



On the self-regulation of sentinel activity among Arabian babbler groupmates



Roni Ostreihier^{a,*}, Roger Mundry^b, Aviad Heifetz^c

^a Department of Life Science, The Open University of Israel, Raanana, Israel

^b Platform Bioinformatics and Biostatistics, VetMedUni, Vienna, Austria

^c Department of Management and Economics, The Open University of Israel, Raanana, Israel

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In many cooperatively breeding species, one of the group members (called a sentinel) flies or climbs up occasionally to a high position, looks around and utters alarm calls if a predator approaches, while other group members are foraging. Bednekoff's (1997, *American Naturalist*, 150, 373–392; 2001, *Annales Zoologici Fennici*, 38, 5–14) game-theoretic model assumes that group members trade the need to forage against the advantages of earlier risk detection when sentinelling. The model predicts that in the presence of another sentinel which may provide timely alerts, a sentinel will terminate its sentinel bout earlier when its energy level drops below a threshold that is higher than the depletion threshold that would incentivize it to resume foraging if it were sentinelling alone. We propose a complementary hypothesis, that this effect of shortened sentinel duration in the presence of another sentinel will be more pronounced for subordinate group members, for whom the fierce competition they suffer while foraging gets attenuated when a groupmate sentinels. We tested these hypotheses in Arabian babbler, *Argya squamiceps*, groups by comparing sentinel activity under natural conditions vis-à-vis sentinel activity in a feeding experiment in which one or two individuals were fed. In natural conditions, dominant males not only acted as sentinels longer and more often, but they also initiated a larger share of their sentinel bouts when another group member was already on guard. Following experimental feeding ad libitum, in line with the game-theoretic predictions (1) the probability of starting a sentinel bout was not affected by the presence of another sentinel, nor by its sex or rank, and (2) sentinel bouts that terminated in the presence of another sentinel were significantly shorter than sentinel bouts ending alone. Our findings suggest that the seemingly systematic exchange of sentinels may be a consequence of differential needs and incentives rather than active coordination.

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Sentinel behaviour has been widely studied in many species of group-living animals (Bednekoff, 2015). Yet, the interactions between successive sentinels still pose unresolved questions. Does a successive sentinel actively replace the previous one, or do both the incumbent and the new sentinel each decide when to start and end their sentinel bout based on their own incentives?

Bednekoff (1997, 2001) proposed a state-variable game-theoretic model, symmetric across all group members, in which group members trade the need to forage against the advantages of earlier risk detection when sentinelling. The model predicts that at equilibrium, the decision to start or terminate a sentinel bout depends on the energetic level of the individual, as well as on whether some other group member already sentinels.

One of the model's predictions is that fully satiated group members will climb up to sentinel irrespective of whether another sentinel is already on guard. A second prediction of the model is that in the presence of another sentinel that is also likely to provide timely alerts, a sentinel that started off fully satiated will terminate its sentinel bout earlier when its energy level drops below a threshold that is higher than the depletion threshold below which hunger would incentivize it to forage if it were sentinelling alone. We conjectured that, additionally, this effect of shortened sentinel duration in the presence of another sentinel is more substantial for subordinate group members, for whom the fierce competition they suffer while foraging becomes less intense when a groupmate sentinels.

We set out to test some aspects of these predictions in the Arabian babbler, *Argya squamiceps*, in an experiment in which two foragers were successively fed ad libitum. The Arabian babbler is a

* Corresponding author.

E-mail address: ronio@arava.co.il (R. Ostreihier).

cooperatively breeding songbird, resident in dry riverbeds along the Rift Valley, and studied intensively in Israel. Their ecology, social organization and sentinel behaviour have already been described (Dattner, Zahavi, & Zahavi, 2015; Edelaar & Wright, 2006; Naguib et al., 1999; Ostreiher & Heifetz, 2017, 2019, 2020; Regosin, 2002; Sommer, 2011; Sommer, Todt, Ostreiher, & Mundry, 2012; Wright, Berg, de Kort, Khazin, & Maklakov, 2001a, b, c; Zahavi, 1989, 1990; Zahavi & Zahavi, 1997 (pp 134–136)). Groups are territorial, composed of 2–22 individuals of both sexes and all ages. Two hierarchical rank orders, usually reflecting age order, exist separately for males and females. Babblers are omnivores, and eat pollen, nectar, fruits, invertebrates and small reptiles. They live in an extreme desert (with less than 30 mm rain per year), their food sources are scattered, and most of their day is dedicated to foraging over large areas. All group members forage simultaneously and close to each other. However, each individual supplies its own needs, and does not, usually, share food with others (except for feeding nestlings and young fledglings). From time to time, dominants shove subordinates aside from plentiful locations, exploit their work and sometimes grab from them food items that they have not consumed immediately. As a consequence, subordinates invest more time in foraging than dominants (Ostreiher, n.d.). Sentinel behaviour is carried out by all group members over 4 months old, and occurs for about 50% of the day (Ostreiher & Heifetz, 2019). Dominants and adult males act as sentinels more frequently and for longer than subordinates and adult females, respectively (Ostreiher & Heifetz, 2017; Wright et al., 2001a).

In this study, we fed Arabian babblers *ad libitum* to investigate the role of the social hierarchy within Bednekoff's model. We predicted that (1) the presence of a sentinel would not prevent a satiated babbler from beginning to sentinel, regardless of their sex and rank, and (2) a sentinel would terminate its sentinel activity sooner after another groupmate set out to sentinel. This phenomenon of shortening the sentinel bout duration would be more pronounced for subordinate group members than for dominant ones.

METHODS

The study was performed with the long-studied population at Hatzeva, Israel. The study area, the research population, the Arabian babbler's social system and our fieldwork methods have been already described (Ostreiher & Heifetz, 2017, 2019; Zahavi, 1989, 1990).

The babblers in the research area are used to close human presence, and all are colour-ringed with a unique combination enabling individual identification.

Following established methods (Ostreiher & Heifetz, 2017, 2019), babblers were considered as sentinels when they stayed on the treetop at least 60 s.

The study was conducted in 10 groups with four focal adults (i.e. at least 2 years old) selected in each: the dominant female, the dominant male, the subordinate adult female and the subordinate adult male. We knew their age (± 1 day) and verified their dominance hierarchy by documenting aggressive–submissive interactions and saw no exceptions. In all 10 groups there were additional yearlings (1–2 years old) or fledglings (up to 1 year old) which were not tested in this study. Group size varied between seven and 11 individuals.

Observation started at first light, when the babblers descended from their roost tree to the ground and continued for 3 h. During this time, we recorded all the sentinel bouts including identity of the sentinel, starting and ending time and physical and vocal interactions with other group members. Each group was observed on

36 days, 3 h per day, equalling a total of 108 h per group and 1080 observation hours for the whole project.

After observing the group for 3 h, we conducted a feeding experiment. As detailed below, on some of the 36 days one individual was fed, and on the others two individuals were fed separately, one after the other.

An individual was fed after it foraged continuously for 10 min. We fed them both the yellow mealworm, *Tenebrio molitor*, and superworm, *Zophobas morio*. Mealworms were offered until the focal babbler stopped eating them and moved away. The number of mealworms eaten was not the main subject of our study, and we therefore present the data in Appendix 1 (and see Tables A1, A2, Fig. A1). We recorded the focal babbler's next behaviour which was one of the four following activities: climbing up and starting to sentinel, initiating mutual interaction (such as allopreening or play), performing personal wellbeing behaviour (such as self-preening or resting inside a bush or a tree) or returning to foraging.

In each group the experiment consisted of two stages (see Table 1 for a summary of the structure of the experiment). In stage A, on one of the mornings, when no sentinel was on guard, one of the following three focal babblers was fed: the dominant female, the subordinate female or the subordinate male. We then recorded which of the four subsequent activities mentioned above it performed. On the previous morning or on the following morning, based on the random number generator in Excel (RANDBETWEEN (1,2)), the dominant male was fed before one of these three focal individuals, with the aim of inducing it to sentinel. We carried out three replicates of a feeding trial for each focal babbler. In about a third of these replicates the dominant male did not start to sentinel after being fed, so the replicate was stopped and a new one was carried out on the following morning, until the dominant male started to sentinel after feeding. In all cases, with each individual involved in the experiment, we performed only one feeding trial per day.

