 group was different: he was the only young bird in the group. He tried to feed everyone. None of the 16 feedings he offered was accepted. On 23 additional occasions this young male was seen moving around purring, displaying the food in his beak.

Discussion

The adaptive significance of allofeeding

We have shown that in babblers, allofeedings were almost always unidirectional: an individual was allofeeding another individual lower than itself in rank. A

Table 4 Rates of allofeeding (interactions/10 h) among breeders in different periods: *a* non breeding, *b* courtship, *c* laying and incubation, *d* feeding of nestlings and fledglings

Group period	Allofeedings of F1 by the breeding males								Allofeedings of Males 1 and 2 by F1				Allofeedings of M2 by M1	
	F1 by M1				F1 by M2 ^a				M1 by F1		M2 ^a by F1		M2 ^a by M1	
	a	b	c	d	a	b	c	d	a	b	a	b	a	b
BAR1 ^b	1.1	4.5	2.0	1.3	0.8	3.5	0.0	1.4	0	0.5	0	1.0	0.18	0
BAR2 ^b	1.7	4.2	1.1	—	0.9	6.3	1.7	—	0	0.2	0	0	0	0.22
BMS	0.2	0.5	—	—	—	—	—	—	0.4	3.2	—	—	—	—
MZR1	0.5	2.6	0	—	—	—	—	—	0.3	0	—	—	—	—
MZR2 ^c	—	2.7	—	—	—	2.7	—	—	—	0	—	0	—	4.42
ZEH1	2.3	9.7	—	—	—	—	—	—	0.2	0	—	—	—	—
ZVA1 ^b	0	2.1	1.0	0.6	0.2	0.6	0.5	0.6	0	0.3	0	0.9	0.63	2.12
ZVA2	1.4	0.9	0	0	—	—	—	—	0	0.9	—	—	—	—

^aOnly when M2 was a potential breeder

^bComplex groups where M2 could be a breeder

^cThree new females in group MZR2

Table 5 Reciprocal allofeeding interactions among youngsters. Within each couple, when one bird acted as a donor the other one was the receiver

Group	Donor				Receiver	Rates of allofeeding (interactions per 10 h)		Number and type of interaction ^a
	Name	Month hatched	Rank	Position in hierarchy ^b		In period ^c		
						a	b	
BAR1	ZTLA	5/91	YF	-2	VLTM	0.7	3.0	+4 -9
	VLTM	5/91	YM	-1	ZTLA	0.2	5.5	+9 -3
BMS	HLHT	5/91	M4	-2	LTAL	1.2	7.7	+15 -5
	LTAL	5/91	F2	-1	HLHT	0.4	4.1	+3 -6
ZEH	AHZT	5/91	YM	-2	CTCV	4.4	17.3	+57 -22
	CTCV	5/91	YF	-1	AHZT	1.2	3.2	+18 -1
ZVA1	CMTM	6/91	YF	-4	MTZL	0.4	1.2	+4 -6
	MTZL	6/91	YM4	-3	CMTM	0	0	0
ZVA2	MTZL	6/91	M5	-4	CMTM	0	0.9	+1
	CMTM	6/91	F2	-3	MTZL	0	0.3	+2
ZVA2	CMTM	6/91	F2	-3	ZZCT	2.9	0.9	+6 -1
	ZZCT	5/92	YM	-2	CMTM	0.5	0.9	+4 -1

^aType of interaction: + item accepted, - item refused

^bPosition in hierarchy: -1 = lowest

^cPeriod: *a* Non-breeding, *b* Courtship

common exception was the allofeeding of breeding males by breeding females (Table 4), which may fall into the category of courtship feeding. The other common exception was reciprocal allofeedings among the very young (Table 5).

The purrs that accompany allofeeding, and the special stance of the feeder, call the attention of other group members to the act. We have often noticed group members watching allofeeding interactions between other individuals. The cases of interference of the dominants in the allofeedings of others, and the interferences of the first males in allofeedings of the second males (Table 3), clearly show that babblers notice allofeedings by other group members.

