

RESEARCH PAPER

The sentineling—Foraging trade-off in dominant and subordinate Arabian babblers

Roni Ostreiher¹  | Aviad Heifetz²

¹Department of Life Science, The Open University of Israel, Raanana, Israel

²Department of Management and Economics, The Open University of Israel, Raanana, Israel

Correspondence

Roni Ostreiher, Department of Life Science, The Open University of Israel, Raanana, Israel.

Email: ronio@arava.co.il

Funding information

The study was supported by The Open University of Israel's Research Fund (grant no. 37142). We are grateful for this support.

Editor: W. Koenig

Abstract

Many cooperative breeders forage under predation risks, sentineling is a central activity, and groupmates have to balance between sentineling and foraging. The optimal balance between sentinel activity and foraging may differ among dominant and subordinate individuals, as dominants are more efficient foragers. Two theoretical models pertain to this balance and predict when individuals with different foraging abilities should switch between the two activities on the basis of their energetic state. In one of these models, individuals must attain a critical energetic level by dusk to pass the night, and in the second model fitness is monotonically increasing with the energetic state. We tested these models in the cooperatively breeding Arabian babbler, *Turdoides squamiceps*. We measured the length of sentinel bouts and the gaps between them both in natural conditions and following experimental feeding. Following feeding ad libitum, subordinates expanded their sentinel bouts significantly more than dominants in comparison with natural conditions. These findings are consistent with the first model, but not with the second. In the experiment, we measured the mass of mealworms consumed by each individual following a sentinel bout relative to its body mass. This ratio was larger for subordinates, indicating that they ended their sentinel bouts at a lower energetic state than dominants. This finding is consistent with the second model, but not with the first. Immediately after eating ad libitum, in 62% of the cases the first behavior performed by the babblers was a new sentinel bout, but in 17% it was a mutual interaction with a groupmate, indicating that social interactions also play a role in the trade-off vis-à-vis sentinel activity.

KEYWORDS

feeding experiment, food mass/body mass ratio, foraging success, sentinel, state-dependent sentinel hypothesis, *Turdoides squamiceps*

1 | INTRODUCTION

Two main necessities shape the regular lives of most animals living in nature: the necessity to eat and the necessity not to be eaten. Most behaviors are derived or influenced by these contradicting demands. Under certain conditions, cooperative breeding may be advantageous for coping with both.

In many cooperative breeders, from time to time one of the group members stops its activity, climbs up or flies to a high and prominent position, keeps steady and looks around. This activity is called sentinel behavior. At the level of the group, coordination of vigilance among the group members has been recognized as the defining feature of sentinel behavior (McGowan & Woolfenden, 1989). If a predator or a raptor approaches, the sentinel is usually the first

to notice and reacts vocally by specific alarm calls. Hearing these calls, other group members usually react by escaping to shelter or climbing up to join the sentinel (Zahavi & Zahavi, 1997).

Sentinelism may enhance fitness via a variety of mechanisms. A sentinel may be safer in virtue of its ability to detect predators earlier than when it forages, and upon detection either to dissuade the predator from attacking by calling toward it or by escaping to shelter in due time (Bednekoff, 1997, 2001). Predators might target sentinels more often than foragers (Ridley, Nelson-Flower, & Thompson, 2013), but this may be more than offset by the sentinel's higher rate of early detection (Bednekoff, 2015). In these senses, sentinels may be considered selfish if one sentinel in a population of nonsentinels would have a fitness advantage, and individuals protect themselves best by being sentinels when other individuals are not sentinels already. Moreover, sometimes the alarm calls emitted by the sentinel may actually divert the attack away from itself toward the foragers (Kareksela, Harma, Lindstedt, Siitari, & Suhonen, 2013). Additionally, since foragers learn from the sentinel's alarm calls about the imminent danger and react accordingly, the sentinel benefits also from the higher survivability of its group mates via group augmentation (Kingma, Santema, Taborsky, & Komdeur, 2014; Kokko, Johnstone, & Clutton-Brock, 2001; Wright, Berg, Kort, Khazin, & Maklakov, 2001b) and kin selection (Hamilton, 1964; Sherman, 1977).

Ideally, each individual should switch among fitness-enhancing activities, like foraging and sentinelism, depending on its energetic state (Wright, Maklakov, & Khazin, 2001), whenever continuing with the current activity yields less additional fitness than the other can yield. For example, if after foraging successfully for long enough the individual approaches satiation, it may be that sentinelism may then become more valuable for enhancing fitness. Conversely, after a long enough sentinel bout, the energetic level of the individual may decrease to a point where foraging is then more valuable than additional sentinelism.

