Animal Behaviour 165 (2020) 143–152

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Context-dependent contributions to sentinel behaviour: audience, satiation and danger effects

Josh J. Arbon [a,*], Julie M. Kern [a,b], Amy Morris-Drake [a], Andrew N. Radford [a]

[a] *School of Biological Sciences, University of Bristol, Bristol, U.K.*
[b] *School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia*

ARTICLE INFO

Article history:
Received 2 October 2019
Initial acceptance 14 November 2019
Final acceptance 13 March 2020
Available online 30 June 2020
MS. number: 19-00663R

Keywords:
audience
contribution
cooperation
danger
investment
playback experiment
risk allocation hypothesis
satiation
sentinel
vigilance

In group-living species, particularly cooperative breeders, all group members contribute to various behaviours but there is considerable variation between and within individuals in their contributions. While it is well established that there is variation due to differences in the costs and benefits for individuals of different sex, age and dominance status, shorter-term social, internal and environmental factors are also likely to be important. Sentinel behaviour, where individuals adopt a raised position to scan for danger while groupmates forage, offers an opportunity to test hypotheses about context-dependent differences in contributions to group behaviour. Here we used field experiments to manipulate the conspecific audience, satiation state and perceived danger level of dwarf mongooses, *Helogale parvula*, to investigate how sentinel contributions are modulated by individual context. In addition to standard measures of sentinel behaviour (likelihood of becoming a sentinel, number of bouts, bout duration), we considered within-bout behaviour in terms of surveillance calls and attentiveness (head-scanning rate and distraction levels). We found that the presence of a neighbouring forager (audience) decreased sentinel contributions, while individuals increased their sentinel investment when satiated and experiencing an increased danger level. Changes in head-scanning rate provided evidence for an interaction between the effect of satiation and danger levels, demonstrating that sentinel attentiveness was influenced by changes in context. Our results demonstrate that sentinel behaviour is strongly context dependent, with effects seen in initial bout and bout quantity decisions, as well as within-bout characteristics, and that individual contributions to group behaviours can vary depending on social, internal and environmental factors.

In group-living species, particularly cooperative breeders, all group members contribute to a variety of behaviours but there is considerable variation in individual contributions. Individuals in groups participate in a range of tasks, including food acquisition (Boesch, 1994; Bshary, Hohner, Ait-El-Djoudi, & Fricke, 2006; Creel & Creel, 1995), territory defence (Radford, 2003; Seddon & Tobias, 2003; Taborsky, 1984), rearing of young (Clutton-Brock, 2002; Jennions & Macdonald, 1994; Koenig & Dickinson, 2004) and prevention of predation (Novaro, Moraga, Briceño, Funes, & Marino, 2009; Owings & Coss, 1977; Seyfarth, Cheney, & Marler, 1980). It is well established that there can be large differences in contributions to such behaviours by different individuals, some of which can be explained by factors such as sex, age and dominance status (Desjardins, Stiver, Fitzpatrick, & Balshine, 2008; Graw & Manser, 2007; Koenig, Mumme, & Pitelka, 1983; Zöttl et al., 2016). However, these relatively fixed characteristics are not the only potential drivers of differences in contributions; in addition to variation between individuals, there is the potential for variation by the same individuals depending on context.

Individual behavioural contributions can vary in response to shorter-term social, internal and environmental factors, such as the presence of an audience, satiation level of the actor and the current predation risk. Audience effects, where individuals change their behaviour due to the presence (and identity) of others (definition adapted from Zuberbühler, 2008), are widespread. With respect to group behaviours, examples include the presence of a conspecific increasing alarm calling in red-legged partridges, *Alectoris rufa* (Zaccaroni, Binazzi, Massolo, & Dessì-Fulgheri, 2013), food-associated calling in chimpanzees, *Pan troglodytes* (Slocombe et al., 2010), and minimizing cheating through ‘false feeding’ (where an individual feigns feeding of young, but consumes the

---

[*] Correspondence and present address: J. Arbon, Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, UK.
E-mail address: ja545@exeter.ac.uk (J. J. Arbon).

