



RESEARCH ARTICLE

REVISED Competition over guarding in the Arabian babbler (*Turdoides squamiceps*), a cooperative breeder [version 2; referees: 2 approved, 1 approved with reservations]

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v2 First published: 24 Aug 2015, 4:618 (doi: 10.12688/f1000research.6739.1)
 Latest published: 04 Feb 2016, 4:618 (doi: 10.12688/f1000research.6739.2)

Abstract

Observations on 12 groups comprised of two adult males and one adult female (some included one or two fledglings), tame, individually marked, Arabian babblers (*Turdoides squamiceps*) in the rift valley in Israel revealed that the babblers compete to guard. The pattern of guarding and the way by which one sentinel replaces another reflect the dominance relationships within the group. The dominant (alpha) male guarded more than any other individual. It interfered with and replaced the guarding by the adult beta male more than it did with the yearlings. About one-third of the replacements occurred less than one minute after the sentinel had assumed guarding. Whereas the dominant often replaced its subordinates directly; subordinates hardly ever replaced their dominants directly. The alpha male often allowed the beta male during the replacement. Replacements and allofeeding of the beta males by the alpha males increased significantly during courtship, when competition over breeding was maximal, and dropped back to their previous level at the start of incubation, highlighting the competitive basis underlying the act of guarding. Competition over altruistic acts, as shown here for guarding, is not compatible with explanations based on the assumption that altruistic acts reduce the fitness (reproductive success) of the altruist. We suggest, in contrast, that by investing in guarding and by intervening in the guarding of its competitors, a babbler demonstrates and signals its quality and its control over its competitors, thereby increasing its prestige and consequently its direct fitness.

Open Peer Review

Referee Status:

	Invited Referees		
	1	2	3
version 2 published 04 Feb 2016	report		
	↑		
version 1 published 24 Aug 2015	report	report	report

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How to cite this article: Dattner A, Zahavi A and Zahavi A. **Competition over guarding in the Arabian babbler (*Turdoides squamiceps*), a cooperative breeder [version 2; referees: 2 approved, 1 approved with reservations]** *F1000Research* 2016, 4:618 (doi: [10.12688/f1000research.6739.2](https://doi.org/10.12688/f1000research.6739.2))

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Grant information: The authors declared that no grants were involved in supporting this work. Arnon Dattner's observation were part of his Msc thesis for the Tel-Aviv University. Carmel Besner was a volunteer.

Competing interests: No competing interests were disclosed.

First published: 24 Aug 2015, 4:618 (doi: [10.12688/f1000research.6739.1](https://doi.org/10.12688/f1000research.6739.1))

REVISED Amendments from Version 1

We have updated the statistical analysis according to the calculations of Prof. Uzi Motro (referee 1).

See referee reports

Introduction

The issue of altruism is still a major question in evolution. Trivers (1985) defined altruism as an “act that confers a benefit on someone at a cost to the other (*the altruist*).” “...cost is measured by a decrease in reproductive success”. Several theories have been posited to suggest that the altruist gains indirectly, among them are group-selection (including group augmentation), kin-selection and reciprocal-altruism. All these theories are based on the assumption that the altruistic act reduces the reproductive success of the altruist, and were developed in order to explain how altruism has persisted despite its supposed shortcomings. Zahavi (1977); Zahavi (1990); Zahavi (1995) and Zahavi & Zahavi (1997) contended that many altruistic acts can be explained as activities that signal the performer’s claim to social prestige, and that increase rather than decrease the fitness of the altruist. Consequently, contestants would be expected to compete to perform the altruistic act. Such competition has already been shown in babblers for allofeeding and feeding at the nest by yearlings (Carlisle & Zahavi, 1986); for mobbing of raptors (Anava, 1992); in confrontations with neighbours (Berger, 2002) and in allofeeding among adults (Kalishov *et al.*, 2005).

Guarding, the activity of one or more individuals taking turns to watch over the group, is a very common phenomenon among group-living birds and animals (see Ridley *et al.*, 2013 for references). Many observations have confirmed that the presence of a sentinel allows the group to forage in comfort (Hollén *et al.*, 2008; Ben-Mocha, 2013). However, that guarding helps the group does not explain why a particular individual may forego foraging or any other occupation, in order to guard.

In this paper we present data showing that the alpha and beta male babblers compete to perform the altruistic act of guarding. Other aspects of the phenomena of guarding are not discussed.

Methods

Arabian babblers are thrush-size, group-living song birds (Zahavi, 1989; Zahavi, 1990; Zahavi & Zahavi, 1997). 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; Zahavi, 1990). Groups are composed of 2–20 individuals. The birds are tame, and observers can make close observations without disturbing them. The lineage and life history of most of the individuals is known from the time they were colour-banded as nestlings for individual recognition. The groups are resident and territorial. They maintain a strict age- and gender-dependent dominance hierarchy. Only the alpha male and female usually reproduce in the single nest, although

sometimes more than one male may father the young and more than one female may lay in the common nest (Lundy *et al.*, 1998).

All group members share in activities such as defending the territory against intruders, sentinel activities, mobbing, incubation, feeding and caring for the young. There is very little overt aggression, except among the very young. The birds spend most of the time in close proximity, and when not foraging often clump, play or allopreen.

The population

Observations were carried out from August 2003 to April 2004, following four years of serious drought, in which reproduction was reduced from 180 nestlings and fledglings, ringed in 1997, to the low number of about 30 ringed in each of the years 2000, 2001 and 2002. As a result the population was old and very stable (Zahavi, 1990), enabling us to select a large number of similar groups, each comprising two adult males (Alpha male, M_1 ; beta male, M_2) and one adult female (F_1). Some of the groups included one or two independent youngsters fledged in 2003 (Table 1). The males were not related to the females and thus competed for reproduction, except in one group (MTE), in which the beta male was the son of the breeding female. In another group (HNC), there was acute competition between father and son culminating in eviction of the father leaving a group of two. Observation of this group ceased following the eviction. Competition over breeding was also intense in the SAL group, in which M_2 was observed to copulate with the female and on several occasions interrupted the copulation of the dominant pair by following them (Perl, 1996).

All the birds in this study were colour-banded for individual recognition and tame to the extent that they readily accepted food from the hand of the observer. None of the groups inhabited a territory bordering directly on agriculture.

Table 1. Group composition, ages and relatedness among the males.

Group	Age ^{*,**}					Relatedness of M_1 to M_2
	M_1	M_2	F_1	Y_1	Y_2	
Main groups						
BOK	8.7	5.8	>3	0.8	0.4	uncle
HOR	8.8	4.6	>03	0.8		father
MTE	9.8	4.6	9.7	0.5	0.5	uncle
MZR	>8	>7	3.8	0.5		unknown
NAV	>9	5.8	>3			father
SAL	9.8	8.7	>3	0.9	0.9	brothers
SZF	>9	>1	9.7			not related
Auxiliary groups						
BOT1	9.5	6.8	6.8	0.8	0.6	not related
BOT2	6.8	0.8	6.8	0.6		not related
POL	7.6	1.6	2.5	0.5	0.5	uncle
TMR	8.8	6.8	3.5	0.4	0.4	brothers
HNC	>11	4.6	>03			father

*Age (years, on 1/1/2004).

** > before the age denotes years since the individual joined the study population as an adult.

Data on group composition, their ages and relatedness among the males are presented in [Table 1](#).