In cooperative breeders, these trade-offs may be different across dominant and subordinate mature individuals. A main difference between the two is that dominants are more efficient foragers, since they sometimes usurp their dominance to push aside subordinate foragers or to confiscate food items that the latter find. In contrast, sentinelism may provide similar value to dominants and to mature subordinates. During a sentinel bout, both have all-round scanning opportunities and can thus benefit directly in a similar manner from the safety enhancement that early detection of threats can provide. Moreover, in cooperative breeders all sentinels, dominant and subordinates alike, emit alarm calls upon predator detection, to which group members react in a like fashion, thus yielding both dominant and subordinate sentinels similar benefit via group augmentation and kin selection.

In view of these similarities and differences, how should the trade-off between foraging and sentinelism be resolved for dominant individuals as opposed to subordinate mature individuals? Two models put forward in McNamara and Houston (1994) are relevant here. The models pertain to the optimal time allocation of more or less efficient foragers between a riskier patch with food and a safer

patch with no food, and to the resulting energetic levels of the foragers. When applied to the foraging-sentinelism trade-offs faced by dominants and subordinates, the dominants are the more efficient foragers, and the no-food patch is the sentinel position.

Previous studies compared sentinel durations of dominants and subordinates in cooperative breeders. In the Arabian babbler, *Turdoides squamiceps* (Wright, Berg, Kort, Khazin, & Maklakov, 2001a; Wright et al., 2001b), Florida scrub-jay, *Aphelocoma coerulescens* (Bednekoff & Woolfenden, 2003, 2006), pied babblers, *Turdoides bicolor* (Hollen et al., 2011), white-browed sparrow weaver, *Plocepasser mahali* (Walker, York, & Young, 2016) and meerkats, *Suricata suricatta* (Clutton-Brock et al., 1999), dominants act as sentinels significantly more than subordinates. In dwarf mongoose, *Helogale undulata*, Rasa (1986) found that subordinates sentinel more than dominants, but these findings were overturned in Kern, Sumner, and Radford (2016).

These studies did not estimate, however, the second important prediction of the above models, namely comparative energetic levels of dominants and subordinates. This is one of the new aspects of the current study, performed on the Arabian babbler, a cooperatively breeding songbird resident year round along the dry riverbeds of southeastern Israel, in territorial groups of two to 20 individuals of both sexes and all ages (Zahavi, 1989, 1990). By manually feeding as much as they wished dominant and subordinate mature Arabian babblers of both sexes right at the end of their sentinel bouts, and measuring how much they ate relative to their body mass, we obtained a comparative proxy for how low their energetic level declined during the sentinel bout. Together with records of sentinel duration following the manual feeding, as well as sentinel durations and the gaps between them in natural conditions, we were able to better assess the above models for this species. We also recorded whether at the end of the experimental feeding there followed immediately an additional sentinel bout, or rather another type of individual or social activity, pointing out additional dimensions of trade-off.

2 | METHODS

The study was carried out at the Shezaf Nature Reserve in the Arava Valley, in the southeastern part of Israel. The study area, the research population, the Arabian babbler's social system, and our fieldwork methods have been described by Zahavi (1989, 1990), by Ostreher (2001, 2003) and by Ostreher and Heifetz (2016, 2017). The study area contained about 160–260 individuals who lived in 25–32 groups. Regularly, each group was observed at least twice a week, and, in the breeding seasons, almost daily. The nestlings were ringed when they were 10 days old, 4 days before fledging, with four colored rings in a unique combination. The babblers were accustomed to human presence, thus we were able to stay in their vicinity as much as needed.

The morning observation started at first light, few minutes before the descending of the babblers from their roost tree, and lasted three hours. We documented each sentinel activity: the identity of the sentinel, starting and ending time (measured with a stopwatch

with 1 s accuracy), different behaviors during the sentinel activity such as autopreening, changing place and uttering alarm calls, replacement of a sentinel, the last activity before starting a sentinel bout and the first activity after ending it.

An individual was defined as carrying out sentinel activity when it flew up or climbed to a high position above the ground (usually on a tree top), stood steady and looked around without foraging until it left its position. However, during flights babblers use to stop on treetops for a while, either for looking ahead or for resting, and then continue to fly. To avoid confusion, babblers were considered as sentinels only when they stayed on the tree top at least 60 s. An additional 3-hr observation was carried out in the afternoon, ending at darkness, when the babblers set to their night roost. The study is based on both natural observations and a feeding experiment.