Stage B was identical to stage A, except that here the focal individuals were either the dominant male, the dominant female or the subordinate male, and on days on which two individuals were fed, the first fed individual was the subordinate adult female (Table 1).

The experiment allowed us to check the propensity of each focal babbler to climb up and start to sentinel after eating a lot in the absence versus in the presence of another sentinel, and whether the identity of the current sentinel (dominant male versus subordinate female) influences this propensity.

In each group we carried out 18 replicates over 36 days. Each replicate lasted two mornings, as detailed above. A gap of at least 7 days was kept between two replicates in the same group. The order of the tested babblers was determined randomly, using a random number generator in Excel (RANDBETWEEN (1,18)), so each replicate was scattered randomly among 18 combinations. All the replicates were carried out in the autumn and winter, outside the breeding season and when no fledglings under 6 months old were present, so breeding and parental care could not influence the babblers' decisions to start or to end sentinel activity.

During the experiment we counted the mealworms that each focal babbler ate when it was fed alone and no sentinel was on guard versus when it was fed when another group member, either the dominant male or the subordinate female, was already sentinelling. Because this was not the main subject of our study, we present these data in Appendix 1.

During the observations and the experiment, we documented each sentinel activity: the identity of the sentinel, start and end times (measured with a stopwatch with 1 s accuracy), the reaction of the sentinel when another sentinel climbed up, and interactions between them. The study was conducted over 4 years, from 1

Table 1

The structure of the experiment carried out in each group

Stage	Focal babbler	Day	Fed no. 1	Fed no. 2	No. of replicates
A	Subordinate male	1	Subordinate male	—	3
		2	Dominant male	Subordinate male	
A	Dominant female	3	Dominant female	—	3
		4	Dominant male	Dominant female	
A	Subordinate female	5	Subordinate female	—	3
		6	Dominant male	Subordinate female	
B	Dominant male	7	Dominant male	—	3
		8	Subordinate female	Dominant male	
B	Subordinate male	9	Subordinate male	—	3
		10	Subordinate female	Subordinate male	
B	Dominant female	11	Dominant female	—	3
		12	Subordinate female	Dominant female	

Stage A: feeding a focal individual in the absence of a sentinel versus feeding the same individual when the dominant male already sentinels. Stage B: feeding a focal individual in the absence of a sentinel versus feeding the same individual when the subordinate female already sentinels. Between days 1+2, 3+4, 5+6, 7+8, 9+10 and 11+12, there was a gap of 1 day between replicates. The order of the two feeding trials was determined randomly. Between each pair of feeding trials and the following pair there was a gap of at least 7 days. The order of the 18 pairs was determined randomly across time.

October 2009 to 28 February 2013, completing two or three groups per year.

Statistical Analysis

Sentinel effort under natural conditions (models 1 and 2)

To estimate how much sentinel activity under natural conditions differed between sexes and ranks we fitted two generalized linear mixed models (GLMMs; Baayen, 2008). In the first of these models (fitted with Poisson error structure and log link; McCullagh & Nelder, 1989) we used the number of sentinel bouts as the response (model 1) and in the second (fitted with Gaussian error structure and identity link) the total duration of sentinel activity per observation session as the response (model 2). As fixed effects we included sex and rank and their interaction, and as random intercepts effects we included individual (nested in group) and group identity; since the data were collected simultaneously for all four focal members of the group and on multiple days per group, we included an additional random intercepts effect for observation day nested in group. To keep type I error rate at the nominal level of 0.05 we included random slopes effects (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009) of sex (manually dummy coded and then centred), rank and their interaction within group and of sex and rank within day nested in group. In both models we originally included the correlations between random intercepts and slopes (Barr et al., 2013). However, in model 1 these appeared all to be close to -1 or 1. As this indicates they were not identifiable (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017) we dropped them from the model, which led to a minor decrease in model fit (log-likelihoods, with correlation parameters: -2708.307; without correlation parameters: -2709.326). Since observations generally lasted 3 h, there was no need to control for observation time. To avoid cryptic multiple testing (Forstmeier & Schielzeth, 2011), we compared each of the two full models with a respective null model lacking the fixed effects of rank, sex and their interaction. Overdispersion was not an issue in model 1 (dispersion parameter: 0.502). From model 2 we excluded sentinel durations of zero and log-transformed sentinel durations since otherwise residuals were too heterogeneous (checked by visual inspection of residuals plotted against fitted values). The sample used for these models comprised a total of 1440 bout numbers observed on 360 days nested in group for 40 individuals of 10 groups (model 1) and a total of 1408 bout durations observed on 360 days nested in group for 40 individuals of 10 groups (model 2).

The feeding experiment

To test whether the tested individuals' decisions to act as a sentinel depended on whether another individual was already acting as a sentinel, and, if yes, which one it was, we fitted two GLMMs (Baayen, 2008; models 3 and 4). Since the response was binary (individual began to sentinel: no or yes) we fitted both models with binomial error structure and logit link function (McCullagh & Nelder, 1989).

We fitted one further mixed model with Gaussian error structure and identity link in which we investigated to what extent the duration of sentinel activity bouts depended on whether the bout ended in the presence or absence of another sentinel, and whether the effect of this factor differed between the subordinate female and the dominant male (model 5).

Influence of sentinel's presence on decision to act as sentinel (model 3)

With this model we asked whether the presence of a sentinel influenced the fed individuals' decisions to begin acting as a sentinel. Hence, we included sentinel presence (no or yes) as our key predictor with a fixed effect in this model. Note that with this model we compared the decisions of the individuals when fed first (and alone) versus second since the first individual was fed when there was no sentinel present, but the second individual was fed while there was a sentinel present. We further controlled for the replicate (covariate with values 1, 2 or 3) as well as the sex (female or male) and rank (dominant or subordinate) of the tested individual, and the two-way interaction between these latter two factors by including them as further fixed effects in the model.

To avoid pseudoreplication we included random intercepts effects for the identity of the individual tested (nested in group) and for the group. Furthermore, we included a random intercepts effect for the trial (nested in group) since two individuals had been tested in each trial. To keep type I error rate at the nominal level of 0.05 we included all theoretically identifiable random slopes (Barr et al., 2013; Schielzeth & Forstmeier, 2009), namely those of sentinel presence and replicate within individual ID and those of sex and rank and their interaction as well as sentinel presence and replicate within group ID. Initially we also included the correlation parameters among random intercepts and slopes. However, the majority were estimated to be essentially 1 or -1 which indicates they were unidentifiable (Matuschek et al., 2017) and, furthermore, a model including these correlation parameters and one lacking them had almost identical log-likelihoods (with correlation parameters: -229.879; without correlation parameters: -230.171). Hence, we removed them from the model.

It seemed possible that the difference between a sentinel being absent or present would not be the same in all combinations of sex and rank. Hence, we fitted an additional model (model 3b) into which we included the three-way interaction between sex and rank of the tested individual and sentinel presence (and all interactions this encompassed; we kept the random effects structure as in the original model). The sample for these models comprised 360 observations made in 180 trials, conducted with 40 individuals of 10 social groups, whereby the individual chose to act as a sentinel in 230 experiments.

Influence of sentinel type on decision to act as sentinel (model 4)

For this model we considered only the decisions made when a sentinel was already present, and our key predictor was the type of sentinel present (dominant male or subordinate female) which we included as a fixed effect. As in model 3 we further included fixed effects of replicate, sex and rank of the individual tested and the interaction between these latter two. As random intercepts effects we included the ID of the tested individual (nested in group), the sentinel (nested in group) and the group. The random slopes we included were those of replicate and type of sentinel present within the ID of the tested individual, replicate, rank and sex of the tested individual within sentinel ID, and replicate, rank and sex of the tested individual and their two-way interaction, as well as the type of sentinel within group ID. As in model 3, most of the correlation parameters were essentially -1 or 1 and the log-likelihoods of a model with and without them hardly differed (without correlation parameters: -109.342; with correlation parameters: -108.787), and we present results for the model without them. We also considered including a random intercepts effect for the dyad as each dyad was tested thrice. However, this random effect would in essence be redundant with the random slopes, and hence we opted to include these latter rather than the random intercepts effect of dyad. The sample for these two models consisted of 180 experiments, during which 40 individuals were tested with 20 sentinels in 10 social groups. In 121 experiments the individual tested began to act as a sentinel after it was fed to saturation.