Descriptions of guarding patterns

a. Guarding. When the group is searching for food, or occupied in some other activity, one individual will stop feeding and climb onto a high place (e.g. a tree), inspecting the neighbourhood. It is usually easy to distinguish the sentinel from an individual that is in the tree for another reason, such as feeding, resting, auto-preening, etc. The height and extent of exposure of the sentinel depends on environmental conditions: in the darkness of dawn or during danger, it perches on the edge of the canopy. With increasing light it takes a more exposed perch, climbing to the top of the canopy, or often onto a dry branch devoid of leaves high above the canopy, from where it can see and be seen for a great distance. Many groups have a preferred guarding perch in their territory, highly exposed above the canopy ([Figure 1](#)). Sometimes the sentinel flies directly to its guard post, but more often it climbs the tree, scanning around, then climbs to a higher and more exposed position and sometimes flies off to another tree. There is usually only a single sentinel, but when a predator or an alien babbler is sighted the whole group may perch for a while on the top of the tree. At the end of the guarding bout the sentinel either flies down directly or moves slowly into the canopy. A new individual starts its guarding bout at variable intervals after the previous sentinel had left its post. However, about 15% of the guarding bouts are started by the replacement of an active sentinel see below.

In contrast to many other species ([Bell et al., 2010](#); [Gaston, 1977](#)), adult Arabian babbler sentinels do not emit regular calls, except for “alarm calls”, or shouts when interacting with distant babblers ([Sommer, 2011](#)). Young sentinels, however, often produce soft sub-songs while they guard. These vocalizations attract attention to the youngster, advertising its activity to the group.

We do not know the proximate cause for a babbler to assume guarding and we do not discuss this issue here. However, we do know that the presence of foreign babblers in the territory increases guarding



Figure 1. A dominant male Arabian babbler on guard on a high and exposed perch.

activity by the residents. The presence of an alien female in the territory greatly increases guarding by both the breeding female and the other females ([Ben-Mocha, 2013](#)). Food availability too has a profound effect: on a rainy day little guarding was observed, but on the following day a maximum duration of almost 45 minutes/h was reached, probably due to the availability of a large number of insects that had drowned in the flooding ([Anava et al., 2002](#)).

b. Replacements of sentinels. We observed several methods of sentinel replacement: it could be direct, with the replacer flying directly to the guarding bird, with or without some food item, and the previous sentinel then leaving its perch; or indirect, with the replacer taking up a guarding position on another perch. If the replacing bird was a subordinate, it often perched below the dominant or on another, usually lower, tree, and climbed to the final guarding position only after the dominant had vacated it. Eventually, mostly within one minute, one of the birds would abandon its position. In most cases, if the original sentinel did not leave its perch the second one retreated. The conflict between the two was often manifested by both of them nervously preening themselves.

c. Allofeeding. Adult babblers sometimes allofeed ([Kalishov et al., 2005](#)). This often happens when the feeder seeks to replace the sentinel. We occasionally observed how a babbler that intended to replace another by allofeeding, first looked at the sentinel, and then started searching for a suitable food item. Upon finding one, it flew directly to the sentinel, fed it and usually replaced it. The sentinel either accepted the food (acceptance), sometimes crouching in a begging position (accepting like a fledgling), or rejected it. Finally it either did or did not leave its post. Often the sentinel, which may well be aware of the intention of the feeder - left its post before the feeder reached it. On rare occasions, when the sentinel did not accept the food item, the replacer (always a dominant) aggressively pushed the food into its beak. On several occasions a subordinate babbler that had just refused food offered by the dominant, immediately approached the observer to take a small crumb of bread, suggesting that despite being hungry it had refused to accept the “gift” from another babbler. Such interactions are not common but we have witnessed several over the years ([Zahavi & Zahavi, 1997](#)).

d. Social phases. We have defined three social phases: a. non-breeding; b. courtship, beginning when sticks are collected and lasting until the last egg has been laid; and c. incubation and feeding the young until independence. Breeding cycles were often aborted for various reasons.

Observation and data collection

Every group was visited on average every 7–10 days. However, visits were not equally distributed – during mate guarding and egg laying a group could be visited daily until the first day of incubation, when frequency of visits usually dropped.

Observations started with first light, usually before the babblers had left their night-roost tree. For the first 2–3 hours they were followed without any interference by the observer. The data presented in this paper were collected during that period. Following these observations the babblers were offered some bread tidbits and water. This was done in order to induce allopreening, which was the main

subject of the study (Dattner, 2005). In one group (MTE) an entire day of observations without interference was conducted once a month. Of those days, only observations from the first three hours of the morning are included in the data presented here. We recorded the time of ascent and descent of the sentinel, its identity, the way by which it took up its perch, whether there was another sentinel at the time, whether it was replaced, the identities of the replacer and the replaced, type of replacement (direct or indirect or with allofeeding, acceptance or rejection of the food). The observations were written up on cards, noting the exact time and circumstances, and were later transferred to Excel spreadsheets. The social phase of the group in relation to the breeding cycle was also recorded. Table 2 presents the number of observation hours for each group, at the different social phases.

Weight was measured occasionally by other researchers who monitored the groups on alternate days, but not on our “observation days”. The babblers were weighed in the morning as soon as they left the night roost. The birds were lured into mounting a scale (Moznei Shekel) by placing tiny tidbits of bread on it. The data presented in Table 3 are averages of several measurements taken over several months. A few individuals were not weighed because they either refused to mount the scale or were absent for some reason.

The data presented in this paper summarize a total of 637 h of observations in the mornings without interference by the researchers: 212 h in the non-breeding phase, 322 h in the courtship phase (179 h during nest building and 143 h during mate-guarding), and 103 h while incubating and feeding the young. When not otherwise noted, numbers are averages per hour of observation.

Table 2. Hours of observation* for the different groups: total and at the different social phases.

Group	Total	Social phase		
		Non-breeding	Courtship**	Incubation and dependent fledglings
Main groups				
BOK	107.3	36.9	37.8	32.6
HOR	46.5	23.3	14.7	8.5
MTE	64.9	45.5	11.9	7.5
MZR	64.3	30.2	21.2	12.9
NAV	56.3	24.8	27.3	4.3
SAL	128.2	24.5	85.7	18.1
SZF	65.8	14.1	42.1	9.67
Auxiliary groups				
BOT1	7.10	7.10		
BOT2	25.80		25.80	
POL	39.80		39.80	
TMR	14.58	6.33	8.25	
HNC	7.9		7.90	

*First three hours of the morning.

**Courtship phase: from collection of sticks to the start of incubation.

Table 3. Weight (g)* of M₁, M₂, and F₁.

Group	M ₁	M ₂	F ₁
Main groups			
BOK	82.7	80.4	71.7
HOR	76.4		66.8
MTE	74.4	75.3	68.2
MZR			
NAV	72.0	77.0	
SAL	80.0	81.0	67.1
SZF	83.8	80.0	77.3
Auxiliary groups			
BOT1	85.0	80.1	81.8
BOT2	80.1		81.8
POL	76.4	79.1	71.0
TMR	72.2		70.0
HNC	74.8	75.1	73.0

*Averages of several dates. See text for details

Statistical analysis: Paired *t*-test was used to compare the behaviour of the alpha male, the beta male and the female in the group (when needed, Bonferroni-type adjustments for multiple comparisons were used). The *P* values are for a two-tailed alternative. Effect size calculations were also carried out using effect size calculators (<http://www.polyu.edu.hk/mm/sizeeffectsizecalculator/calculator.html>).

Results

Dataset 1. Source data for the statistical analyses together with effect-size calculations

<http://dx.doi.org/10.5256/f1000research.6739.d97780>

a. Daily activity. Foraging for food was the main activity in the morning. Later in the day, when the birds were partly satiated, other activities dominated, such as allopreening (Dattner, 2005), play (Pozis-Francois *et al.*, 2004) and, mainly in summer, sleep. Activity in the afternoon was mixed. This pattern of activity is reflected in the number of guarding bouts during the day (Supplementary material 1). In the first three hours the number of bouts was maximal, between 8–9 bouts per group per hour. Later, the number fell below 5, and averaged less than one bout per hour in the middle of the day (and down to zero in the hot hours of the summer). Sentinel activity was resumed together with the other activities in the afternoon, but did not reach the same level as in the mornings.

b. Guarding. The mean (\pm SE) duration in which a sentinel was present in the morning was 22.75 ± 1.3 ($n = 10$ groups) minutes per hour of observation, meaning that even in the morning, at the time of maximal sentinel activity, a sentinel was present only for about one-third of the time. In every group there was great daily

variability in the amount of sentinel activity, ranging from a minimum of 6.5 minutes to a maximum of 50.5 minutes per hour of observation (Supplementary material 2).