2.1 | Natural observations

The observations were performed in 12 groups. In each group, four adult birds (adult means older than two years) had been chosen as focal birds: The dominant male, the dominant female, the most subordinate adult male, and the most subordinate adult female. In the Arabian babbler's social system, for each sex elder babblers are dominant over younger ones, even within the same brood (Ostreiher, 1997, 2001; Zahavi, 1990). We verified their dominance hierarchy by documenting aggressive–submissive interactions between the group members, and saw no exceptions. Group size varied between six and 11: Three groups were composed of six individuals, four groups of seven individuals, three groups of eight individuals, one group of nine individuals, and one group of 11 individuals. A total of 10 groups contained in addition to the focal birds one to five adults. A total of eight groups contained fledglings (younger than 1 year old) and/or yearlings (younger than 2 years old). Only the four focal babblers were tested in this study.

For each of the four focal birds, we measured the duration of two subsequent sentinel bouts, starting with the second sentinel bout after our arrival, in order to let the babblers to get used to our presence. We also measured the duration of the gap between these two subsequent sentinel bouts. We repeated these observations during three subsequent days. In each class (dominant male, subordinate male, dominant female, subordinate female), for half of the individuals two repetitions were performed in the morning and one repetition in the afternoon, and for the other half one repetition was performed in the morning and two repetitions in the afternoon. We measured, therefore, the duration of 288 sentinel bouts (12 groups, four focal babblers, two sentinel bouts per bird, 3 days) and 144 periods of time between two subsequent sentinel bouts ($12 \times 4 \times 3$). The rest of the time was used to learn the relationships between the group members in order to manage the experiment efficiently (see below). For each group, the natural observations were completed within 4–8 days. With each group, we completed the natural observations before starting the experiment.

2.2 | Feeding experiment

The experiment was carried out in the same 12 groups. Immediately after descending of a focal babbler from a sentinel bout, it was attracted to the scale, weighed, and obtained from our hand one mealworm after the other, as many as it was willing to eat. We pre-weighed each mealworm separately before offering it to the babbler. We used two species of mealworms: The yellow mealworm, *Tenebrio molitor*, and superworm, *Zophobas morio*. After eating as many mealworms as they wanted, the focal babblers moved away. We categorized their ensuing behavior to 4 classes: Climbing up and starting a new sentinel bout, mutual interaction (such as allopreening or play), personal well-being behavior (such as autopreening or resting inside a bush or a tree) and foraging in some distance from the scale, ignoring additional mealworms that were offered. We recorded also the time until the start of the next sentinel bout of the focal babbler, as well as its length. The experiment had two stages: pre-experiment and the experiment itself.

2.3 | Stage 1: Pre-experiment

The four focal babblers in each of these 12 groups had been trained to get up onto a digital top-pan scale (And, model HL-200i, accuracy 0.1 g) in order to obtain mealworms. In this way, we could weigh both the babblers and the mealworms that were given as food. The babblers were already habituated to close human presence, but there were huge differences between individuals. Some of them were already used to take a mealworm directly from a human's hand, while others did not dare to approach closer than 5 m from the observer. This stage of habituating the focal babblers to stay steady on the scale for at least one minute, and accepting mealworms directly from our hand, allowing us to weigh the babbler and to give the food to the focal bird alone, lasted between a week up to 4 weeks per group, visiting and training the babblers daily. During this stage, we gave up one group in which we failed to train a subordinate female and chose another group instead of it. In each group, we completed this stage before starting the experiment itself.

2.4 | Stage 2: Feeding experiment

As mentioned above, immediately after descending of a focal babbler from a sentinel bout, it was attracted to the scale, weighed and obtained as many mealworms as it was willing to eat. Three repetitions were carried out for each focal bird, with at least 1 day gap between subsequent repetitions. With each group, we performed only one repetition per day, either in the first three hours of the morning or in the last three hours of the afternoon, before night roosting. As in the natural observations part of the study, for half of the individuals of each class two repetitions were performed in the morning and one repetition in the afternoon, and for the other half one repetition was performed in the morning and two repetitions in the afternoon. When we started to work with a group, we worked with it daily, and there was a gap of about

TABLE 1 The duration of sentinel bouts, in minutes, in natural conditions and following supplemental food, \pm SD

	Natural conditions	Feeding experiment	Time difference between feeding experiment and natural conditions
Dominant males (N = 12)	10.9 \pm 3.2	11.9 \pm 3.1	0.9 \pm 1.7
Subordinate males (N = 12)	9.1 \pm 2.1	10.6 \pm 2.3	1.4 \pm 1.3
Dominant females (N = 12)	7.9 \pm 1.6	8.9 \pm 1.9	1.0 \pm 0.8
Subordinate females (N = 12)	5.2 \pm 1.4	9.0 \pm 1.7	3.8 \pm 0.6
All babblers (N = 48)	8.3 \pm 3.0	10.1 \pm 2.6	1.8 \pm 1.7

24 hr between subsequent repetitions. For each group, we needed about 3–6 weeks in order to complete 12 successful repetitions. In most cases, we worked with two groups in parallel, performing one repetition with one group in the morning and a second repetition with another group in the afternoon.