Table 6 Number and type of interactions where non-breeding individuals tried to allofeed higher-ranking individuals (except those presented in Table 5)

Group	Donor			Receiver's rank	Number and type of interaction ^a
	Name	Rank	Position in hierarchy ^b		
Females					
BAR1	ZTLA	YF	-2	M2	+1
BAR2	HCTA	YF	-1	F2	+1
BMS	LTAL	F2	-1	M3	-1
ZVA1	CMTM	YF	-2	YM1	-1
ZVA2	TTSS	YF	-1	M1	-2
Males					
BAR1	VLTM	YM	-1	F1	-1
MZR1	MLTA ^c	YM	-1	M1	-5
				M2	-9
				F1	-2
ZVA1	AMTA	YM3	-5	YM1	-2
				YM2	-1 + 1

^aType of interaction: + item accepted, - item refused

^bPosition in hierarchy: -1 = lowest^a

^cSee text

There are several possible explanations of the adaptive significance of allofeeding among adult birds.

Altruism Allofeeding may be considered altruism in so far as the donor donates some of its food to another individual while it is still hungry itself (in 62% of the cases the donor searched for food immediately following the interactions). However, if the aim of allofeeding were to aid individuals who need help, we would expect donations to be given mainly by older birds to the very young. In fact, we often find that young individuals allofeed more than, and certainly not less than, older and more mature individuals higher in the hierarchy (Table 2). Also, we found that the number of allofeeding interactions greatly increased during food supplementation to the group, in spite of the fact that food was available ad libitum to all group members.

The fact that in most cases low-ranking individuals did receive more feedings than higher-ranking ones (Fig. 2; Table 2) may simply be a consequence of the fact that there were more individuals higher than them in rank that were eligible to allofeed these birds.

Other details of the interactions also are not consistent with the idea that the purpose of allofeeding is to support the needy. Babblers often refuse food offered by their peers, then eagerly accept food from the observer. Also, in **Experiment 2** we would have expected M2 to increase its allofeeding interactions when it alone was supplemented with food. We found instead that these satiated babblers often refused food offered to them by the observer, rather than use it to allofeed other group members that were hungry.

Delayed reciprocity Delayed reciprocity was suggested by Ligon and Ligon (1983) to explain allofeeding among green wood hoopoes. They suggested that feeding the young might encourage behaviors that are

of benefit to the donor: assistance in defending the donor's territory, feeding the donor's offspring at a later time, etc. This suggestion cannot be applied to the frequent cases of reciprocal allofeedings between young females and young male babblers (Table 5), since these youngsters will never breed in the same group; usually the females disperse from the group to breed, and in the rarer cases when alien males take over the group to breed with the females, all the male members of the original group are chased away (Zahavi 1990). Also, the frequent refusals of offered food again argue against such an explanation.

Reinforcing social bonds Craig (1988) observed allofeeding among pied starlings. In these birds, the pattern of allofeeding did not follow the pattern of dominance as indicated by aggression. He therefore suggested that allofeeding served to establish or reinforce social bonds between individuals. Pied starlings live in family groups within large, complex flocks; thus their social structure is very different from that of babblers. In babblers, as we have seen, allofeeding is closely connected to dominance. The fact that recipients often refrain from accepting food offered them by other babblers, and are sometimes attacked when they refrain from accepting food offered to them (see also Carlisle and Zahavi 1986), suggests that, in babblers, allofeeding is more a display of dominance than a display of social bonds.

Allofeeding as a claim for social prestige As we have shown above, in most interactions an individual feeds another individual lower in rank. We therefore agree with Woolfenden and Fitzpatrick (1977) and with Kemp and Kemp (1980), that allofeeding may be considered an expression of dominance. The many cases of reciprocal allofeeding occurring where dominance was being challenged strengthen this notion.