The alpha male guarded for longer duration (a) and more frequently (b) than the other two adults (Figure 2). (a). The mean duration of guarding was different between M_1 (the alpha male) and M_2 (the beta male) and between M_1 and F_1 (the female) (t -test for paired observations, $t_9 = 5.157 P = 0.0012$ and $t_9 = 5.642 P = 0.0006$, respectively – P values are given after Bonferroni’s correction). In both cases, the mean values for M_1 were larger than for M_2 and for F_1 . (b). The mean frequency of guard bouts was different between M_1 and M_2 and between M_1 and F_1 (t -test for paired observations, $t_9 = 4.583 P = 0.0026$ and $t_9 = 6.239 P = 0.0003$, respectively – P values are given after Bonferroni’s correction). In both cases, the mean values for M_1 were larger than for M_2 and for F_1 . Effect sizes (Es) for the differences in the duration of guarding and for the number of bouts between M_1 and M_2 were both large (see Dataset, Figure 2). In 80% of the 241 observation days the alpha male guarded more than any other individual in the group. Only on 20% of the days did the beta male or the female guard somewhat more than the alpha. This often happened when the latter was busy incubating (Figure 11). There were no consistent differences in the number of bouts or in the duration of guarding between a beta male and a female.

As soon as a subordinate male became dominant – following the eviction or disappearance of the alpha male – its guarding increased to the level of dominant (Figure 3). (Before: 1.7211 ± 1.1953 (mean \pm SD) After: 3.8738 ± 1.1465 . After minus Before: t -test for paired observations, $t_9 = 9.378 P = 0.0026$). One could argue that the former M_2 was now guarding against the former M_1 , which might still be present at the border of the territory. However, in group BOT1 the eviction of the M_1 occurred early on in the observation period (with the group thus becoming BOT2), and the former M_2 maintained a high rate of guarding until it was itself evicted. All other cases of eviction occurred towards the very end or after the end of the present study.

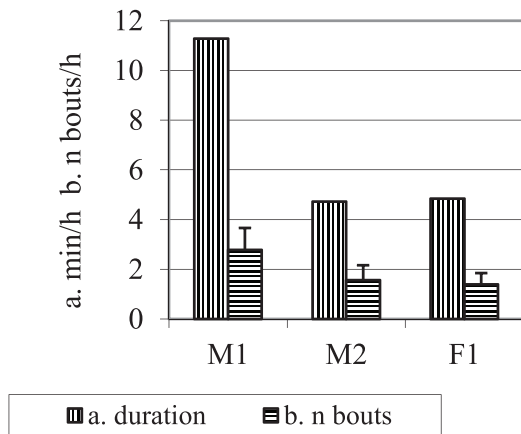


Figure 2. a. Duration of guarding (minutes/h) and b. number of guarding bouts/h by M_1 by M_2 and by F_1 .

c. Relationship of guarding to body mass is presented in Figure 4. Within each category (M_1 , M_2 and F_1) there was no significant correlation between the babbler’s weight and its guarding effort (Linear regressions: $R = -0.310$ for M_1 , $R = 0.089$ for M_2 , $R = -0.116$ for F_1 – all are non-significant).

In five of the seven groups for which the weight of both males was known M_2 was heavier than M_1 (Table 3) and in all of them M_1 guarded much more than M_2 (see Dataset, Figure 4). As soon as an M_2 became dominant, its guarding increased to match that of the previous dominant (Figure 3), without a corresponding change in its weight.

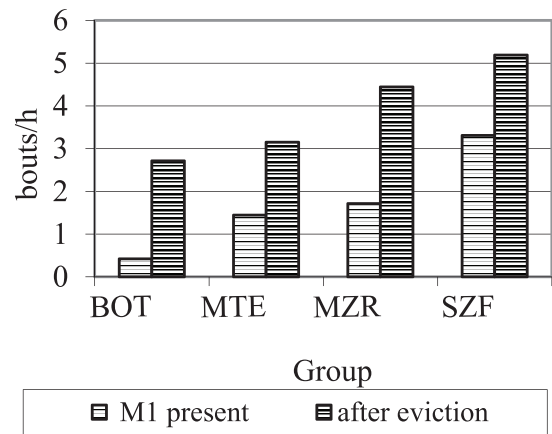


Figure 3. Guarding (bouts/h) by M_2 before and after it evicted M_1 in groups BOT1 MTE MZR SZF.

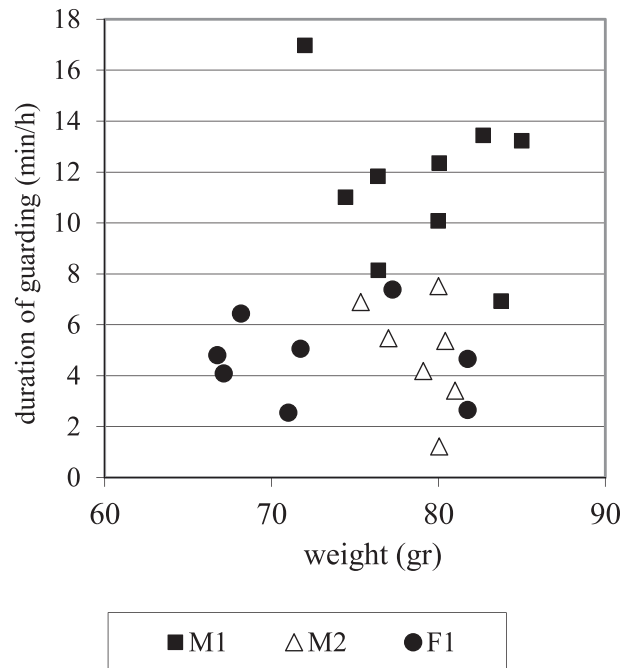


Figure 4. Relationship between a babbler’s weight (g) and its duration of guarding (min/h).

d. Replacements of the sentinel. Replacements of a sentinel occurred on average about once per hour of observation. Thirty-percent of the replacements ($32\% \pm 1.57$, $n = 14$) occurred within 0–1 minutes after the original sentinel had started its guarding bout. When not interrupted, only about 10% (± 1.24 , $n = 14$) of the bouts lasted less than 1 minute. There was a significant difference between interrupted and uninterrupted bouts ($P < 0.01$, $W = 0$, $n = 14$, Es: large.) (Supplementary material 3).

The number of replacements/h as well as the percentage of guarding bouts starting with the replacement of an active sentinel is presented in Figure 5. Mean frequency of replacements by M_1 is significantly larger than by M_2 or by F_1 (t -test for paired observations with Bonferroni's correction, $t_7 = 4.829$ $P = 0.0038$ and $t_7 = 7.657$ $P = 0.0002$, respectively, Es: large), whereas mean frequency of replacements by M_2 and by F_1 are not significantly different.

In about 20% of its guarding bouts M_1 started its session by replacing an active sentinel. M_2 did so in 11% and an F_1 in 18% of their guarding bouts respectively (Figure 5b.) (Es: large).