For this model, a three-way interaction between the type of sentinel, rank and sex of the tested individual seemed possible. However, this could not be fitted since not all sex–rank combinations of the tested individual could be tested with both sentinel types (e.g. the dominant male could not be tested while acting as a sentinel). We hence combined all three factors into a single factor with six levels indicating the sex–rank combination of the sentinel and the tested individual and included it in the model (model 4b), replacing type of sentinel as well as rank and sex of the tested individual and their two-way interaction (we kept the random effects structure as in the original model). We then compared this model with model 4 by means of Akaike's information criterion, corrected for small samples (AICc; Burnham & Anderson, 2002). The rationale behind this approach was that if the behaviour of the subordinate male or the dominant female depends on with which type of sentinel they are tested, then the second model would be better at explaining the observed behaviour, leading to a smaller AICc. We used an information criterion for this comparison since neither model is nested in the other.

Sentinelling duration with and without another individual (model 5)

With this final model we investigated the extent to which the duration of sentinel activity was influenced by whether another sentinel was present when the sentinel bout ended and how much this potential influence differed between the subordinate female and the dominant male. More precisely, we analysed the durations of all sentinel bouts (response variable) of these two types of

individuals and modelled them as a function of sentinel type (subordinate female or dominant male), whether the bout ended in the presence or absence of another sentinel ('sentinel presence') and their interaction (all included as fixed effects).

Since we were mainly interested in the effects of sentinel presence and its interaction with sentinel type, we excluded these two terms from the full model to obtain the null model. The random intercepts effects we included were group, individual and trial ID (the latter because in some trials both the subordinate female and the dominant male of a group participated). We included random slopes of sentinel presence, sentinel type and their interaction within group and of sentinel presence within individual. As the estimated correlation between the random intercept and slope within individual was essentially 1 and hence not identifiable, we excluded it from the model, which led to a minor decrease in model fit (log-likelihoods: model with the correlation: 1426.67; without the correlation: -1426.70). The sample used for this model comprised 203 sentinel bout durations of 20 individuals of 10 groups, tested in 147 trials. The five models are summarized in Table 2.

General considerations

We fitted the models in R (version 3.6.1; R Core Team, 2019) using the functions `lmer` or `glmer` of the package `lme4` (version 1.1–21; Bates, Maechler, Bolker, & Walker, 2015). Prior to fitting the models, we z-transformed replicate (if present in the model) to a mean of zero and a standard deviation of one to ease model convergence and achieve more easily compared coefficients. Before including factors as random slopes we manually dummy coded and then centred them. For models 2 and 5 we checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visual inspection of a qq plot of the residuals and residuals plotted against fitted values. This did not reveal any strong violations of these assumptions although residuals were correlated with fitted values, presumably due to shrinkage (Baayen, 2008) which tends to become obvious in the presence of random effects that have many levels with a single observation such as trial ID. For all models we estimated model stability by dropping levels of random effects one at a time and comparing the estimates obtained when fitting the full model to those subsets of data with those obtained for the entire data set. This revealed all models to be of acceptable stability (see Results). We tested the significance of individual effects by means of likelihood ratio tests (Dobson, 2002) comparing the respective full model with models lacking testable terms one at a time (R function `drop1`; Barr et al., 2013). We obtained confidence intervals by means of parametric bootstraps ($N=1000$) which we obtained using the function `bootMer` of the package `lme4`.

Ethical Note

The research was done in the Arabian babbler research site in Hatzeva, Israel, in the babblers' natural habitat. In 10 groups (of 32 in the research area) 40 individuals (out of 260) were fed three times on 3 separate days without physical contact. No other procedures, except observations, were done. The research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research and the requirements of the Nature Reserve Authority in Israel (Permissions No. 32915 and 41723).

RESULTS

Sentinel Effort under Natural Conditions (Models 1 and 2)

The 40 focal babblers performed 5531 sentinel bouts during 1080 h. Of these, 4858 sentinel bouts (87.8%) started when no sentinel was on guard and 673 (12.2%) started when another group

Table 2
Overview of the models fitted

Model	Response	Fixed effects ^a	Random effects ^b	Error structure
1	No. of sentinel bouts	Sex*rank	(1 Subject ID) + (1+sex*rank group ID) + (1+sex+rank observation day)	Poisson
2	Sentinel duration	Sex*rank	(1 Subject ID) + (1+sex*rank group ID) + (1+sex+rank observation day)	Gaussian
3	Begins to act as sentinel (no/yes)	Sentinel presence (no/yes) + <i>sex*rank</i> + <i>replicate</i>	(1+Sentinel presence (no/yes) + replicate Subject ID) (1 Sentinel presence (no/yes) + replicate + sex*rank group ID) + (1 trial ID)	Binomial
3b	Begins to act as sentinel (no/yes)	Sentinel presence (no/yes)*sex*rank + replicate	(1+Sentinel presence (no/yes) + replicate Subject ID) (1 Sentinel presence (no/yes) + replicate + sex*rank group ID) + (1 trial ID)	Binomial
4	Begins to act as sentinel (no/yes)	Sentinel type (dominant male/subordinate female) + <i>sex*rank</i> + <i>replicate</i>	(1+Sentinel type+replicate subject ID)+ (1+sex*rank + replicate sentinel ID)+ (1+Sentinel type (dominant male/subordinate female) + sex*rank + replicate group ID)	Binomial
4b	Begins to act as sentinel (no/yes)	Sex rank combination of subject and sentinel	(1+Sentinel type+replicate subject ID)+ (1+sex*rank + replicate sentinel ID)+ (1+Sentinel type (dominant male/subordinate female) + sex*rank + replicate group ID)	Binomial
5	Duration of sentinel bout	Sentinel presence (when the bout is terminated; no/yes)* <i>sentinel type</i> (dominant male/subordinate female)	(1+how ended subject ID)+ (1+how ended*sentinel type group ID)+ (1 trial ID)	Gaussian

^a Fixed effects only included to control for their potential effects and hence kept in the respective null model are depicted in italics; asterisks denote an interaction and all lower order terms it encompasses (e.g. A*B*C corresponds to the main effects of A, B and C, the three two-way interactions A*B, A*C and B*C and the three-way interaction between A, B and C); models 3b and 4b were not compared with a respective null model.

^b Random effects are denoted in the lme 4 specific way, that is, (1+A+B|C) denotes a random intercepts effect of C, random slopes of A and B within C and parameters for the correlations among all random intercepts and slopes, whereas (1+A+B|C) means that the correlation parameters are not included.

member was already sentinel. All four focal babblers initiated sentinel bouts when others were already sentinels, and new sentinel bouts started during the sentinel bouts of all four (Table 3).

During the 1080 observation hours, a sentinel was present for 553.8 h (51.3%). Of these hours, in 475.2 (85.8%) there was only one sentinel at a time, in 58.6 (10.6%) there were two sentinels at the same time and in 20.0 (3.6%) there were more than two sentinels at the same time (Fig. 1).

Both the number of sentinel bouts and their total duration were clearly influenced by sex and rank (full–null model comparisons, likelihood ratio tests, number of bouts (model 1): $\chi^2_3=92.387$, $P<0.001$; total duration (model 2): $\chi^2_3=46.682$, $P<0.001$), and in both models the interaction was clearly significant (number of bouts: $\chi^2_1=16.955$, $P<0.001$; total duration: $\chi^2_1=16.309$, $P<0.001$). More specifically, males sentinelled more than females of the same rank, and in subordinates this difference between the sexes was more pronounced (Fig. 2; for details see Tables A3, A4 in Appendix).

The Feeding Experiment

After eating as much as they chose (the number of worms eaten by the focal babblers is presented in Fig. A1 in Appendix 1), the focal

babblers climbed up and started to sentinel in 230 cases (63.9% of 360 replicates), initiated a mutual interaction with another group member in 81 cases (22.5%), started a wellbeing behaviour in 42 cases (11.7%) or returned to foraging in seven cases (1.9%).