Still, the question remains: why should babblers daily reinforce their claim to dominance when their rank is stable? We suggest that, although rank does not change, the degree of dominance an individual can exert over another may well change. We introduced the term 'prestige' to enable us to express the *degree* of dominance of each individual within the social composition of its group (Zahavi 1989; Zahavi and Zahavi 1997). In earlier publications (Carlisle and Zahavi 1986) we used the term 'social status' instead of 'prestige.'

Allofeeding interactions often change according to changes in social conditions. When a breeding female is replaced by alien ones, a major change occurs: males that could not breed with the previous female because of incest avoidance become potential and actual breeders as demonstrated in the present study within the MZR group. In group MZR1, M2 did not allofeed F1, who was his mother. As soon as three alien females joined the group, which now became MZR2, M2 started allofeeding them, and M1 greatly increased the allofeeding

of his son, M2, who now became his competitor over breeding.

Changes in group composition may affect the social condition of every member of the group. For the lowest-ranking individuals, major changes occur upon the addition of new fledglings. Such changes in group composition do not change the dominance hierarchy. However, it may be assumed that the degree of control a dominant exercises over his subordinate may change.

It makes sense that the degree of dominance of M1 depends on the extent to which he needs the collaboration of his subordinates, and on whether the subordinates have alternative options. In babblers, the need for subordinate collaborators depends mainly on the ability to defend the group's territory. This ability probably depends on, and varies with, the size and the social composition of the group—the number and age of its males, and the physical ability of its members—and also on the composition of neighboring groups. In the present observations, second males (M2) never allofed the first (M1). However, during the 30 years of our study we encountered three groups (out of about 20 groups \times 30 years) in which M2 regularly allofed M1. In all three cases, the groups consisted of two breeding males and one female, surrounded by stronger groups. Under such circumstances, it stands to reason that M1's need for M2 was especially high, and he might thus allow displays usually reserved solely to the dominant individual in the hierarchy.

Lundy et al. (1998), studying the paternity of babblers using DNA fingerprinting, found that, in six groups that resided in their natal territory, M1 fathered all the offspring. In six other groups in which the coalition between M1 and M2 was newly formed or in cases in which the groups were new to the territory, M2 shared in fathering the young. Although we do not have DNA data for the above-mentioned three groups where M2 was allowed to allofeed M1, it seems probable that they likewise shared in reproduction.

Intra-group fighting among babblers is very costly (Zahavi and Zahavi 1997). Adult babblers of the same group rarely display overt aggression or even ritualized pecks at each other. Still, during our long-term study, we encountered some such fights. Once an intra-group fight starts, babblers make no compromise: in all observed cases, one of the adversaries was either killed or chased from the group (in a single case the loser was later accepted into the group).

We suggest that, in the constant social interactions within groups including allofeeding, donors display both their claim for prestige and their willingness to collaborate, and receivers display their acceptance of the situation. Thus conflicts that in other birds are resolved by overt aggression and threat are replaced for babblers by competition over prestige, expressed and assessed by allofeeding as well as by other "altruistic activities" such as guarding, feeding the young and defending the territory (Zahavi and Zahavi 1997)