Figure 6 and Figure 7 show which individual replaced which other individual. Figure 6 presents the total number of replacements and number of direct and indirect replacements of M_2 or F_1 by M_1 and of M_1 or F_1 by M_2 . In over 50% of encounters M_1 replaced M_2 directly. M_2 never replaced M_1 directly but they did replace the females directly (see Dataset, Figure 6). Total: M_1/M_2 more than M_2/M_1 (t -test for paired observations, $t_6 = 7.994$ $P = 0.0002$). If we break the Total into its components (Direct and Indirect), we still have M_1/M_2 significantly more than M_2/M_1 for each component. (Direct: $t_6 = 5.943$ $P = 0.0010$ Indirect: $t_6 = 8.357$ $P = 0.0002$)

In Figure 7 replacements of the young are also shown. In this figure replacements are presented as a percentage of the guarding bouts of the babbler being replaced. This was done to compensate for the low number of bouts by the young. Only groups that included young birds are presented in this figure.

The figure clearly reveals that M_1 replaced the sentinels much more often than M_2 . M_1 also replaced its adult partners as sentinels much more often than it replaced the young inexperienced birds ($p < 0.05$, $W = 0$, $n = 5$, Es: large). M_2 rarely replaced M_1 but it did replace females and young.

e. Allofeeding. (Figure 8, Table 4). On average, allofeedings during replacements were observed about once per observation session. Data in Figure 8 clearly show that M_1 replaced M_2 with allofeedings significantly more than it replaced and allofed the young (t -test for paired observations, $t_4 = 9.418$ $P = 0.0007$, Es: large), although the young were surely more in need of it. It is also apparent that the youngsters allofed each other more than they received from the adults. We never observed an M_2 allofeeding an M_1 , although they do, on rare occasions, as was observed in other studies (unpublished report). M_2 allofed both the females (Table 4) and the young (Figure 8). M_2 , and to a lesser extent the females, sometimes received the food in a crouching position, like fledglings. However, the food was also sometimes refused (Table 4).

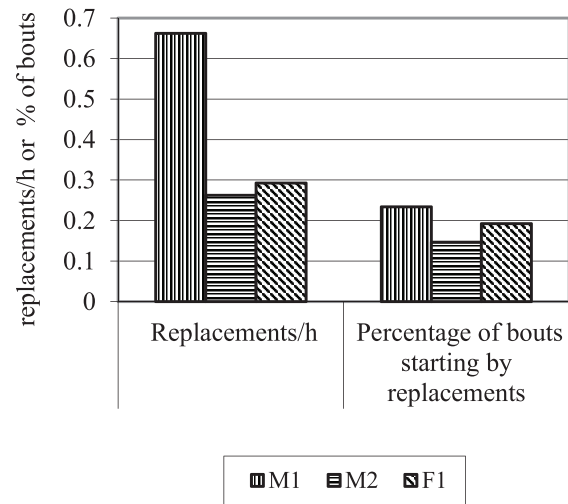


Figure 5. a. Number of replacements/h and **b.** percentage of guarding bouts that started by replacing an active sentinel.

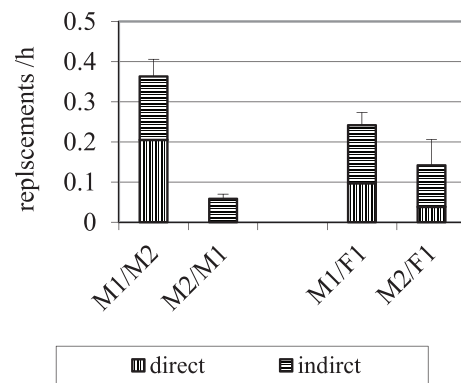


Figure 6. Direct and indirect replacements/h by M_1 and by M_2 (\pm SE for the total number of replacements).

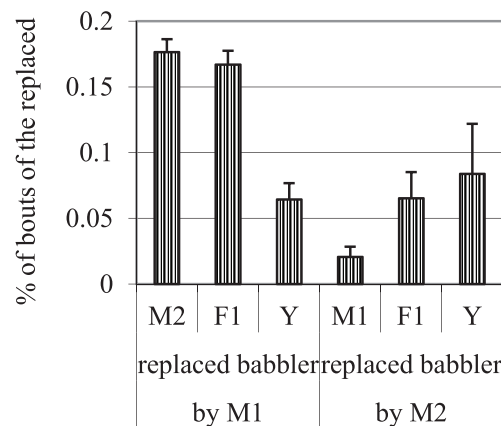


Figure 7. Replacements of adult or young sentinel by M_1 or by M_2 , as percentage of the number of guarding bouts of the replaced babblers (groups with young only).

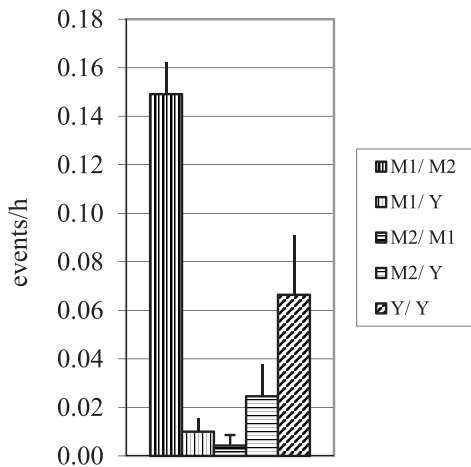


Figure 8. Replacing the sentinel by means of allofeeding (events/h±SE) among the males, among the males and the young, and among the young.

f. Social phase. The breeding phase had a profound effect on all aspects of guarding, especially on that of the alpha male (Figure 9–Figure 11). The number of guarding bouts by M₁ increased significantly during the courtship phase but dropped back as soon as incubation started. Frequency of guarding bouts by M₁ during Breeding is significantly larger than during Non-breeding: $t_5 = 4.413$ $P = 0.0139$. Breeding vs. Incubation: $t_5 = 2.088$ $P = 0.1823$, which is not significantly different (Bonferroni’s correction has been applied). (Es: large). In some of the groups the M₂ also slightly increased its guarding bouts (Figure 9) in the courtship phase but it did not drop during incubation and feeding of the young.

The number of replacements of M₂ by M₁ as well as the number of allofeedings of M₂ by M₁ also increased significantly during mate-guarding and then declined at the start of incubation: Replacements/h: Breeding vs. Non-breeding: $t_5 = 5.945$ $P = 0.0038$, Breeding vs. Incubation $t_5 = 1.579$ $P = 0.3504$.

Allofeedings/h: $t_5 = 5.458$ $P = 0.0056$ Breeding vs. Non-breeding: Breeding vs. Incubation: $t_5 = 4.670$ $P = 0.0110$.

During the first days of incubation the breeding-pair often monopolized incubation. On those days the guarding by M₁ declined and those of M₂ increased significantly in all groups ($P < 0.05$ $W = 0$; $n = 5$ Figure 11).

M₁ Mate Guarding vs. M₁ Incubation: $t_4 = 3.740$ $P = 0.0403$

M₂ Mate Guarding vs. M₂ Incubation: $t_4 = -6.043$ $P = 0.0076$ (Please note a reversed direction).

M₁ Mate Guarding vs. M₂ Mate Guarding: $t_4 = 3.054$ $P = 0.0757$

M₁ Incubation vs. M₂ Incubation: $t_4 = 3.848$ $P = 0.0367$

(Bonferroni’s correction has been applied). Note that the first, the second and the fourth comparisons (but not the third) are significant.

Different types of replacements: indirect, direct and with allofeedings can be visualized in this video clip: https://youtu.be/H_EdXA-bRu2g

Discussion

The data provided in this paper demonstrate that the alpha and beta males compete to guard. In addition to the alpha bird guarding more than any other individual, it also replaces and thus interrupts the guarding by other birds, especially that of the beta male, which competes with it over reproduction. The alpha male replaced the guarding beta male more than it replaced the young inexperienced birds (Figure 7 and Figure 8). About one-third of guarding replacements took place less than one minute after a particular individual had mounted the guarding perch (Supplementary material 3). This indicates that the sentinel that had just started its guarding bout was not yet hungry or tired, unlike what was suggested by Bell *et al.* (2010) for the pied babbler.