Probability of Acting as a Sentinel (Models 3 and 4)

Overall, we did not find any obvious evidence for sentinel presence (no or yes) or the type of sentinel (subordinate female or dominant male) affecting the probability of beginning to act as a sentinel. More specifically, whether a sentinel was present or not did not obviously affect the probability of beginning to act as a sentinel (model 3; Fig. 3a, Table A5 in Appendix 2). The type of sentinel also did not strongly influence the probability of individuals beginning to act as a sentinel, although there was a marginally nonsignificant tendency for individuals to be less likely to act as a sentinel when the current sentinel was the subordinate female (model 4; Fig. 3b, Table A6 in Appendix 2). In both models, the interaction between sex and rank was not significant whereas replicate was significant in model 3.

Including the interaction between sentinel presence, sex and rank of the tested individual in model 3 (model 3b) did not reveal

Table 3
Number of sentinel events that started when another sentinel was already on guard

Second sentinel	Total no. of sentinel bouts	First sentinel				
		Dominant male	Dominant female	Subordinate male	Subordinate female	Total
Dominant male	1887	X	119	108	56	283 (15.0)
Dominant female	1400	89	X	43	23	155 (11.1)
Subordinate male	1440	93	51	X	17	161 (11.2)
Subordinate female	804	39	14	21	X	74 (9.2)
Total	5531	221 (11.7)	184 (13.1)	172 (11.9)	96 (11.9)	673 (12.2)

The rows show how many times a certain individual started to sentinel as a second sentinel when another group member was already on guard. The columns show how many times another sentinel started to sentinel when that individual was already on guard. Percentages are given in parentheses.

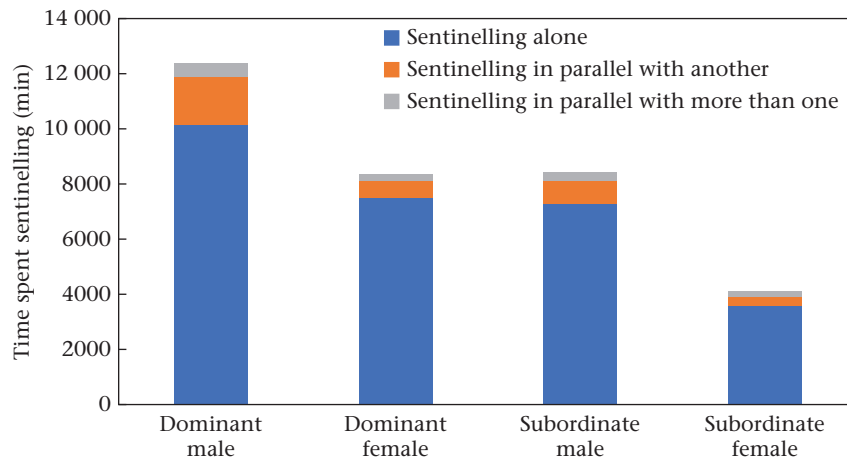


Figure 1. Time spent by dominant and subordinate males and females sentinelling alone and in parallel with others, out of 33 231 min (553.8 h).

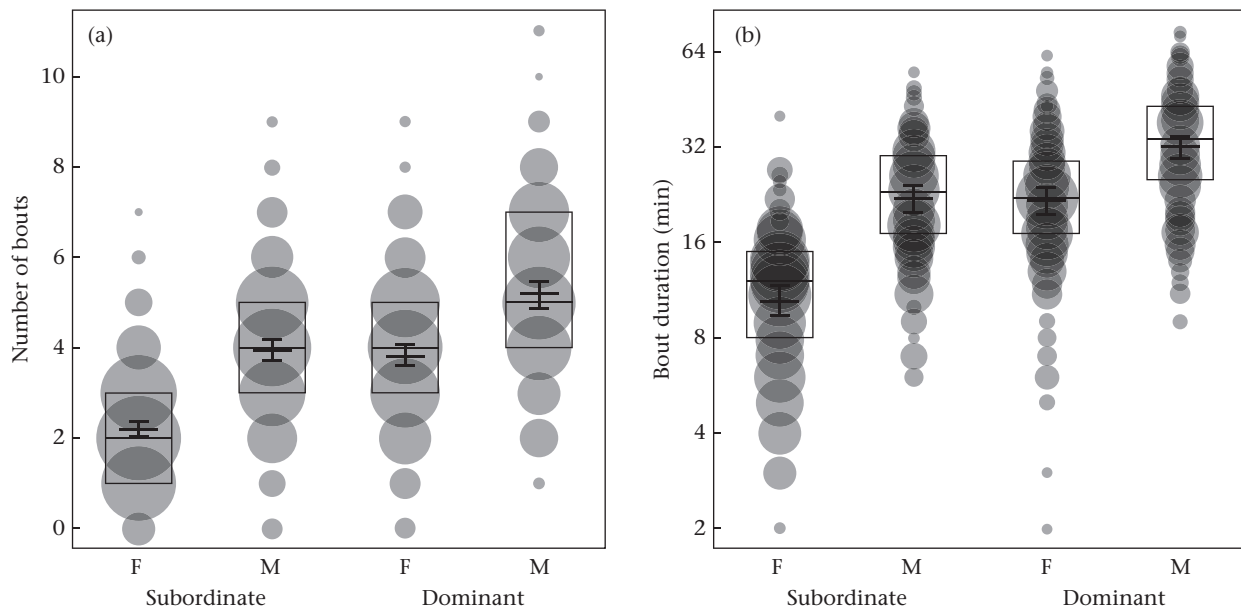


Figure 2. Sentinel effort in terms of (a) number of bouts (model 1) and (b) total bout duration (min; model 2) per 3 h observation period for dominant and subordinate females (F) and males (M). Dots depict the raw data (dots) whereby larger dots depict tied observations (range of number of observations per dot: (a) 1–114; (b) 1–30). Horizontal lines and boxes indicate medians and quartiles and thick horizontal lines with error bars depict the fitted model and its confidence interval.

this to have an obvious effect (Table A7, Fig. A2a in Appendix 2). Substituting model 4 with one in which type of sentinel as well as rank and sex of the tested individual were all combined in a single factor (model 4b) led to a slightly larger AICc (original model: 261.434; model with combined factor: 263.757; Fig. A2b in Appendix 2) indicating that the probability of subordinate males and dominant females beginning to act as a sentinel did not obviously vary with the type of current sentinel.

Duration of Sentinel Bouts

Fig. 4 presents descriptive statistics about sentinel bout durations in the experiments, classified into sentinelling alone, sentinelling first and sentinelling second. In 20% of the cases in which the first sentinel was the dominant male, and in 30% of the cases in which it was the subordinate female, the focal individual that began sentinelling second nevertheless terminated its sentinel bout first.

Duration of Sentinel Bouts according to End Type

When we analysed the duration of the sentinel bouts ending alone versus ending when another individual was also on guard (model 5), we found a clearly significant overall effect of the two test predictors sentinel presence (no/yes) and its interaction with sentinel type (dominant male/subordinate female; $\chi^2_2=13.002$, $P=0.002$). There was no significant interaction between sentinel presence and sentinel type ($\chi^2_1=2.005$, $P=0.157$; Table A8 in Appendix 2, Fig. 5a) suggesting that the effect of whether the bout ended in the absence or presence of another sentinel was not obviously different between subordinate females and dominant males. After dropping the interaction, we found that sentinel bouts that ended in the presence of another sentinel were on average shorter than bouts that ended in the absence of another individual (Table A9 in Appendix 2, Fig. 5b).