During the experiment, many repetitions failed. In many cases, after descending from a sentinel position, the focal babbler ignored us, flew further away for foraging or started a social interaction with other group members. We considered a repetition as successful when we succeeded to see the focal bird continuously from the start of a sentinel bout, through descending from the sentinel position and until the beginning of its first activity following our feeding, the babbler came to the scale immediately after descending from the sentinel position without eating anything else except what we gave it, and it could eat without disturbance of its group mates. In order to test each bird three times and achieve a total of 144 successful repetitions (12 groups, four babblers per group, three repetitions per bird), we repeated the experiment more than 430 times. The most frequent reason for failure of a repetition was the disturbance of group mates to the focal bird to obtain mealworms. A total of 41 repetitions failed when a raptor flew above us, causing all group members to climb up to treetops, and 26 repetitions failed when the group members reacted to vocalization or approach of a neighboring group and flew toward them.

The study has been completed in winters, when babblers were not busy with breeding, they did not need to allocate part of their food to their offspring, and their body mass (Anava, Kam, Shkolnik, & Degen, 2000) as well as their sentinel rate (Wright et al., 2001a) were both higher than in summer. When we started to work with a group, we worked with it continuously from the beginning of the natural observations (4–8 days per group), through the pre-experiment stage (7–28 days per group) till the end of the experiment (21–42 days per group). We completed each stage before starting the following one. On average, we worked with each group 41.6 ± 11.7 days. (range

32–78 days). The study was performed during five winters of 2009–2010 through 2014–2015, and we worked with two or three groups each winter.

2.5 | Statistical analysis

Wilcoxon signed rank tests were conducted to test differences between natural conditions and following supplemental feeding regarding (a) the duration of sentinel bouts and (b) the time gap between consecutive sentinel bouts. For the duration of sentinel bouts, Mann–Whitney tests were conducted to examine differences between dominants and subordinates and between males and females in each condition separately.

Generalized estimating equation (GEE) full models were used to examine the effects of sex and rank on the differences between natural conditions and following supplemental feeding regarding (a) the duration of sentinel bouts, (b) the time gap between sentinel bouts, and also, in the experiment, and (c) Worms mass/Babbler mass ratio. In each model, the dependent variable was predicted using Sex and Rank as fixed effects, as well as the interaction between them. Individual ID, Group ID, and Replication were entered as random effects. In addition, to control for possible influence of sentinel timing (morning vs. afternoon) and group size, these variables were also entered to the GEE models as co-variables.

Because the study was carried out over five years, we conducted a preliminary test to check whether the babblers' behavior differed among years, using analysis of variance. All analyses (duration of sentinel bouts in natural conditions and following supplemental food, the difference in the gap between two subsequent sentinel bouts, between natural conditions and following experimental feeding, babblers' weight before experimental feeding and weight of food intake in the experiment) were non-significant: Therefore, the years were not entered as factors in the GEE models.

We also carried out a preliminary test whether the presence of fledglings/yearlings who may require adults' attention affects the focal babblers' behavior, using analysis of variance. Fledglings/yearlings presence was not found to be correlated with duration of sentinel bouts in natural conditions ($p = 0.31$) or following supplemental food ($p = 0.66$), with the difference in the gap between two subsequent sentinel bouts, between natural conditions and following experimental feeding ($p = 0.18$), with babblers' weight before experimental feeding ($p = 0.37$), and with the weight of food intake in the experiment ($p = 0.41$). Therefore, the presence of fledglings/yearlings was not entered as a factor in the GEE models.

We ran a logistic regression mixed model testing whether or not the first behavior after the experimental feeding was a new sentinel bout, with sex, rank and the interaction among them as fixed effects, and individual ID, group ID, replication, sentinel timing, and group size as random terms. Statistical analyses were conducted using SPSS version 24.

3 | RESULTS

3.1 | The duration of sentinel bouts in natural conditions and following supplemental food

The average duration of sentinel bouts following supplemental feeding was significantly longer than its duration in natural conditions (Wilcoxon signed rank test: $Z = 3.70$, $p < 0.001$) (Table 1).