Table 4. Number of allofeedings by M₁ or by M₂ and type of acceptance. n/h= interactions per hour.; crouch= accepting as a fledgling (percentage of interactions); refusals (percentage of interactions).

Feeder	M ₁						M ₂			
	M ₂			F ₁			M ₁	F ₁		
Receiver	n/h	Crouch	Refusal	n/h	Crouch	Refusal	n/h	no./h	Crouch	Refusal
BOK	0.17	53%	6%	0.13	14%	37%	0	0.05	15%	44%
HOR	0.19	23%	43%	0.25	36%	11%	0	0.09	16%	47%
MTE	0.17	15%	0	0.01	0	0	0	0		
MZR	0.17	0	13%	0.08	0	56%	0	0		
NAV	0.34	33%	0	0.13	0	0	0	0.16	22%	0
SAL	0.26	14%	21%	0.04	0	20%	0	0.10	24%	37%
SZF	0.60	44%	0	0.04	0	0	0	0.03	0	0

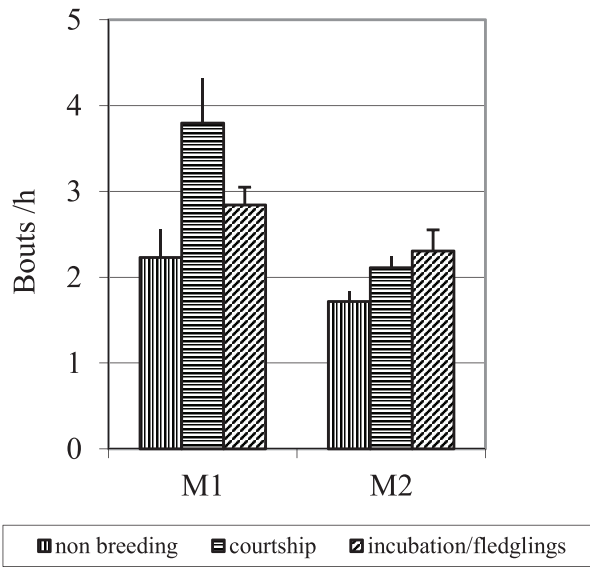


Figure 9. Effect of the social phase on the number of guarding bouts by M₁ and by M₂.

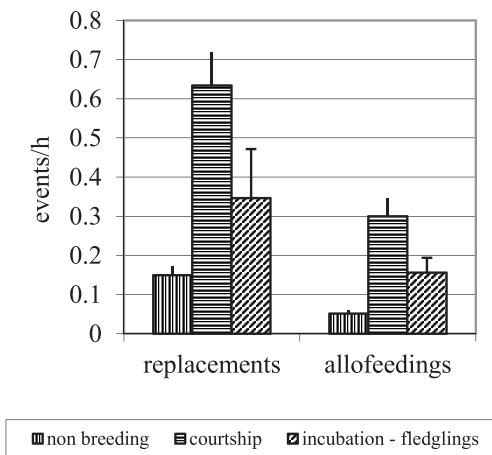


Figure 10. Effect of the social phase on replacements/h and allofeedings/h of M₂ by M₁ (+SE).

The dominant often replaced its subordinate directly (Figure 6) by landing next to its perch, whereas the subordinate did not replace the alpha directly, but indirectly, by perching below it or taking a post on a lower tree, waiting for it to leave. The motivation of the beta male to replace the alpha was evident, for as soon as the latter had vacated its perch the beta male often climbed up to occupy the same perch. The alpha male also allofed the beta male during the replacement, sometimes forcing it to accept the gift, while the latter often reacted by fluttering its wings like a fledgling (Figure 8, Table 4). The fact that all these behaviours increased significantly during courtship, when competition over breeding was maximal, and then declined at the start of incubation, after paternity had been decided and competition over immediate paternity was over (Figure 9 and Figure 10), highlights the competitive basis underlying the act of guarding.

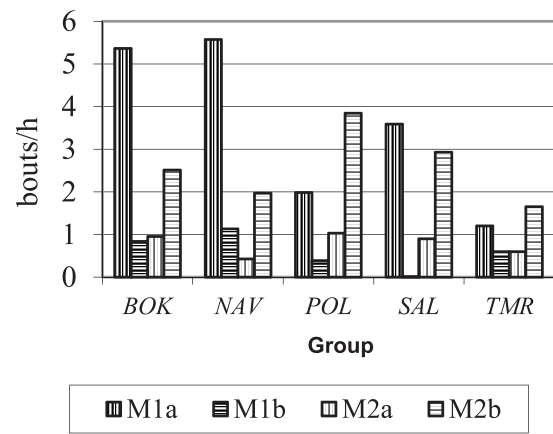


Figure 11. Guarding (bouts/h) by M₁ and by M₂ during a. mate guarding and b. the first day of incubation, in groups BOK, NAV, POL, SAL and TMR.

It should be stressed that most of the replacements were performed quite gently. The replacing bird often clumped with and sometimes allopreened the soon to be replaced sentinel for a few seconds or more before the latter left. However, when it refused to leave, it was sometimes pushed and even pecked at by the alpha male. As already noted, although overt aggression among adult males within the group is rare, aggressive replacements do occasionally occur.

Wright *et al.* (2001a,b,c) contended that a direct relation exists between a babbler’s mass (weight) and the extent of its guarding: “Overall, body mass explained much of the variation in individual sentinel effort both within and between birds”, and “...found relatively little evidence that individuals compete for the chance to act as sentinels”.

Our data not only clearly contrast these statements, but some of the data presented in the figures of Wright *et al.*, contradict their own statements. They obtained a positive regression of mass vs. guarding effort (Figure 4 of Wright *et al.*, 2001b) due to the inclusion of guarding by young immature group members, which were both lighter in weight and guarded much less than the adults. Indeed, the upper part of their figure differs little from our Figure 4, and clearly shows that within each of the upper three social categories (M₁, M₂, and F₁) there is no correlation between body mass and guarding. In another study (Wright *et al.*, 2001c), the average body mass of the beta males was given as greater than that of the alpha males (Figure 3 of that study); but in eight out of the ten control days the sentinel effort by the alpha male was higher than that of the beta (their Figure 2, see also Figure 1 of Wright *et al.*, 2001b). Five of our beta males were heavier than the alpha males in their groups (Table 3), but guarded much less than the alpha. In yet another paper, Wright *et al.* (2001a) state that “Change-overs between sentinels rarely revealed any social context”; but Figure 3 of the same study reveals large differences in change-overs between the alpha and beta males. Moreover, it has frequently been shown that supplementing the babblers with food greatly increased sentinel activity (Bell *et al.*, 2010; Cordovi, 1988, unpublished report; Wright *et al.*, 2001b), suggesting that food availability constitutes a

constraint on guarding, especially in the desert. However, except for the case of artificial differential feeding of one particular individual for single days (Wright *et al.*, 2001b), food availability for the group did not alter the relative extent of guarding by the different hierarchical categories.

Wright *et al.* (2001a) also suggested that in large groups the load of guarding per bird was reduced. This argument was based on the division of the total time when a sentinel was present, by the number of birds in the group. However, our data show that the time that a babbler spends guarding depends mainly on its place in the hierarchy and other social and ecological aspects (including food availability), rather than on the mean number of birds in the group. Guarding by the maturing young does extend the overall period in which a sentinel is present (Supplementary material 2), but it does not reduce the “load” of any particular individual.

Wright *et al.* (2001b) concluded that “...sentinel behaviour in Arabian babblers appears entirely consistent with recent (Bednekoff’s) models of selfish state-dependent sentinel behaviour”. Bednekoff (1997); Bednekoff (2001) proposed a model suggesting that “the sentinel position is the safest place to be... when no other group member is on guard” If that were indeed the case, why replace that sentinel? In contrast, in a recent paper, Ridley *et al.* (2013) found that in the pied babbler the sentinel is at a greater risk of predation and further from cover than the foragers. Our observations (unpublished report) suggest that this is the case also for the Arabian babbler.