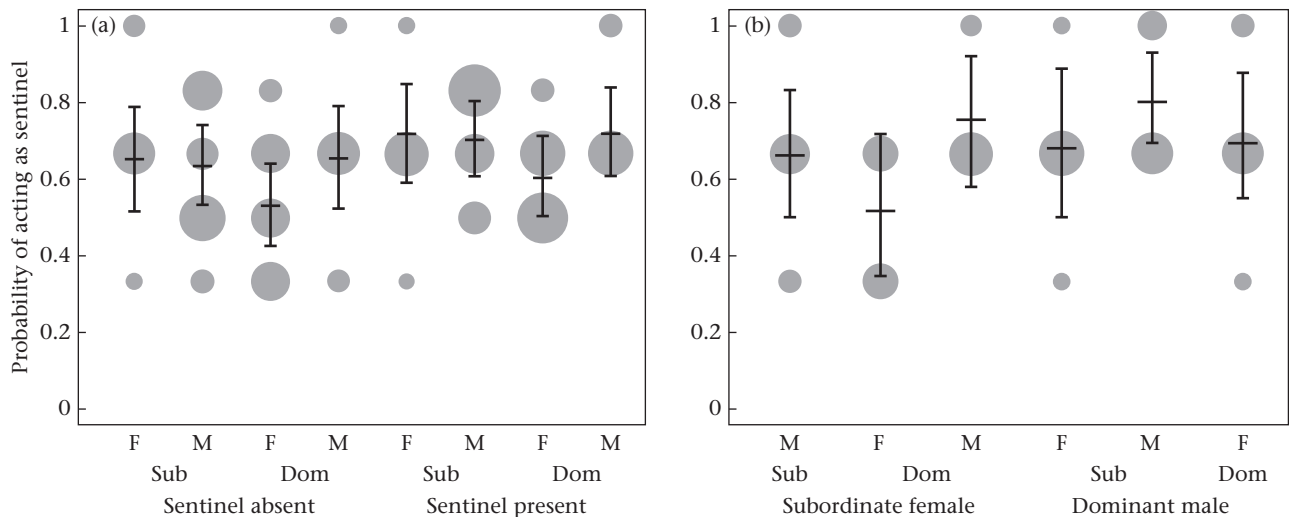


Figure 3. Probability of acting as a sentinel as a function of whether (a) there was a sentinel already present or not (model 3) and (b) the sentinel was the subordinate female or the dominant male (model 4), for subordinate (Sub) and dominant (Dom) females (F) and males (M). Dots depict the average probability of acting as a sentinel per individual and condition (sentinel present or absent), whereby the area of the dots is proportionate to the number of individuals with the given probability (range 3–30). The vertical lines with error bars depict the fitted model and its confidence interval with all other predictors at their average.

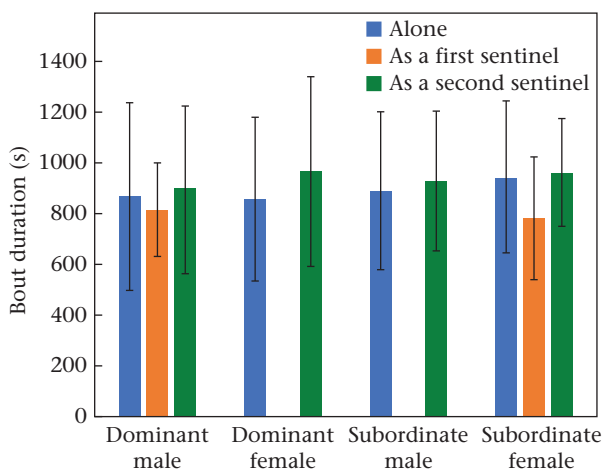


Figure 4. Sentinel bout duration (s) \pm SD for dominant and subordinate males and females, when each sentinel was alone, the first (out of two) and the second (out of two).

Interactions Between First and Second Sentinels

After eating ad libitum, in 64 of 90 cases (71.1%) one of the focal babblers began a sentinel bout when the dominant male was already on guard. In an additional 57 of 90 cases (63.3%) a group member started to sentinel when the subordinate female was already on guard. In all these cases, without exception, the former sentinel remained on guard and did not react by descending, and we were unable to identify any reaction towards the new sentinel, either by movement or by calls. In none of the cases did we see any behaviour performed by the second sentinel towards the first.

DISCUSSION

After eating as much as they wished, apparently to satiation (babblers returned to foraging following feeding ad libitum in only seven of 360 or 1.9% of the feeding events), the babblers that were tested climbed or flew up and began to act as a sentinel in 230 cases

(64%). No significant difference was found between cases in which another sentinel was already on guard and those in which no sentinel was present at that moment. When there was a sentinel, it did not obviously matter whether the sentinel was the most dominant adult male or the most subordinate adult female in the group, nor did it obviously matter who was the second-fed individual. Moreover, in 121 cases in which a second individual began to sentinel, no interaction was observed between the first and the second, regardless of their sex and rank. Altogether, these findings support the equilibrium prediction of Bednekoff's (1997) model which predicts that under full satiation, individuals should prefer to begin sentinelling, irrespective of whether another group member is already on guard, but with the important caveat that in 34% of the cases of full satiation the individuals resorted neither to sentinelling nor to foraging, but rather to social or personal wellbeing activities, options that were not included in Bednekoff's model.

These findings are completely different from those in natural conditions, where full satiation is apparently rare. Under natural conditions, dominants sentinel more than subordinates, and adult males sentinel more than adult females (Dattner et al., 2015; Ostreiher & Heifetz, 2017, 2019; Wright et al., 2001a; this study, models 1 and 2, Fig. 2). Similar findings were also found in other cooperatively breeding species, including mammals such as vervet monkeys, *Chlorocebus pygerythrus* (Horrocks & Hunte, 1986), and meerkats, *Suricata suricatta* (Clutton-Brock et al., 1999, 2002), as well as birds, such as pied babblers, *Turdoides bicolor* (Hollen et al., 2011), jungle babblers, *Turdoides striatus* (Gaston, 1977), Florida scrub jays, *Aphelocoma coerulescens* (Bednekoff & Woolfenden, 2003; Hailman, McGowan, & Woolfenden, 1994), white-browed sparrow weavers, *Plocepasser mahali* (Ferguson, 1987; Walker, York, & Young, 2016) and others.

Under natural conditions solitary sentinelling was much more common than parallel sentinelling, possibly because when a group member is already on guard and is likely to provide timely alerts if a predator approaches, the trade-off between continuing to forage and first-hand information from sentinelling shifts towards the latter only after the forager reaches a higher level of satiation (Bednekoff, 1997). The feeding experiment corroborated this prediction: it induced a high level of satiation, and, indeed, after eating ad libitum, an individual's probability of starting sentinelling was

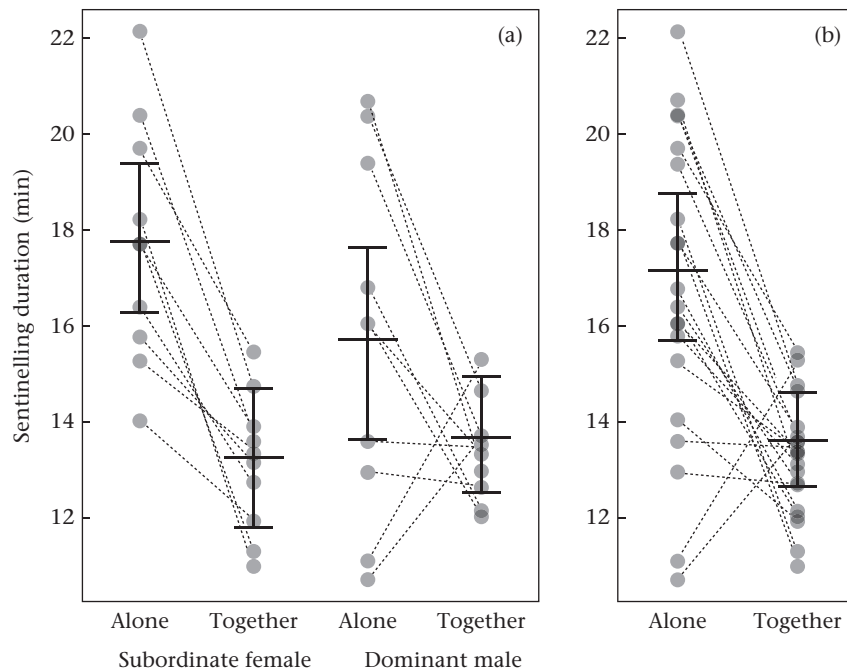


Figure 5. Duration of sentinel bouts that ended in the absence or presence of another sentinel, for the subordinate female and dominant male. Each point represents one individual. In 10 groups there were 10 dominant males and 10 subordinate females. Dots show the individual observations with darker shading indicating similar durations. The horizontal lines with error bars depict the fitted model (model 5) and its confidence intervals for (a) the full model including the interaction between the two factors and (b) the reduced model lacking the interaction. Pairs of points connected by a dotted line depict average durations of the same individual.

not obviously affected by the absence or presence of a sentinel or by the identity of the sentinel (models 3 and 4, Fig. 3).