https://doi.org/10.1016/j.anbehav.2020.04.021

food itself) in white-winged choughs, *Corcorax melanorhamphos* (Boland, Heinsohn, & Cockburn, 1997a). Satiation level (also referred to as state) has been shown to influence brood provisioning, for example, with increased satiation leading to higher rates in both breeding white-winged choughs (Boland, Heinsohn, & Cockburn, 1997b) and nonbreeding helper Arabian babblers, *Turdoides squamiceps* (Wright & Dingemanse, 1999); false feeding in crows, *Corvus corone*, occurs less frequently when individuals are satiated (Canestrari et al., 2010). Danger levels relating to predation risk can also drive variation in behavioural investment: for instance, red-breasted nuthatches, *Sitta canadensis*, preferentially contribute to mobbing behaviour when the threat to themselves is greater (Templeton & Greene, 2007), while herring gulls, *Larus argentatus*, increase their alarm calling as danger increases (Shah, Greig, MacLean, & Bonter, 2015).

Sentinel behaviour offers an excellent opportunity to test hypotheses about context-dependent differences in contributions to group behaviours. Sentinel behaviour, where an individual adopts a raised position to look out for danger while its groupmates continue with other activities such as foraging (Bednekoff, 2015), has evolved in various mammals (Clutton-Brock et al., 1999; Rasa, 1986) and birds (Bell, Radford, Rose, Wade, & Ridley, 2009; McGowan & Woolfenden, 1989). In many cases, sentinels use low-amplitude surveillance calls (also known as the ‘Watchman's song’) to announce their presence (Hollén, Bell, & Radford, 2008; Kern & Radford, 2013). The presence of a sentinel, and the production of surveillance calls, enables foragers to be less vigilant (Hollén et al., 2008; Rauber & Manser, 2017) and thus benefit from a higher food intake rate (Hollén et al., 2008). Sentinel investment is influenced by fixed or relatively stable factors such as sex, dominance rank and group size (Clutton-Brock et al., 1999; Kern, Laker, & Radford, 2017; Kern, Sumner, & Radford, 2016; Rasa, 1986, 1989; Ridley & Raihani, 2007; Wright, Berg, De Kort, Khazin, & Maklakov, 2001). There is also some evidence that sentinel contributions (here we use the phrases ‘sentinel contributions’ and ‘sentinel investment’ interchangeably) can be modulated by personal context. For instance, investment levels can vary depending on the conspecific audience, with individuals more likely to act as a sentinel when with young than in their absence (Santema & Clutton-Brock, 2013; Sorato, Gullett, Griffith, & Russell, 2012), although this is likely to be a cooperative response to risk rather than a targeted change in social investment. Theory predicts that individuals are more likely to perform sentinel bouts when satiated (Bednekoff, 1997), with some corroborating empirical evidence (Bednekoff & Woolfenden, 2003; Wright, Maklakov, & Khazin, 2001); group members are also less likely to act as a sentinel if others are in a more favourable state (Bell, Radford, Smith, Thompson, & Ridley, 2010). Moreover, individuals contribute more to sentinel behaviour (Ridley, Raihani, & Bell, 2010; Sorato et al., 2012), and adjust their surveillance calls accordingly (Bell et al., 2009), when danger levels are higher. However, most of this work has considered just general measures of sentinel investment (e.g. likelihood of bouts occurring, bout rate, proportion of time a sentinel is present). Only rarely are within-bout behaviours considered (Bell et al., 2010; Kern & Radford, 2013), with no experimental work examining differences in sentinel attentiveness; this could be affected by context and alter the value of the contribution. Furthermore, while animals are known to integrate multiple stimuli into other decision-making processes (Hebets & Papaj, 2005; Morris-Drake, Kern, & Radford, 2016), experimental testing in relation to sentinel decisions has been confined to single contexts or factors.