Why did the beta males guard much less than the alpha males? In our groups the beta males were all mature and not much younger than the alphas in their group (Table 1). Whenever they had the opportunity they guarded as much as the alphas. During the first days of incubation the breeding pair monopolize the incubation. Later on the beta male as well as the young may share in the incubation. In the few groups that were observed on the first day of incubation, the alpha male spent most of its time incubating rather than replacing the beta male. Consequently, the beta male increased its guarding almost to the average level of the alpha on other days (Figure 11). One could argue that M_2 was compensating for the absence of M_1 – however, the large day-to-day fluctuations in the total amount of guarding (Supplementary material 2) are not compatible with the notion that there is a certain daily “quota” of guarding. Indeed, in most cases, on days in which the alpha bird reduced its guarding - it still guarded more than any other individual in the group. The large increase in guarding by the beta male following its eviction of the alpha (Figure 3) also indicates that the beta male’s previous lower extent of guarding was not due to incompetence, or laziness or lack of desire to guard. We suggest rather, that guarding by the beta male was restricted by the alpha male.

Many observations have confirmed the fact that the presence of a sentinel allows the group to forage in comfort (Hollén *et al.*, 2008 and references cited therein; Ben-Mocha, 2013). However, this does not explain why a particular individual will feel obliged to stop feeding, or any other activity, and stand guard over the group. Our calculations show that even in the morning, at the time of maximal guarding activity, a sentinel was present only for about one-third of the time. Why should a babbler choose frequently to replace an

active sentinel rather than to start guarding when no other individual is guarding, and thus extend the overall time during which a sentinel is present? That the alpha male guards more than any other member of the group, and often replaces a subordinate as soon as the latter seeks to begin guarding, suggests that the primary concern of the alpha male is to demonstrate that it is the one that is performing the altruistic act, and that it can control the beta male and replace it whenever it wishes.

Anava (1992) studying mobbing of raptors in Arabian babblers, observed a similar competition among the males as well as among the females. In most groups the alpha male participated more than any other individual in all aspects of mobbing, and interfered with the mobbing of other group members, mainly that of the beta male; except in one group in which there was a single male and three adult females that competed over breeding. In that group the alpha female participated in the mobbing and guarding more than the male and interfered in the mobbing by the other females.

Competition over altruistic acts was also described in babblers with regards to: allofeeding and feeding at the nest by yearlings (Carlisle & Zahavi, 1986); confrontations with neighbours (Berger, 2002); and allofeeding among adults (Kalishov *et al.*, 2005). All these altruistic activities confer benefit on the group and require investment by their performers.

Competition makes sense if the contestants gain from winning. Any sentinel, not necessarily the alpha male, will satisfy the need of the group for a guard. If the reason for guarding is solely for the benefit to the group, why should a dominant not let a willing subordinate individual guard? We suggest (Zahavi, 1990; Zahavi & Zahavi, 1997) that by investing effort in guarding and by intervening in the guarding of its competitors, a babbler demonstrates and signals its general ability and its control over its competitors.

Group members are aware of the presence of the sentinel, because in its presence they can feed and move about with greater ease; they know who is guarding (Bell *et al.*, 2010) and are also attentive to the replacements and how these replacements are carried out. By guarding and by replacing a competitor, a babbler thus retains or increases its own prestige and reduces that of the competitor. We have suggested previously (Zahavi, 1995; Zahavi, 2008) that this investment constitutes the handicap that proves the honesty of the claim to prestige.

Why should a babbler care so much about its prestige? High prestige provides the individual with a greater share in the group’s resources. Prestige functions like an invisible “peacock’s tail”: it attracts collaborators and deters rivals. Zahavi & Zahavi (1997) suggested that whereas rank is stable, the prestige of an individual changes constantly. Every individual in the group, including the females and the very young, has and cares about its own prestige, especially in relation to those closest to it in the hierarchy.

In more general terms, because acting altruistically may confer prestige on the performing individual, altruism can substitute for other means of obtaining prestige, such as overt aggression or wasteful display. This is especially important in such closely-knit

social groups as the Arabian babblers. Threats and aggression can easily turn into fights that may result in the killing or eviction of the loser. The loser, if it survives the fight, becomes a refugee, while the winner loses a partner in the defense against its neighbours.

An altruist gains directly from the investment of performing altruistic acts, and the competition increases the likelihood that there will usually be a willing candidate to take upon itself the duty of the sentinel. Members of a social group are attentive to such acts because they both benefit from them and gain information regarding the social relationships among other members of the group. This may explain why altruistic acts are so common among animals living in cooperative groups.

Ethics

The birds were banded and tamed under a permit from the Israel Nature and National Parks Protection Authority. No other permits were required.

Data availability

F1000Research: Dataset 1. Source data for the statistical analyses together with effect-size calculations., [10.5256/f1000research.6739.d97780](https://doi.org/10.5256/f1000research.6739.d97780) (Dattner *et al.*, 2015).

Supplementary materials

Supplementary material 1. **Guarding (bouts/h, per group) throughout the day.** Figure and source data for MTE group.

[Click here to access the data.](#)

Supplementary material 2. **Duration of guarding (min/h, in the first three hours of the morning) by different members of SAL group on observation days in February 2004 (breeding phase).** Figure and source data for SAL group.

[Click here to access the data.](#)

Supplementary material 3. **Brief bouts (0–1min).** A. As a percentage of uninterrupted guarding bouts or B. Bouts replaced 0–1 minutes after the start of the bout, as a percentage of total replacements of the replaced babbler.

[Click here to access the data.](#)

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Author contributions

Data presented in this paper were collected by Arnon Dattner and Carmel Bezner (Dattner, 2005). Arnon Dattner designed, collected and summarized the observations. More recently (2015) he produced the attached video clip. Avishag Zahavi wrote the manuscript and Amotz Zahavi supervised the thesis and was involved in every detail of the presentation.

Competing interests

No competing interests were disclosed.

Grant information

The author(s) declared that no grants were involved in supporting this work. Arnon Dattner's observations were part of his Msc thesis for the Tel-Aviv University. Carmel Besner was a volunteer.

Acknowledgments

We are grateful to Carmel Bezner for assistance in the observations; Oded Keinan, Yitzhak Ben-Mocha, Mandy Ridley, Ally Harari, Arnon Lotem, Tirtza Zahavi and Naama Zahavi-Ely for critical reading and suggestions and to Naomi Paz for editorial assistance. We also thank our referees for careful reading and comments. Special thanks are due to Uzi Motro for revising the statistical calculations.

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Open Peer Review

Current Referee Status:



Version 2

Referee Report 05 February 2016

doi:10.5256/f1000research.8394.r10064



Uzi Motro

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I approve the revised version, without reservations.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Competing Interests: No competing interests were disclosed.

Version 1

Referee Report 09 December 2015

doi:10.5256/f1000research.7238.r11476



Raghavendra Gadagkar

Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India

The evolutionary origins and maintenance of altruism are indeed major unsolved problems in the study of animals and humans. Most people attempt to find ways in which altruistic behaviour, which is believed to be detrimental to the fitness of the actors, is nevertheless favoured by natural selection. Zahavi and his co-workers on the other hand, have consistently pursued the idea that so-called altruistic behaviour is actually beneficial to the actor. This is because the very fact that the altruist is willing (and capable) to undertake costly altruistic behaviour increases his prestige and therefore his access to mates.