At the same time, the feeding experiment did not nullify the gradual energy depletion that a sentinel experienced while guarding without eating. Consequently, fully satiated sentinels did end their sentinel bouts sooner when at that point in time another group member was sentinelling (model 5, Fig. 4b). This finding is also in line with the predictions of Bednekoff (1997).

Bednekoff's model is symmetric across group members. For a more realistic situation of heterogeneity within the group, our complementary prediction was that for subordinate individuals, like the subordinate female, which suffer fiercer competition over food while foraging than do strong individuals, like the dominant male, the shortening of sentinel bouts in the presence of another sentinel would be more pronounced. In other words, when another sentinel joins, subordinate female sentinels are expected to have a higher incentive to 'seize the moment' with fewer competitors on the ground to resume foraging. Dominant males, in contrast, are hardly inhibited by others when they forage, so their incentive to shorten their sentinel bout when somebody else joins in sentinelling derives only from the collateral benefit of being warned of danger and not, unlike subordinate females, from reduced competition.

In the experiment, subordinate females shortened their sentinel bouts when another individual started to sentinel more than dominant males, although not significantly (Fig. 5a). We think that the nonsignificant result derives from the fact that in the experiment, in contrast to natural conditions, subordinate females started to sentinel when they were fully satiated. However, further studies are needed to corroborate this hypothesis. Nevertheless, we suggest that the group members' competitive foraging abilities are not equal, and this should be incorporated into Bednekoff's (1997) original model. This suggestion is supported by the finding that, in the experiment, subordinate females ate significantly more and dominant males significantly less than others.

Under natural conditions, dominants may seem to 'replace' subordinates in sentinelling (Dattner et al., 2015; Zahavi, 1989; Zahavi & Zahavi, 1997). However, the apparent replacement may be a consequence of differential needs and incentives, rather than an intention to prevent somebody else from sentinelling. In fact, the apparent replacement might be a by-product of dominants sentinelling more frequently and in longer bouts than subordinates, and because parallel sentinelling was relatively rare (Table 2, Fig. 1). When a dominant joins a subordinate in sentinelling it is likely that the subordinate is already hungry, which might then cause the subordinate to terminate its sentinel activity soon after. This is supported by our finding that fully satiated first-fed subordinate females did not go down immediately when joined by an additional sentinel, regardless of its sex and rank. In other words, if a sentinel is not hungry enough, it transpires that it has no immediate reason to stop sentinelling, even when the new sentinel has a higher rank.

It thus seems that Arabian babblers do not coordinate their sentinel behaviour, at least not directly. Each group member individually maximizes its foraging–sentinelling trade-off at each given moment. This, in turn, depends, among additional factors, on the foraging behaviour of its groupmates. The result is indirect and partial coordination, which, at the group level, leads both to times without a sentinel (in 48.7% of our observation time in natural conditions) and times with more than one sentinel (in 14.2% of the sentinel time we observed without interference).

We should emphasize once again that our experiment induced satiation. Between the two extreme situations, being so hungry that nothing but foraging is acceptable and being so satiated that continued foraging has low value and the presence of a sentinel does not inhibit parallel sentinelling, there is a wide range in which the decision to stop foraging and start sentinelling is influenced by, among other factors, the presence of a sentinel, competition for food on the ground, predation risk and other environmental variables, as well as the need for social interactions and individual wellbeing activities. Additional theoretical and empirical studies

are required to fine-tune the relative influence of all these factors on the decision to sentinel.

Acknowledgments

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References

- Baayen, R. H. (2008). *Analyzing linguistic data*. Cambridge, U.K.: Cambridge University Press.
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68, 255–278.
- Bates, B., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bednekoff, P. A. (1997). Mutualism among safe, selfish sentinels: A dynamic game. *The American Naturalist*, 150, 373–392.
- 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. *Advances in the Study of Behavior*, 47, 115–146.
- 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.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference* (2nd ed.). Berlin, Germany: Springer.
- 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.
- Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S., et al. (1999). Selfish sentinels in cooperative mammals. *Science*, 284, 1640–1644.
- 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>
- Dobson, A. J. (2002). *An introduction to generalized linear models*. Boca Raton, FL: Chapman & Hall/CRC.
- Edelaar, P., & Wright, J. (2006). Potential prey makes excellent ornithologists: Adaptive, flexible responses towards avian predation threat by arabian babblers *Turdoides squamiceps* living at a migratory hotspot. *Ibis*, 148, 664–671.
- Ferguson, J. W. H. (1987). Vigilance behaviour in white-browed sparrow weavers *Plocepasser mahali*. *Ethology*, 76, 223–235. <https://doi.org/10.1111/j.1439-0310.1987.tb00685.x>
- Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65, 47–55. <https://doi.org/10.1007/s00265-010-1038-5>
- Gaston, A. J. (1977). Social behaviour within groups of jungle babblers, *Turdoides striatus*. *Animal Behaviour*, 25, 828–848.
- Hailman, J. P., McGowan, K. J., & Woolfenden, G. E. (1994). Role of helpers in the sentinel behaviour of the Florida scrub jay (*Aphelocoma c. coerulescens*). *Ethology*, 97, 119–140. <https://doi.org/10.1111/j.1439-0310.1994.tb01034.x>
- Hollen, L. I., Bell, M. B. V., Wade, H. M., Rose, R., Russell, A., Niven, F., et al. (2011). Ecological conditions influence sentinel decisions. *Animal Behaviour*, 82, 1435–1441.
- Horrocks, J. A., & Hunte, W. (1986). Sentinel behaviour in vervet monkeys: Who sees whom first? *Animal Behaviour*, 34, 1566–1567.
- Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing type I error and power in linear mixed models. *Journal of Memory and Language*, 94, 305–315.
- McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models*. London, U.K.: Chapman & Hall.
- Naguib, M., Mundry, R., Ostreither, R., Hultsch, H., Schrader, L., & Todt, D. (1999). Cooperatively breeding Arabian babblers call differently when mobbing in different predator-induced situations. *Behavioral Ecology*, 10, 636–640.
- Ostreither, R. (n.d.). Changes in Arabian babblers' daily schedule following changes in the social hierarchy within the group. (Manuscript in preparation).
- Ostreither, R., & Heifetz, A. (2017). *The sentinel behaviour of Arabian babblers floaters* (Vol. 4). Royal Society Open Science. <https://doi.org/10.1098/rsos.160738>
- Ostreither, R., & Heifetz, A. (2019). The sentinelling—foraging trade-off in dominant and subordinate Arabian babblers. *Ethology*, 125, 98–105. <https://doi.org/10.1111/eth.12833>
- Ostreither, R., & Heifetz, A. (2020). The function of sentinel alarm calls in the Arabian babblers. *Journal of Avian Biology*, 51(10), 1–5. <https://doi.org/10.1111/jav.02513>
- R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Regosin, J. V. (2002). Alarm calling and predator discrimination in the arabian babblers (*Turdoides squamiceps*). *Bird Behavior*, 15, 11–19.
- Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, 20, 416–420.
- Sommer, C. (2011). Alarm calling and sentinel behaviour in Arabian babblers. *Bioacoustics*, 20, 357–368.
- Sommer, C., Todt, D., Ostreither, R., & Mundry, R. (2012). Urgency-related alarm calling in arabian babblers, *Turdoides squamiceps*: Predator distance matters in the use of alarm call types. *Behaviour*, 149, 755–773.
- 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 babblers. *Animal Behaviour*, 62, 973–979.
- Wright, J., Berg, E., de Kort, S. R., Khazin, V., & Maklakov, A. A. (2001c). Safe selfish sentinels in a cooperative bird. *Journal of Animal Ecology*, 70, 1070–1079.
- Wright, J., Maklakov, A. A., & Khazin, V. (2001b). State-dependent sentinels: An experimental study in the arabian babblers. *Proceedings of the Royal Society of London B*, 268, 821–826.
- Zahavi, A. (1989). The Arabian babblers. In I. Newton (Ed.), *Lifetime reproduction in birds* (pp. 253–275). London, U.K.: 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). Cambridge, U.K.: Cambridge University Press.
- Zahavi, A., & Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. Oxford, U.K.: Oxford University Press.