Cooperatively breeding dwarf mongooses, *H. parvula*, provide an ideal study species in which to investigate experimentally, and in detail, the possibility of context-dependent contributions to sentinel behaviour. Dwarf mongooses forage in groups for predominantly invertebrate prey and are vulnerable to a wide range of predators, including raptors, small felids and snakes (Kern & Radford, 2014; Sharpe, Joustra, & Cherry, 2010). While foraging, individuals spend considerable time with their heads down searching or digging for prey, and therefore face a trade-off between vigilance and food finding. Perhaps as a consequence, dwarf mongooses have evolved a sentinel system (Kern & Radford, 2013, 2014; Rasa, 1986) as well as a range of alarm calls (Collier, Radford, Townsend, & Manser, 2017) and they also eavesdrop on the alarm calls of other species such as fork-tailed drongos, *Dicrurus adsimilis*, and tree squirrels, *Paraxerus cepapi* (Morris-Drake, Bracken, Kern, & Radford, 2017; Rasa, 1986). Previous work has shown that dwarf mongoose behaviour can be context dependent: they respond differently to conspecific alarm calls depending on the signaller's spatial position, the receiver's satiation and prior information about current predation risks (Kern et al., 2017), and increase their sentinel contributions in response to conspecific alarm calls (Kern & Radford, 2014). Collection of detailed information on sentinel behaviour, as well as controlled field-based experimentation, is facilitated because wild dwarf mongooses can be habituated to the close presence of observers (Kern & Radford, 2013, 2014, 2017, 2018).

Here, we used call playbacks and supplementary feeding to investigate how variation in within-individual sentinel contributions is affected by context, specifically conspecific audience effects and the influence of satiation and danger levels (and their interaction). Alterations in investment could arise with respect to three main elements of sentinel behaviour: initial bout decisions (whether to perform a bout, when to start the first bout); bout quantity decisions (how many bouts to perform, the durations of bouts); and within-bout characteristics (the production or not of surveillance calls, ‘attentiveness’ as indicated by head-scanning rate and levels of distraction). Table 1 provides definitions for each element and response variable, as well as general predictions relating to an increased investment in each case; specific predictions relating to different contexts are provided below.

We predicted that simulating a conspecific audience, in this experiment standardized as an opposite-sex dominant, would result in increased investment in sentinel behaviour. Individuals might use sentinel contributions either to signal their quality as a potential social partner and to gain prestige (Zahavi, 1990; Zahavi & Zahavi, 1997) or to gain more immediate cooperative grooming rewards (as in Kern & Radford, 2018); these ideas are not mutually exclusive. Specifically, we expected to see increases in investment in all three main elements of sentinel behaviour: for example, an increased bout likelihood and longer bouts, as well as an increased production of surveillance calls, both to signal the presence of the sentinel and to benefit the perceived audience through increased social information (Kern & Radford, 2013).

We predicted that supplementary feeding would result in an increase in sentinel investment as a positive relationship between current state and sentinel behaviour has been modelled theoretically (Bednekoff, 1997) and has been demonstrated empirically in other systems (Clutton-Brock et al., 1999; Wright, Maklakov, et al., 2001). For example, a trade-off switch from foraging to vigilance (Lima & Bednekoff, 1999a) would result in individuals becoming a sentinel sooner, more often and for longer. With respect to danger level, we predicted that a simulated increase in predation risk would also result in individuals increasing investment in sentinel behaviour, owing to a heightened personal risk (Ridley et al., 2010; Wright, Berg, et al., 2001). Here we also expected changes in each of the three elements with, for example, increases in bout number and duration, a greater likelihood of surveillance calls and a heightened attentiveness (i.e. an increased head scan rate and a reduced

Table 1
Sentinel response variables: how they were defined and a general prediction of change that would reflect an increased sentinel investment

Element	Response	Definition	Prediction
Initial bout decisions	Was a bout performed?	Binary measure of whether a sentinel bout was performed during the trial	Increased likelihood
	Time to first bout	Seconds until the first sentinel bout was performed since the start of the trial	Reduced time until first bout
Bout quantity decisions	Number of bouts	Number of discrete sentinel bouts performed during the trial	More bouts
	Mean bout duration	The mean duration of all bouts performed during the trial	Increased duration
Within-bout characteristics	Surveillance call	Binary measure of whether the sentinel produced surveillance calls during a given bout	Increased likelihood
	Mean scan rate	Rate of head scanning by a sentinel, measured as the number of times the sentinel moved between discrete head positions per min for a given sentinel bout	Increased rate
	Distraction	Binary measure of whether the sentinel became distracted during a given sentinel bout	Decreased likelihood