In this paper the authors attempt to provide support for their idea (often refereed to as the Handicap Principle), by showing that males of the Arabian babbler compete with each other to have the opportunity to undertake presumably costly, altruistic sentinel or guarding behaviour. Such a claim has been made by this group before but has been criticised by others who were either unable to find such pattern in sentinel behaviour of this species or argued that the observed pattern can be explained by other means. It may be very hard to conclusively demonstrate that males do or do not compete to perform sentinel behaviour or that all other explanations have been ruled out. The best way therefore to test the Handicap Principle in this case is to measure the actual costs and benefits of sentinel behaviour. This has not yet been done and is perhaps hard to do. Thus until such costs and benefits can be measured, we continue to rely on

understanding and explaining the patterns of sentinel behaviour. In such a situation, wide acceptance of the Handicap Principle will necessarily depend on other researchers finding evidence in support of it. More research, more data and reiteration by the same authors and their associates are unlikely to be sufficient.

I would therefore argue that this is treated as an open question and researchers finding evidence for and against the Handicap Principle should have the opportunity to publish their findings and their interpretations, as long as they are scientifically rigorous. In this spirit I support the dissemination of this paper but to make it scientifically rigorous I recommend that the authors revise their manuscript in response to my comments below.

1. Introduction, last paragraph: If the authors wish to argue that altruistic acts are not actually altruistic, they should not continue to say “altruistic act of guarding”. Perhaps they should say something like “supposedly altruistic act of guarding”.
2. Under the heading “Descriptions of guarding patterns a. Guarding”, the authors state that: “It is usually easy to distinguish the sentinel from an individual that is in the tree for another reason, such as feeding, resting, auto-preening, etc.” The authors should say clearly how to make such a distinction between a sentinel and a bird that is in the tree for another reason, so that other researchers can try to make the same distinction and it does not remain only a tacit knowledge of the present authors. I first assumed that the few sentences that follow this describe how to make the distinction but I am not sure of that. If that is indeed so, the authors should be explicit about it. More generally speaking, many things that Zahavi and his co-workers ‘know’ is a kind of tacit knowledge to which outsiders have no access. For Zahavi’s ideas to become more widely acceptable, they will have to make the effort to describe the sources of their knowledge and the reason for their convictions more transparent and thus allow others to enter into the same knowledge space.
3. In the same section at the end the authors mention that “but on the following day a maximum duration of almost 45 minutes/h was reached, probably due to the availability of a large number of insects that had drowned in the flooding (Anava *et al*, 2002)”. It is not clear why “high availability of insects” should increase guarding. Please explain.
4. Under the heading “Descriptions of guarding patterns b. Replacement of sentinels”, the authors state in the last line: “The conflict between the two was often manifested by both of them nervously preening themselves”. How do we know there was conflict?
5. Under the heading “Descriptions of guarding patterns c. Allofeeding”, the authors state in the end “... suggesting that despite being hungry it had refused to accept the “gift” from another babbler”. What is the interpretation of refusing to accept food despite being hungry, especially for a subordinate? Please elaborate.
6. In Fig. 2, there is no mention of F1.
7. In all the figures, the colour contrast between different bars is very poor.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Competing Interests: No competing interests were disclosed.

Author Response 11 Jan 2016

Amotz Zahavi, Tel Aviv University, Israel

1-Q. If the authors wish to argue that altruistic acts are not actually altruistic, they should not continue to say "altruistic act of guarding". Perhaps they should something like "supposedly altruistic act of guarding".

Answer: Although altruism is defined by biologists as an act that helps others at a cost in fitness to the altruist, this is not the only definition of the term. Ordinary dictionaries define altruism as an investment that helps others. It is not dependent on whether or not the fitness of the altruist is reduced as a result, consequently, guarding when the rest of the group is feeding is indeed an altruistic act.

We have repeatedly suggested that, on average, the direct fitness of the altruist is increased, and that "This may explain why altruistic acts are so common among animals living in cooperative groups." See also: "Altruism and moral behaviour." (page 149, in Zahavi A, Zahavi A: The Handicap Principle).

In a more recent paper (~Zahavi, A. and Zahavi, A. (2012). The logic of analog signaling and the theory of signal selection. *Israel Journal of Ecology & Evolution*. 58, 269-278) we suggest use of the term "investment" rather than "cost" because observers of altruistic acts can evaluate the investment of the altruist; whereas, when the investment is described as "cost" this already implies that it reduces the fitness of the altruist which is not necessarily the case

2. Description of Guarding. Our "questionable sentence" is preceded by a description of sentinel activity. This description does not differ from that used in almost every study dealing with sentinel activity

3. This is a short way of writing: "Food availability has a profound effect: On a rainy day (for instance, Feb 22 in figure 2, supplementary material) little guarding was observed - because it was difficult to find food while on the following day (for instance Feb 23, in the same figure) a maximum guarding duration of almost 45 minutes/h was reached, probably due to the availability of a large number of insects that had drowned in the flooding, facilitating spending less time on looking for food and more time on guarding"

4. See the attached video clip.

5. If allofeeding may be considered an expression of dominance (Woolfenden and Fitzpatrick (1977) Kemp and Kemp (1980), Kalishov Zahavi and Zahavi, (2005)), then refusing to be fed reduces the prestige of the donor and increases that of the receiver. The fact that the recipient came to us to get food showed that it had not refused the food from the would-be donor because it was satiated.

Competing Interests: We thank our referee and there are no competing interests between us

Referee Report 02 October 2015

doi:10.5256/f1000research.7238.r10649



Stephen Rothstein

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This paper reports observations of guarding in Arabian babblers in considerable detail and does an excellent job of relating various aspects of guarding to variables such as a bird's dominance rank and its manner of replacing an individual who is already guarding. The results are new and important and the paper convincingly shows what looks like an element of competition in terms of who guards. This is a fascinating and valuable result which suggests that individuals that guard receive some increase in fitness from their guarding behavior. The paper argues that this fitness increment is via an increase in an individual's prestige because time spent guarding is a handicap that takes away from time that could be spent feeding and because guarding may increase the guarding individual's risk of predation. All of this train of logic holds together although I am not sure there is much actual evidence for the existence of prestige and its assumed effect on fitness.

A problem as I see it is that there may be alternate explanations for the reason that dominant individuals seem to go out of their way to guard and even displace individuals that are already guarding. First, the alpha male may guard the most because he has the most to gain from guarding as he has fathered the offspring produced in the territory. Second, the assumption seems to be that guarding is done to reduce predation. But what if it is also done to repel conspecific intruders, especially males that might try and mate with the breeding female? The individual that would gain the most from repelling conspecific intruders is the alpha male and this could explain why alpha males do most of the guarding and even displace subordinate males from guarding as the latter would have less to gain from taking action against conspecific intruders. Guarding against intruding rival males explains why alpha males greatly increase guarding during the courtship because that is when extra-pair copulations would be most costly to their fitness. I did not see any clear explanation for this change in alpha males' guarding under the prestige explanation. Guarding against intruding rival males could also explain why so many alpha male guarding sessions start with a direct displacement of another guarding bird as intruders are not as much of a threat (or any threat) to the fitness of other group members. Alpha males may sometimes allofeed birds already guarding because that may ease the transition and allofeeding may occur when an alpha males has found abundant food and is already satiated. Group members other than the alpha male may engage in guarding because they may eventually become the dominant male or female, i.e. they may benefit from maintaining the integrity of the group territory.

If demonstrating to other group members a male's ability to engage in seemingly altruistic acts is an important aspect of guarding, then alpha males should be more likely to initiate a guarding session when another group member is already guarding than when no one is guarding. The authors seem to have the data to test that prediction. The issue is admittedly complicated because there might be a greater need to guard against predators when no one else is guarding than when someone else is already guarding. But the relevant analysis might still be worth doing because it does have the potential to support the authors' line of reasoning.