Appendix 1. Number of Worms Eaten ad libitum

During the experiment we counted the mealworms that each focal babblers ate when it was fed. The descriptive statistics for the different combinations of sex and rank appear in Fig. A1.

To estimate the extent to which the number of worms eaten depended on the type of tested individual (dominant male, subordinate male, dominant female, subordinate female) and whether there was a sentinel present, we fitted a GLMM (Baayen, 2008) with Poisson error structure and log link function (McCullagh & Nelder, 1989; model A1). Since it seemed possible that the effect of sentinel presence depended on the individual tested, we also included the interaction between these two factors as an additional fixed effect.

We included random intercepts effects for the identity of the individual tested, the social group and the day nested in group. The latter we included as on half of the days of the experiment the focal individual was fed in addition to the dominant male or subordinate female. We included random slopes (Barr et al., 2013; Schielzeth & Forstmeier, 2009) of (1) sentinel presence within type of tested individual and (2) type of tested individual, sentinel presence and their interaction within social group.

Originally, we also included parameters for the correlations between random intercepts and slopes, but as the correlation between the random intercept of individual identity and the random slope of sentinel presence within individual identity was estimated to be 1, we excluded it from the model (Matuschek et al., 2017). This did not lead to a recognizable decrease in the log likelihood of the model.

We compared the full model with a null model lacking all fixed effects. The model was not overdispersed (dispersion parameter: 1.109). The sample analysed for this model comprised 540 trials, conducted on 360 days with 40 individuals of 10 groups.

All models we fitted in R (version 3.6.3; R Core Team, 2020) using the function glmer of the package lme4 (version 1.1–21; Bates et al., 2015). We estimated confidence intervals of estimated coefficients by means of a parametric bootstrap (function bootMer of the package lme4) and determined model stability by dropping levels of random effects one at a time. All tests presented are likelihood ratio tests.

We found a clearly significant full–null model comparison (likelihood ratio test: $\chi^2_7=36.462$, $P<0.001$) but the interaction

Table A1

Results of the full model with the number of worms eaten by different individuals in the absence or presence of a sentinel

Term	Estimate	SE	Lower CI	Upper CI	Minimum	Maximum
Intercept	2.365	0.066	2.231	2.485	2.330	2.414
TestedF2 ¹	0.252	0.087	0.087	0.414	0.202	0.298
TestedM1 ¹	-0.312	0.074	-0.451	-0.169	-0.359	-0.279
TestedM2 ¹	0.046	0.080	-0.114	0.209	-0.002	0.083
Sentinel presence ²	0.013	0.076	-0.128	0.163	-0.017	0.060
TestedF2*sentinel presence	-0.100	0.152	-0.400	0.178	-0.184	-0.026
TestedM1*sentinel presence	-0.047	0.130	-0.293	0.193	-0.101	0.015
TestedM2*sentinel presence	-0.031	0.099	-0.218	0.170	-0.077	0.008

Estimates are given with SEs, confidence interval (CI) and the range of estimates obtained when excluding levels of random effects one at a time.

¹ Dummy coded with F1 (dominant female) being the reference category; the other levels are F2: subordinate female; M1: dominant male; M2: subordinate male.² Dummy coded with no sentinel present being the reference category.**Table A2**

Results of the reduced model with the number of worms eaten by different individuals in the absence or presence of a sentinel

Term	Estimate	SE	Lower CI	Upper CI	χ^2	df	P
Intercept	2.389	0.041	2.301	2.471			¹
TestedF2 ²	0.208	0.047	0.104	0.302	26.902	3	0.001
TestedM1 ²	-0.332	0.054	-0.451	-0.221			
TestedM2 ²	0.035	0.055	-0.071	0.156			
Sentinel presence ³	-0.031	0.035	-0.110	0.045	0.740	1	0.390

Estimates are given with SEs, confidence interval (CI) and significance test results.

¹ Not indicated because has limited interpretation.² Dummy coded with F1 (dominant female) being the reference category; the indicated test refers to the overall effect of the factor; the other levels are F2: subordinate female; M1: dominant male; M2: subordinate male.³ Dummy coded with no sentinel present being the reference category; the indicated test refers to the overall effect of the factor.**Table A3**

Results of model 1 investigating the influence of sex and rank on the number of sentinel bouts per 3 h observation under natural conditions

Term	Estimate	SE	Lower CI	Upper CI	Minimum	Maximum
Intercept	1.347	0.031	1.286	1.408	1.335	1.361
Rank ¹	-0.555	0.044	-0.650	-0.472	-0.577	-0.537
Sex ²	0.299	0.035	0.231	0.367	0.285	0.314
Rank*sex	0.284	0.056	0.185	0.394	0.265	0.317

Estimates are given with SEs, confidence interval (CI) and the range of estimates obtained when excluding levels of random effects one at a time.

¹ Dummy coded with dominant being the reference category.² Dummy coded with female being the reference category.

between the tested individual and sentinel presence did not appear significant ($\chi^2_3=4.953$, $P=0.175$; Table A1). After removal of the interaction, we found that dominant males ate the fewest and significantly less than all others and that subordinate females ate the most worms and significantly more than all others until satiation (Table A2, Fig. A1).

In summary, there was a large variation in the number of consumed mealworms between individuals and by the same

Table A4

Results of model 2, investigating the influence of sex and rank on the total duration of sentinel activity per 3 h observation under natural conditions

Term	Estimate	SE	Lower CI	Upper CI	Minimum	Maximum
Intercept	3.067	0.052	2.966	3.172	3.035	3.107
Rank ¹	-0.720	0.042	-0.795	-0.642	-0.749	-0.681
Sex ²	0.397	0.026	0.347	0.451	0.382	0.411
Rank*sex	0.343	0.052	0.243	0.444	0.304	0.378

Estimates are given with SEs, confidence interval (CI) and the range of estimates obtained when excluding levels of random effects one at a time.

¹ Dummy coded with dominant being the reference category.² Dummy coded with female being the reference category.

individual across replicates. Subordinate females ate more than all the others, while dominant males ate less than others. This corroborates the hypothesis that in natural conditions dominants and males enjoy better access to food sources. The presence of a sentinel and its identity did not cause the focal babbler to eat more, or less, in relation to itself when no sentinel was present.