Mean scan rate and distraction likelihood together indicated sentinel ‘attentiveness’.

likelihood of distraction). We also predicted that satiation and danger levels would interact in their effect, as is theoretically predicted by the risk allocation hypothesis (Lima & Bednekoff, 1999b). As the costs and benefits of the foraging/vigilance trade-off change with both satiation state and danger level, individuals would be expected to display maximal vigilance when passing a certain satiation threshold. Therefore, we might expect to see a difference in investment between danger treatments in nonsatiated individuals which would disappear when satiated.

METHODS

Study Site and Population

The study was conducted at the Dwarf Mongoose Research Project (DMRP), based on the Sorabi Rock Lodge reserve, Limpopo Province, South Africa (24°11′S, 30°46′E); full details are given in Kern and Radford (2013). Data were collected between March and July 2018 from six wild groups of dwarf mongooses (mean ± SE group size $= 13.8 \pm 1.9$, range 9–22). The study animals are habituated to the close presence of human observers and individually identifiable from blonde dye marks (Wella, Weybridge, U.K.) added to their fur; individuals are trained to climb on a balance scale using a reward of hardboiled egg (Kern & Radford, 2013, 2014). The DMRP has been running constantly since 2011; therefore, the age, sex and dominance status of each individual are known. Only adult individuals (those at least 1 year old) were used in the study; adults were categorized as either dominants (one pair per group) or subordinates (all other adults) through observations of aggressive behaviour, foraging displacements and scent marking (Kern et al., 2016; Kern & Radford, 2013). All groups had produced litters of pups the previous October/November and December/January, such that all pups were foraging self-sufficiently by the start of experimentation; pups in all groups were of equivalent ages.

Dwarf mongooses face a high predation risk and have therefore evolved both sentinel behaviour and alarm calls; they also eavesdrop on heterospecific alarm calls. At the study site, dwarf mongooses have many aerial and terrestrial predators. These include raptors such as African hawk-eagles, *Hieraaetus spilogaster*, brown snake-eagles, *Circaetus cinereus*, and pale chanting goshawks, *Melierax canorus*, mammals such as black-backed jackals, *Canis mesomelas*, and servals, *Leptailurus serval*, and reptiles such as black mambas, *Dendroaspis polylepis*, puff adders, *Bitis arietans*, Mozambique spitting cobras, *Naja mossambica*, and rock monitors, *Varanus albigularis* (Kern & Radford, 2014; Sharpe et al., 2010). Dwarf mongooses exhibit both personal vigilance and sentinel behaviour (Kern & Radford, 2013, 2014; Rasa, 1986). They spend a lot of time digging with their head down for arthropod prey, so there is a trade-off between foraging and personal vigilance as the two behaviours are mutually exclusive (Rasa, 1989). A sentinel provides updates on current danger levels through surveillance calls, and produces alarm calls when a predator is spotted, allowing groupmates to focus more fully on foraging (Kern & Radford, 2013, 2014, 2018; Kern et al., 2016). Dwarf mongooses also commonly associate with other nonpredatory species, including fork-tailed drongos, yellow-billed, *Tockus leucomelas*, and red-billed, *Tockus erythrorhynchus*, hornbills, grey go-away birds, *Corythaixoides concolor*, and tree squirrels (Sharpe et al., 2010), and respond to their alarm calls. Tree squirrel calls were used in the present study because previous research has shown that dwarf mongoose foragers exhibit a similar flee response to the alarm calls of tree squirrels and conspecifics (Morris-Drake et al., 2017).