In natural conditions, males sentineled longer than females (Mann-Whitney test: $U = 23.0$, $p < 0.001$), and dominants sentineled longer than subordinates (Mann-Whitney test: $U = 152.0$, $p = 0.005$). In the experiment, males sentineled longer than females (Mann-Whitney test: $U = 82.0$, $p < 0.001$), but dominants did not sentinel differently than subordinates (Mann-Whitney test: $U = 224.0$, $p = 0.5$).

Subordinates increased their sentinel duration in reaction to additional food significantly more than dominants ($F_{1,42} = 5.42$, $p < 0.05$). Both males and females increased their sentinel duration similarly in reaction to additional food, and the difference between the sexes was not significant ($F_{1,42} = 0.87$, $p = 0.88$). In addition, no interaction effect was found between sex and rank; that is, no different pattern of duration of sentinel bouts in reaction to additional food was found between males and females among both subordinates and dominants ($F_{1,42} = 0.75$, $p = 0.46$).

3.2 | The time gap between two subsequent sentinel bouts

The average time gap between two subsequent sentinel bouts following supplemental feeding was significantly shorter than its duration in natural conditions (Wilcoxon signed rank test: $Z = 5.91$, $p < 0.001$) (Table 2).

TABLE 2 The time gap, in minutes, between two subsequent sentinel bouts in natural conditions and following supplemental food, \pm SD

	Natural conditions	Feeding experiment	Time difference between feeding experiment and natural conditions
Dominant males (N = 12)	64.1 \pm 14.2	11.4 \pm 5.9	52.7 \pm 13.1
Subordinate males (N = 12)	75.2 \pm 13.8	10.6 \pm 4.3	64.6 \pm 13.9
Dominant females (N = 12)	80.1 \pm 18.1	11.4 \pm 5.3	68.5 \pm 19.7
Subordinate females (N = 12)	102.8 \pm 14.5	11.2 \pm 4.4	91.6 \pm 15.0
All babblers (N = 48)	80.5 \pm 20.8	11.2 \pm 5.1	69.4 \pm 21.0

The difference between natural conditions and the experiment in the gap between consecutive sentinel bouts was larger for females in comparison with males ($F_{1,42} = 26.31$, $p < 0.001$). In addition, the gap between two subsequent sentinel bouts was larger for subordinates in comparison with dominants ($F_{1,42} = 15.58$, $p < 0.001$). However, no interaction effect was found for sex and rank; that is, no different pattern of duration of gap between two subsequent sentinel bouts was found for males and females among subordinates and dominants ($F_{1,42} = 1.87$, $p = 0.20$).

3.3 | Babblers' weight and food intake in the experiment

In the experiment, the babblers' body mass at the end of their sentinel bout, the consumed worms' mass and the ratio between them, in %, are presented in Table 3.

No difference was found between females and males ($F_{1,42} = 2.83$, $p = 0.10$). However, a main effect for rank was found ($F_{1,42} = 9.53$, $p < 0.001$). Worms mass/Babbler mass ratio was larger among subordinates in comparison with dominants. When food was abundant and competition was avoided, subordinates ate more than dominants in relation to their body mass.

No interaction effect was found for sex and rank; that is, no different pattern of the ratio between body mass and consumed food mass was found for males and females among both subordinates and dominants ($F_{1,42} = 1.10$, $p = 0.27$).

3.4 | The first behavior after feeding

After eating and moving away from the experimenter, the babbler's first behavior was defined according to four categories: climbing up and starting a sentinel bout, mutual interaction with another group member, personal well-being behavior and foraging (Table 4). Among those, starting a sentinel bout was carried out more often than all other three potential behaviors together (61.8% vs. 38.2%).

To establish a binary model, behaviors were classified into two categories—climbing up and starting a sentinel bout in one category,

TABLE 3 The babblers' average body mass and the consumed worms' body mass, \pm SD

	Babbler body mass, g	Worms body mass, g	% Worms mass/babbler mass
Dominant males (N = 12)	79.1 \pm 3.2	3.9 \pm 0.7	4.9 \pm 0.8
Subordinate males (N = 12)	77.4 \pm 4.0	4.4 \pm 0.8	5.7 \pm 1.0
Dominant females (N = 12)	72.3 \pm 4.6	3.5 \pm 0.5	4.8 \pm 0.7
Subordinate females (N = 12)	71.0 \pm 3.6	3.7 \pm 0.7	5.2 \pm 0.9
All (N = 48)	74.9 \pm 5.1	3.8 \pm 0.8	5.1 \pm 0.9

TABLE 4 The first behavior after the experimental feeding (number of events)