Appendix 2. Results for Models 1–5

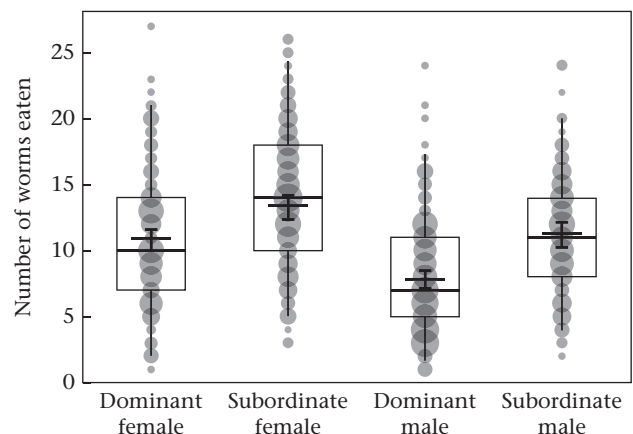


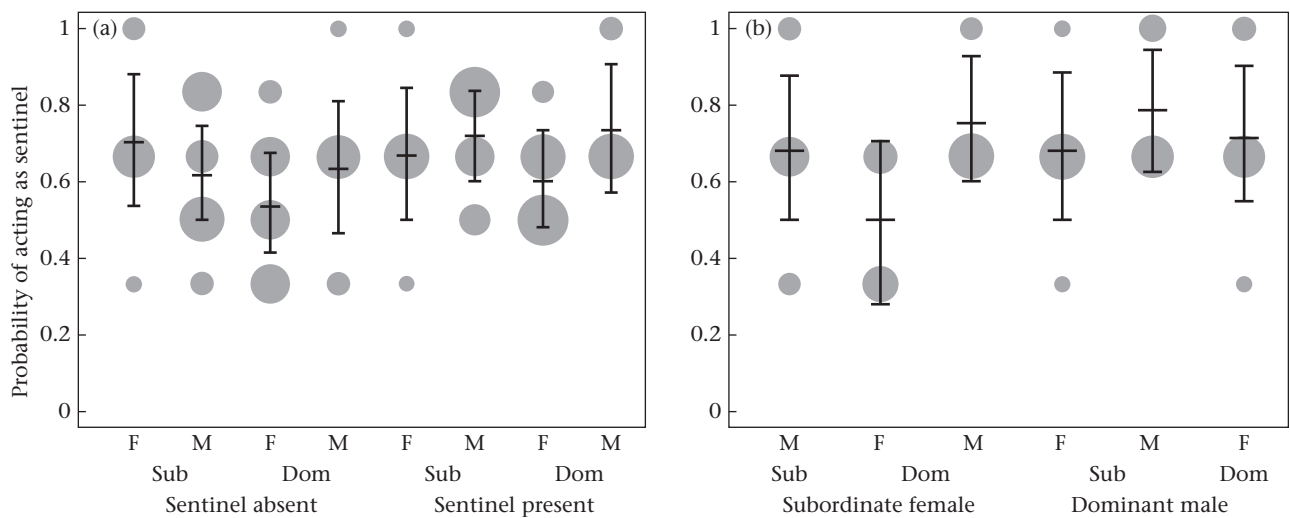
Figure A1. Number of worms eaten until satiation by the different individuals tested. Dots show the number of worms eaten, whereby the area of the dots is proportionate to the number of experiments (1–15). Horizontal lines with boxes indicate medians and quartiles and vertical lines indicate percentiles (2.5 and 97.5%). Vertical lines with error bars depict the fitted reduced model and its confidence limits after removal of the interaction between the tested individual and sentinel presence and with sentinel presence centred to a mean of zero.

Table A5

Results of model 3 comparing the probabilities of beginning to act as a sentinel between when a sentinel was currently present or absent

Term	Estimate	SE	Lower CI	Upper CI	χ^2	df	P	Minimum	Maximum
Intercept	0.125	0.216	-0.287	0.578			¹	0.049	0.180
Condition ²	0.297	0.223	-0.152	0.793	1.780	1	0.182	0.231	0.360
replicate ³	0.242	0.113	0.002	0.504	3.850	1	0.050	0.166	0.323
Sex ⁴	0.510	0.336	-0.115	1.238			¹	0.322	0.618
Rank ⁵	0.510	0.336	-0.186	1.273			¹	0.316	0.624
Sex*rank	-0.588	0.479	-1.681	0.332	1.524	1	0.217	-0.745	-0.322

Estimates are given with SEs, confidence interval (CI), significance test results and the range of estimates obtained when excluding levels of random effects one at a time.

¹ Not indicated because has limited interpretation.² Dummy coded, sentinel absent = 0, sentinel present = 1.³ z-transformed to a mean of zero and SD of one; mean and SD of the original variable were 2.000 and 0.818, respectively.⁴ Sex of the tested individual, dummy coded, female = 0, male = 1.⁵ Rank of the tested individual, dummy coded, dominant = 0, subordinate = 1.**Figure A2.** Probability of acting as a sentinel as a function of whether (a) there was a sentinel present or not (model 3b, including the three-way interaction between sentinel presence, sex and rank of the tested individual) or (b) the sentinel was the subordinate female or the dominant male (model 4b including a factor specifying the particular sex–rank combination of the sentinel and the tested individual) for subordinate (Sub) and dominant (Dom) females (F) and males (M). Dots depict the average probability of acting as a sentinel per individual and condition (sentinel present or absent), whereby the area of the dots is proportionate to the number of individuals with the given probability (range 3–30). The vertical lines with error bars depict the fitted model and its confidence interval with all other predictors at their average.**Table A6**

Results of model 4 addressing how probabilities of beginning to act as a sentinel depended on the type of current sentinel

Term	Estimate	SE	Lower CI	Upper CI	χ^2	df	P	Minimum	Maximum
Intercept	0.821	0.358	0.208	1.972			¹	0.645	0.968
Sentinel type ²	-0.741	0.414	-1.863	-0.002	3.301	1	0.069	-0.898	-0.580
Sex ³	1.034	0.558	-0.055	2.490			¹	0.746	1.162
Rank ⁴	-0.065	0.537	-1.340	1.207			¹	-0.268	0.156
Replicate ⁵	0.288	0.199	-0.102	0.824	2.148	1	0.143	0.205	0.401
Sex*rank	-0.380	0.725	-2.164	1.058	0.277	1	0.598	-0.619	-0.026

Estimates are given with SEs, confidence interval (CI), significance test results and the range of estimates obtained when excluding levels of random effects one at a time.

¹ Not indicated because has limited interpretation.² Dummy coded, dominant male = 0, subordinate female = 1.³ Sex of the tested individual, dummy coded, female = 0, male = 1.⁴ Rank of the tested individual, dummy coded, dominant = 0, subordinate = 1.⁵ z-transformed to a mean of zero and SD of one; mean and SD of the original variable were 2.000 and 0.819, respectively.

Table A7

Results of model 3 comparing probabilities of beginning to act as a sentinel between a sentinel being currently present or absent after including the interaction between sentinel presence 'condition' and sex and rank of the tested individual

Term	Estimate	SE	Lower CI	Upper CI	χ^2	df	P
Intercept	0.136	0.261	-0.347	0.735			¹
Condition ²	0.276	0.372	-0.537	1.042			¹
Sex ³	0.419	0.462	-0.502	1.485			¹
Rank ⁴	0.724	0.478	-0.154	1.872			¹
Replicate ⁵	0.243	0.114	0.035	0.509	3.850	1	0.050
Condition*sex	0.195	0.676	-1.187	1.711			¹
Condition*rank	-0.432	0.672	-1.897	0.904			¹
Sex*rank	-0.796	0.668	-2.332	0.503			¹
Condition*sex*rank	0.420	0.961	-1.681	2.408	0.191	1	0.662

Estimates are given with SEs, confidence interval (CI) and significance test results.

¹ Not indicated because has limited interpretation.

² Dummy coded, sentinel present = 0, sentinel absent = 1.

³ Sex of the tested individual, dummy coded, female = 0, male = 1.

⁴ Rank of the tested individual, dummy coded, dominant = 0, subordinate = 1.

⁵ z-transformed to a mean of zero and SD of one; mean and SD of the original variable were 2.000 and 0.818, respectively.

Table A9

Results of the reduced model 5 lacking the interaction comparing the duration of sentinel bouts that ended in the absence or presence of another sentinel for the subordinate female versus the dominant male

Term	Estimate	SE	Lower CI	Upper CI	χ^2	df	P
Intercept	1051	48	957	1145			¹
Ended ²	-213	44	-294	-126	10.997	1	0.001
Sentinel ³	-42	35	-115	34	1.133	1	0.287

Estimates are given with SEs, confidence interval (CI) and significance test results.

¹ Dummy coded with alone being the reference category.

² Dummy coded with ending in the absence of another sentinel being the reference category.

³ Dummy coded, subordinate female = 0, dominant male = 1.

Table A8

Results of the full model 5 comparing the duration of sentinel bouts that ended in the absence or presence of another sentinel for the subordinate female versus the dominant male

Term	Estimate	SE	Lower CI	Upper CI	Minimum	Maximum
Intercept	1066	49	977	1164	1023	1096
Ended ¹	-271	59	-388	-168	-298	-227
Sentinel ²	-123	64	-251	-6	-162	-72
Ended*sentinel	149	100	-31	354	86	190

Estimates are given with SEs, confidence interval (CI) and the range of estimates obtained when excluding levels of random effects one at a time.

¹ Dummy coded with ending in the absence of another sentinel being the reference category.

² Dummy coded, subordinate female = 0, dominant male = 1.