There is no doubt that the babbler system is a very complicated one and that the Zahavis' long term observations have made this into a classic system that has been very valuable to research on avian breeding and behavioral ecology in general. This paper adds to the novelty of the babbler system and it is only the final bit of the authors' logic stream, that individuals incur a handicap so as to demonstrate their prowess and accrue prestige that remains unconvincing to me. More attention to alternative hypotheses

and to testing these against the favored hypothesis might in the end provide more convincing support for the latter.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Competing Interests: No competing interests were disclosed.

Author Response 11 Jan 2016

Amotz Zahavi, Tel Aviv University, Israel

Q.---First, the alpha male may guard the most because he has the most to gain from guarding as he has fathered the offspring produced in the territory.
Second, the assumption seems to be that guarding is done to reduce predation. But what if it is also done to repel conspecific intruders, especially males that might try and mate with the breeding female? The individual that would gain the most from repelling conspecific intruders is the alpha male and this could explain why alpha males do most of the guarding and even displace subordinate males from guarding as the latter would have less to gain from taking action against conspecific intruders

Answer -There is no doubt that the detection of conspecifics is one of the most important aims of guarding. However, the idea that the subordinate male would have less to lose if the territory is taken over is incorrect, because when alien males or females take over the group in order to breed, all the members of the same sex as the alien in the original group (except sometimes the very young fledglings) are chased away (Zahavi A: (1990). Arabian Babblers: The quest for social status in a cooperative breeder. In Stacey PB and Koenig WD editors. Cooperative breeding in birds. Long-term studies of ecology and behavior. Cambridge: Cambridge University press. 1990; 103–130). The expelled individuals become refugees. It is therefore in the interest of every individual in the group to insure that intruders of the same sex will not take-over the group.

Q .---Extra-pair copulations. The referee suggests that guarding against intruding rival males explains why alpha males greatly increase guarding during the courtship because that is when extra-pair copulations would be most costly to their fitness. "I did not see any clear explanation for this change in alpha males' guarding under the prestige explanation."

Answer. Breeding females do not copulate with males of neighbouring groups, but may copulate with subordinate males of their own group that are not their offspring. Such extra-pair copulations are indeed of great concern for the alpha male. –Mate-guarding by the alpha male is aimed against copulations by the beta or lower ranking males that are not the descendants of the breeding female. This is why competition among same-sex members of the group increases during the breeding season. As there is almost no aggression among the same-sex adults, the competition is expressed mainly by increased guarding and by allofeeding – as demonstrations of dominance.

Q.---Alpha males may sometimes allofeed birds already guarding because (1) that may ease the transition and (2) allofeeding may occur when an alpha males has found abundant food and is already satiated.

Answer. (1) It has repeatedly been suggested that allofeeding is a demonstration of dominance

(Kalishov A, Zahavi A, Zahavi A: (2005). Allofeeding in Arabian Babblers (*Turdoides squamiceps*). *J Ornithol.* 2005; 146(2): 141–150.; Kemp AC, Kemp MI (1980). The biology of the southern ground hornbill *Bucorvus leadbeateri* (Vigors). *Ann Transvaal Museum* 32:65–100.; Woolfenden GE, Fitzpatrick JW (1977). Dominance in the Florida scrub jay. *Condor* 79:1–12). As such it aggravates rather than mitigates the situation. This is manifested by the recipient often trying to avoid being fed (see "refusals" in Table 4).

(2) In most cases the alpha male is not necessarily satiated when allofeeding. It often flies down to take tidbits from the observer immediately after taking up its guarding post following the allofeeding. Similarly, the individual that has just refused to accept food from its replacer will often readily accept the same kind of food when offered by the observer. Satiated individuals usually do not approach the offered food .

Competing Interests: There are no competing interests

Referee Report 07 September 2015

doi:10.5256/f1000research.7238.r10220



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A very stimulating paper, looking at the vigilance conflict in a different, original way.

The idea that taking on a social task (such as guarding the group) that inflicts an obvious burden on the performer, is not necessarily an altruistic act, has already been presented by Zahavi and their associates. Their assertion is that although such a behavior looks altruistic, indeed it is not – by accepting the burden, the performer reliably indicates its high quality, thus gaining a prestige which increases its reproductive success. The contribution of the present paper is in providing real data, which unequivocally confirm their handicap assertion.

However, I have some concern with the statistical analysis of the data. The units of sampling are, obviously, the various groups. Thus, the observations on the alpha males, on the beta males and on the females do not represent independent samples, but constitute paired observations. The correct statistical tool should be a paired-observation comparison, such as a paired *t*-test. Moreover, Bonferroni-type adjustments for multiple comparisons are needed in some places.

I took the liberty of performing paired *t*-tests on the source data (Dataset 1), and to my satisfaction, although the *p*-values have changed, the conclusions remain valid.

And a small comment: In the Introduction, the authors claim that "However, that guarding helps the group does not explain why a particular individual may forego foraging or any other occupation, in order to guard." There are several works that demonstrate how guarding can be evolutionarily stable in certain situations (see below some examples). The novelty in the present paper is that it can explain the *competition* over performing the act of guarding.

Pulliam, H. R., Pyke, G. H. & Caraco, T. (1982). [The scanning behaviour of juncos : a game-theoretical approach](#). *Journal of Theoretical Biology* 95: 89-103.

Parker, G. A. & Hammerstein, P. (1985). Game theory and animal behaviour. In: *Evolution: Essays in Honour of John Maynard Smith*. (Greenwood, P. J., Harvey, P. & Slatkin, M., eds.) pp. 73-94. New York: Cambridge University Press.

Motro, U. & Cohen, D. (1989). [A note on vigilance behavior and stability against recognizable social parasites](#). *Journal of Theoretical Biology* 136:21-25.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Competing Interests: No competing interests were disclosed.

Author Response 11 Jan 2016

Amotz Zahavi, Tel Aviv University, Israel

~~The statistical analysis was corrected using Motro's calculations. See new version.

Competing Interests: There are No competing interests

Discuss this Article

Version 1

Reader Comment 10 Sep 2015

Doron Shultziner, Hadassah Academic College Jerusalem, Israel

This is a great empirical paper. The paper strongly demonstrates that Arabian babblers are competing over "altruistic acts" in a way that defied all competing explanations of altruism: Kin Selection, Reciprocal Altruism, and Group Selection. Indeed, the only thing I found missing in the paper is a more direct rebuttal of those competing explanations, though it is pretty clear from the paper why they are irrelevant in explaining the data. I just want to make that a bit clearer:

1. The authors show an ironic pattern in which the Alpha male is more concerned with helping the Beta male than its direct offspring. Namely, competition between the Alpha and Beta birds is more important than helping direct kin. In fact those closest to each other in rank are more likely to help each other or more correctly put - compete. This is quite astonishing in itself, but first and foremost this contradicts Kin Selection explanations of altruism which would predict the exact opposite.
2. The paper also shows that replacements in sentinel positions are *far from reciprocal*. The evidence is very clear and consistent that the alpha and beta are not engaging in "you'll scratch my back and I'll scratch yours"; quite the opposite. The babblers compete over the altruistic acts. The alpha is guarding more than any other member in all situations and year cycles. In fact, instead of waiting to

be reciprocated, the alpha is interfering in the guarding of other members who just started to guard, and does so most obsessively toward the beta male.

3. The competition over the sentinel position has other paradoxical aspects. For example, instead of maximizing the time of guarding by letting every able and willing individual serve as sentinel until it is tired or hungry, the babblers interfere with each other's job soon after it started. The most efficient way to conduct the sentinel function for the group would be to allow each individual to go up the tree when the previous sentinel has gone down. Instead, the babblers rush to replace one another, especially the alpha, soon after those closest in rank went up. This does not make sense from the standpoint of the group and in fact it is clear that the competition over performing altruistic acts is sometimes hindering the group interest. This is another demonstration how considerations of altruism based on the whole group (or groups selection reasoning) does not hold up even in places where it should have been relevant (if there was any truth to it).

Competing Interests: I have no competing interests but the principle author is my colleague.