	Sentinel (%)	Mutual interaction (%)	Personal well-being (%)	Foraging (%)	Total
Dominant males (N = 12)	24 (66.7)	4 (11.1)	3 (8.3)	5 (13.9)	36
Subordinate males (N = 12)	23 (63.9)	5 (13.9)	4 (11.1)	4 (11.1)	36
Dominant females (N = 12)	21 (58.3)	6 (16.7)	6 (16.7)	3 (8.3)	36
Subordinate females (N = 12)	21 (58.3)	10 (27.8)	2 (5.6)	3 (8.3)	36
All (N = 48)	89 (61.8)	25 (17.4)	15 (10.4)	15 (10.4)	144

and all other types of behavior in the other category. Results did not show effects for sex (OR = 2.55, 95% CI [0.06, 101.32], $p = 0.272$), for rank (OR = 2.12, 95% CI [0.78, 22.74], $p = 0.314$) or the interaction between them (OR = 0.28, 95% CI [0.03, 3.29], $p = 0.42$).

4 | DISCUSSION

Our findings in the natural observations and in the experiment enable us to assess the theoretical predictions in McNamara and Houston (1994). In one of their models, each individual must survive and reach some critical energetic level at the end of a defined time interval (e.g., from dawn to dusk). Hence, in this model more efficient foragers, who attain more food per unit of time in the riskier but food-abundant patch, reach the needed critical energy level in less time, and have more time to spend in the safer patch with no food (p. 989, equation 14).

In a second model presented in the same paper, attaining a higher energetic level at the end of the defined time interval implies higher fitness (in contrast with the first model, where additional energy level increases beyond the critical level do not enhance fitness further). The prediction of this second model is that more efficient foragers will forage mildly more in the riskier patch and maintain a higher energetic level (when they survive), whereas less efficient foragers, for whom additional time in the riskier patch is less effective in increasing their energetic level, resort mildly more to the safe haven (p. 992, equation 17), thus increasing their fitness via enhanced survivability rather than by further increases in their energetic levels.

When applying these models to the case of dominants and subordinates, dominants are the more efficient foragers, because they have priority in access to food and they sometimes take over food items collected by subordinates. We found that dominants' sentinel

bouts are longer (Table 1, left column) and with shorter gaps between them (Table 2, left column), leaving them less time for foraging, in line with the predictions of the first model but not of the second.

At the same time, we also found that at the end of sentinel bouts subordinates ate significantly more relative to their own body mass than did dominants. This is an indication that subordinates ended their sentinel bouts at a lower energetic state than did dominants (Table 3, right column). This comparative indication may be less relevant in incidences in which babblers turned to forage right after feeding on mealworms, but these constituted only 10.4% of the cases, and were distributed almost equally between dominants and subordinates (Table 4).

This indication on comparative energetic levels is in line with the second theoretical model, which predicts higher energetic levels of the more efficient foragers. However, this finding does not yield support to the first model which predicts that both types will aim at the same energetic levels, leading them to attain toward sunset just the critical energetic level to pass the night.

To sum up, our findings provide partial support for each of the two models, but corroborate none of them in full.

After feeding on mealworms as much as they wished, subordinates expanded their sentinel bouts significantly more than dominants in comparison with natural conditions. In particular, following experimental feeding subordinates' sentinel activity was not oppressed or limited (Dattner, Zahavi, & Zahavi, 2015) by dominants' behavior toward them.

Unlike in Bell, Radford, Smith, Thompson, and Ridley (2010) and as in Clutton-Brock et al. (1999), Wright, Maklakov et al. (2001) and Clutton-Brock et al. (2002), our experimental design did not include an additional control treatment of feeding each focal babbler with a single mealworm. Despite the additional information that such a control could have provided, for example, on the potential effect of the interaction with the experimenter, adding such a control would not have been feasible given the already demanding design described above in the methods section, in particular completing the ad libitum feeding treatment for all four focal individuals following the completion of the natural observations for them, all within the same winter to avoid seasonal effects. Our finding that experimental feeding shortened significantly the time gap to the next sentinel bout (Table 2, right column) is in line with the findings in the above-mentioned studies.

Sentinel activity is impeded by different factors: hunger, self well-being behaviors (such as resting and autopsyching), mutual physical interactions (such as allopreening, play and antagonist interactions with group mates), breeding activities, and presence of another sentinel. On the other hand, sentinel behavior is enhanced by danger (Ridley, Raihani, & Bell, 2010), close presence of foreign babblers (floaters or neighboring groups) and apparently also by the need to gather additional information (such as the behavior of other group members, the behavior of other animals, the behavior of neighboring groups, change in weather and maybe also the behavior of the human observer). Our findings indicate that while hunger

is the main factor that impedes sentinel activity, social interaction (and, in particular, maintaining hegemony for the dominant) is an important factor as well. Further studies will be needed to assess the trade-off among such additional activities vis-à-vis sentinel activity.