Zusammenfassung

Gegenseitiges Füttern beim Graudrossling *Turdoides squamiceps*

Gegenseitiges Füttern ist ein häufiges soziales Verhalten bei adulten Graudrosslingen (*Turdoides squamiceps*). Wir untersuchten das soziale Gefüge und die Häufigkeit dieses Verhaltens in fünf zahmen Gruppen von Graudrosslingen im Shezaf Nature Reserve im Rift Valley in Israel. Die Häufigkeit von gegenseitigem Füttern variierte mit der Jahreszeit und der Verfügbarkeit von Nahrung. Experimentelle Zufütterung in der gesamten Gruppe oder auch nur von einzelnen Individuen erhöhte die Häufigkeit erheblich, doch änderten sich dadurch die sozialen Beziehungen nicht. Diese waren meist unidirektional: der Geber fütterte immer einen rangniedrigen Vogel. Die meisten der wenigen Ausnahmen erfolgten innerhalb eines Paares niedrigrangiger Vögel verbunden mit einem Wechsel in der Dominanz zwischen einem jungen Männchen und einem jungen Weibchen. Hochrangige Vögel mischten sich teilweise in das Füttern niedrig rangigerer Vögel ein. Häufig verweigerten die Empfänger die Annahme des Futters. Gegenseitiges Füttern dürfte deshalb vor allem Ausdruck der Dominanz sein. Da Dominanzwechsel mit Ausnahme bei sehr jungen Vögeln sehr selten sind, nehmen wir an, dass gegenseitiges Füttern das Ansehen des Gebers anzeigt, also das Ausmaß von Dominanz gegenüber einem anderen Vogel.

Acknowledgments We wish to acknowledge with thanks Roni Ostreicher, Arnon Lotem, Richard Wagner, Dietmar Todt, Naama Zahavi-Ely and Melvin Patrick Ely for their comments and help, and Amir Balaban for the drawings. The experiments conducted comply with the laws of Israel.

References

- Carlisle TR, Zahavi A (1986) Helping at the nest, allofeeding and social status in immature Arabian Babblers. *Behav Ecol Sociobiol* 18:339–351
- Craig AJFK (1988) Allofeeding and dominance interactions in the cooperative breeding pied starling. *Anim Behav* 36:1251–1253
- Dagai Y (2002) Aggression and social heirarchy in Arabian babbler groups (*Turdoides squamiceps*) (in Hebrew). MSc Thesis, Tel-Aviv University
- Feldman DSJ, Hofmann R, Gagnon J, Simpson J (1987) Abacus concepts, StatView II. Abacus Concept Inc, Berkely
- Kalishov A (1996) Allofeeding among babblers (*Turdoides squamiceps*) (in Hebrew, with English summary). MSc Thesis, Tel-Aviv University
- Kemp AC, Kemp MI (1980) The biology of the southern ground hornbill *Bucorvus leadbeateri* (Vigros). *Ann Transvaal Musuem* 32:65–100
- Ligon JD, Ligon SH (1983) Reciprocity in the green wood hoopoe (*Phoeniculus purpureus*). *Anim Behav* 31:480–489
- Lundy KJ, Parker PG, Zahavi A (1998) Reproduction by subordinates in cooperatively breeding Arabian babblers is uncommon but predictable. *Behav Ecol Sociobiol* 43:173–180
- McGraw KJ, Hill GE (1999) Induced homosexual behaviour in male house finches (*Carpodacus mexicanus*): the “Prisoner Effect.” *Ethol Ecol Evol* 11:197–201
- Thiollay JM (1991) Foraging, home range use and social behaviour of a group-living rain-forest raptor, the red-throated caracara (*Daptrius americanus*). *Ibis* 133:382–393
- Woolfenden GE, Fitzpatrick JW (1977) Dominance in the Florida scrub jay. *Condor* 79:1–12
- Zahavi A (1976) Cooperative nesting in Eurasian birds. In: Frith HJ, Calaby JH (eds) *Proceedings of the 16th international ornithology congress*. Canberra, Australia, pp 685–93
- Zahavi A (1989) Arabian babbler. In: Newton I (eds) *Lifetime reproduction in birds*. Academic Press, London, pp 253–276
- Zahavi A (1990) Arabian babblers: the quest for social status in a cooperative breeder. In: Stacey PB, Koenig WD (eds) *Cooperative breeding in birds: long-term studies of ecology and behaviour*. University Press, Cambridge, pp 13–30
- Zahavi A, Zahavi A (1997) *The handicap principle: a missing piece of Darwin’s puzzle*. New York, Oxford University Press