The fact that subordinates, who face difficulties in achieving food in comparison with dominants, nevertheless allocate time for sentineling even at relatively low energetic states indicates the importance of sentinel activity also for them. It therefore seems that gathering all kinds of information available from the sentinel position, serves, first and foremost, the sentinel itself. This stands in line with the finding that floater babblers, with no group mates around and moving between foreign territories, act as sentinels to a similar extent, irrespective of their sex and their rank in their original group (Ostreiher & Heifetz, 2017). It also stands in line with the finding that meerkat males increase their guarding before dispersal and reduce it once they establish themselves in a new group, apparently in order to collect information about potential mates in the surroundings (Clutton-Brock et al., 2002). Our findings also support both the safe selfish sentinel hypothesis and the state-dependent sentinel hypothesis (Bednekoff, 1997, 2001; Clutton-Brock et al., 1999; Wright et al., 2001b; Wright, Maklakov et al., 2001).

To conclude, we suggested an experimental approach to compare energetic states of different individuals, and used it together with measurements of sentinel duration and frequency to test the predictions of theoretical models regarding the trade-off between sentineling and foraging for dominants and subordinates.

ACKNOWLEDGEMENTS

R.O. is grateful to the Society for Protection of Nature in Israel (SPNI) and Hazeva Field Study Center for hosting the research project. R.O. is also grateful to Avner Anava, Yoel Perel, Amir Kalishow, Yuval Dagay, and Arnon Datner for field assistance. We are grateful to Yaron Sela for his statistical advice. Lastly, we are deeply grateful to Walter Koenig, Sjouke Kingma and to an anonymous referee for their useful and inspiring comments.

ORCID

Roni Ostreiher  <https://orcid.org/0000-0002-2841-2491>

REFERENCES

- Anava, A., Kam, M., Shkolnik, A., & Degen, A. A. (2000). Seasonal field metabolic rate and dietary intake in Arabian babbler (*Turdoides squamiceps*) inhabiting extreme deserts. *Functional Ecology*, 14, 607–613.
- Bednekoff, P. A. (1997). Mutualism among safe, selfish sentinels: A dynamic game. *American Naturalist*, 150, 373–392. <https://doi.org/10.1086/286070>
- Bednekoff, P. A. (2001). Coordination of safe, selfish sentinels based on mutual benefits. *Annales Zoologici Fennici*, 38, 5–14.
- Bednekoff, P. A. (2015). Sentinel behavior: A review and prospectus. In M. Naguib, L. Barrett, S. Healy, L. W. Simmons, P. J. B. Slater, & H. J. Brockmann (Eds.), *Advances in the study of behavior* (Vol. 47, pp. 115–146). San Diego, CA: Academic Press.
- Bednekoff, P. A., & Woolfenden, G. E. (2003). Florida scrub-jays (*Aphelocoma coerulescens*) are sentinels more when well-fed (even with no kin nearby). *Ethology*, 109, 895–904. <https://doi.org/10.1046/j.0179-1613.2003.00926.x>
- Bednekoff, P. A., & Woolfenden, G. E. (2006). Florida scrub-jays compensate for the sentinel behavior of flockmates. *Ethology*, 112, 796–800. <https://doi.org/10.1111/j.1439-0310.2006.01227.x>
- Bell, M. B. V., Radford, A. N., Smith, R. A., Thompson, A. M., & Ridley, A. R. (2010). Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. *Proceedings of the Royal Society of London B*, 277, 3223–3228.
- Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S., & Manser, M. (1999). Selfish sentinels in cooperative mammals. *Science*, 284, 1640–1644. <https://doi.org/10.1126/science.284.5420.1640>
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z., & McIlrath, G. M. (2002). Evolution and development of sex differences in cooperative behavior in meerkats. *Science*, 297, 253–256. <https://doi.org/10.1126/science.1071412>
- Dattner, A., Zahavi, A., & Zahavi, A. (2015). Competition over guarding in the Arabian Babbler (*Turdoides squamiceps*), a Cooperative Breeder. *F1000Research*, 4, 618. <https://doi.org/10.12688/f1000research.6739.1>
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, 7, 1–52.
- Hollen, L. I., Bell, M. B. V., Wade, H. M., Rose, R., Russell, A., Niven, F., ... Radford, A. N. (2011). Ecological conditions influence sentinel decisions. *Animal Behaviour*, 82, 1435–1441. <https://doi.org/10.1016/j.anbehav.2011.09.028>
- Kareksela, S., Harma, O., Lindstedt, C., Siitari, H., & Suhonen, J. (2013). Effect of willow tit *Poecile montanus* alarm calls on attack rates by pygmy owls *Glaucidium passerinum*. *Ibis*, 155, 407–412.
- Kern, J. M., Sumner, S., & Radford, A. N. (2016). Sentinel dominance status influences forager use of social information. *Behavioral Ecology*, 27, 1053–1060. <https://doi.org/10.1093/beheco/arv240>
- Kingma, S. A., Santema, P., Taborsky, M., & Komdeur, J. (2014). Group augmentation and the evolution of cooperation. *Trends in Ecology & Evolution*, 29, 476–484. <https://doi.org/10.1016/j.tree.2014.05.013>
- Kokko, H., Johnstone, R. A., & Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London B*, 268, 187–196.
- McGowan, K. J., & Woolfenden, G. E. (1989). A sentinel system in the Florida scrub jay. *Animal Behaviour*, 34, 1000–1006. [https://doi.org/10.1016/0003-3472\(89\)90144-9](https://doi.org/10.1016/0003-3472(89)90144-9)
- McNamara, J. M., & Houston, A. I. (1994). The effect of a change in foraging options on intake rate and predation rate. *American Naturalist*, 144, 978–1000. <https://doi.org/10.1086/285721>
- Ostreiher, R. (1997). Food division in the Arabian babbler nest: Adult choice or nestling competition? *Behavioral Ecology*, 8, 233–238.
- Ostreiher, R. (2001). The importance of nestling location for obtaining food in open cup-nests. *Behavioral Ecology and Sociobiology*, 49, 340–347. <https://doi.org/10.1007/s002650000308>
- Ostreiher, R. (2003). Is mobbing altruistic or selfish behaviour? *Animal Behaviour*, 66, 145–149.
- Ostreiher, R., & Heifetz, A. (2016). The blessing of having younger nestmates: The case of the Arabian Babbler. *Behavioral Ecology*, 27, 393–400. <https://doi.org/10.1093/beheco/arv161>
- Ostreiher, R., & Heifetz, A. (2017). The sentinel behaviour of Arabian babbler floaters. *Royal Society Open Science*, 4, 160738. <https://doi.org/10.1098/rsos.160738>
- Rasa, O. A. E. (1986). Coordinated vigilance in dwarf mongoose family groups: The 'watchman's song' hypothesis and the costs of guarding. *Ethology*, 71, 340–344. <https://doi.org/10.1111/j.1439-0310.1986.tb00598.x>

- Ridley, A. R., Nelson-Flower, M. J., & Thompson, A. M. (2013). Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour*, 85, 137–142.
- Ridley, A. R., Raihani, N. J., & Bell, M. B. V. (2010). Experimental evidence that sentinel behavior is affected by risk. *Biology Letters*, 6, 445–448.
- Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science*, 197, 1246–1253. <https://doi.org/10.1126/science.197.4310.1246>
- Walker, L. A., York, J. E., & Young, A. J. (2016). Sexually selected sentinels? Evidence of a role for intrasexual competition in sentinel behavior. *Behavioral Ecology*, 27, 1461–1470. <https://doi.org/10.1093/beheco/arw064>
- Wright, J., Berg, E., de Kort, S. R., Khazin, V., & Maklakov, A. A. (2001a). Cooperative sentinel behaviour in the Arabian babbler. *Animal Behaviour*, 62, 973–979.
- Wright, J., Berg, E., de Kort, S. R., Khazin, V., & Maklakov, A. A. (2001b). Safe selfish sentinels in a cooperative bird. *Journal of Animal Ecology*, 70, 1070–1079.
- Wright, J., Maklakov, A. A., & Khazin, V. (2001). State-dependent sentinels: an experimental study in the Arabian babbler. *Proceedings of the Royal Society of London B*, 268, 821–826.
- Zahavi, A. (1989). The Arabian babbler. In I. Newton (Ed.), *Lifetime reproduction in birds* (pp. 253–275). London, UK: Academic Press.
- Zahavi, A. (1990). Arabian babblers: The quest for social status in a cooperative breeder. In P. B. Stacey, & W. D. Koenig (Eds.), *Cooperative breeding in birds* (pp. 103–130). London, UK: Cambridge University Press.
- Zahavi, A., & Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. Oxford, UK: Oxford University Press.

How to cite this article: Ostreier R, Heifetz A. The sentinel—Foraging trade-off in dominant and subordinate Arabian babblers. *Ethology*. 2019;125:98–105. <https://doi.org/10.1111/eth.12833>