Experimental Overview

The ‘audience’ experiment tested how the presence of a simulated conspecific ‘audience’ affects sentinel behaviour, with particular reference to potential benefits relating to social prestige and cooperative rewards. This experiment had a matched design, with each focal individual (a forager) presented with two playback treatments: close calls (low-amplitude vocalizations given while foraging) from the opposite-sex dominant within their group (chosen as the standardized experimental audience) and ambient sound (as a control). This specific audience was chosen as the best candidate to elicit the predicted response; the majority of individuals have their strongest social bond with an opposite-sex individual (Kern & Radford, 2020), while a strong bond with a dominant individual is likely to convey more benefits than with a subordinate and therefore be more desirable. Twenty individuals (14 males, six females; 19 subordinates, one dominant) received both playback treatments while foraging; all focal individuals could be readily followed within 5 m by an observer.

The ‘satiation and danger’ experiment tested the effects of satiation level and danger level (and any interaction between the two) on sentinel behaviour. This experiment adopted a 2 × 2 matched design to control for variation between focal individuals. Each focal individual (a forager) received four combinations of a feeding treatment and a playback treatment: Fed (the provision of a quarter of a hardboiled egg) or Control-Fed (the provision of a few egg crumbs, as a control), followed by Danger (the playback of tree squirrel alarm calls) or No-Danger (the playback of tree squirrel close calls, as a control). Fifteen individuals (seven males, eight females) were targeted to receive all four treatment combinations (Fed × Danger, Fed × No-Danger, Control-Fed × Danger, Control-Fed × No-Danger) but, for logistical reasons, four individuals only received two combinations. All focal individuals would readily feed from a pot held by the experimenter and could be followed within 5 m.

Playback Track Preparation

Playback tracks were prepared from original recordings of dwarf mongoose close calls, tree squirrel close and alarm calls and ambient sound. All recordings were made using a Sennheiser MKE600 shotgun microphone (Sennheiser, Wedemark, Germany) paired with a Marantz PMD661 MkIII solid-state recorder (Marantz, Kanagawa, Japan). The microphone was mounted in a Rycote lyre shock mount (Rycote, Stroud, U.K.) to isolate handling noise, with all recordings taken in still conditions to maximize audio clarity. Recordings of dwarf mongoose close calls were made from up to 3 m away, whereas the tree squirrels were recorded from up to 10 m as they were not habituated to human observers. Ambient-sound recordings were made from the centre of each dwarf mongoose group's territory. Measures of sound pressure level were taken using a HandyMAN TEK1345 sound meter (Metrel U.K. Ltd., Normanton, U.K.) to determine the natural amplitude for use during playbacks. Recordings were isolated using the noise reduction functions in Adobe Audition CC (Adobe Systems, San Jose, CA, U.S.A.). Playback tracks were compiled in Reaper (Cockos Inc., New York, U.S.A.), and exported at a sample rate of 44.1 kHz.

For the audience experiment, 10 min playback tracks were created for both treatments. In the ‘audience present’ treatment, close calls were played at a naturally determined rate (5 calls/min) overlaid on an ambient-sound recording; each individual received a unique ambient-sound track ($N = 20$) containing 10 unique close calls ($N = 200$). In the control treatment, only the ambient-sound track was played, with each pair of tracks played to an individual created using the same ambient-sound recording.

For the satiation and danger experiment, 230 s tracks were created for both playback treatments. Each track contained eight calls: tree squirrel alarm calls in the Danger treatment and tree squirrel close calls in the No-Danger treatment. These eight calls were spaced in two 25 s blocks each containing four calls, with 3 min of silence between the blocks. In total, 19 unique alarm calls and 17 unique close calls were used, with four unique calls used per track. The design was blocked so that within any mongoose group, no individuals would be played the same calls and thus habituation effects were minimized. Each individual received the same playback track for both Danger trials and for both No-Danger trials; different tracks were used for different individuals.

Experimental Trials

For both experiments, trials were conducted during the morning (0700–1200) and afternoon (1300–1800) field sessions, when the group were foraging away from a sleeping burrow. Trials on the same individual were run within the same 2 h window on separate days. All trials on any one individual occurred over a maximum period of 14 days. Multiple trials were run on separate individuals within a group on a given day, with at least 30 min between the end of one trial and the start of the next to minimize potential carryover effects.

A trial was commenced and considered completed only if a set of environmental and behavioural criteria were met. For a trial to start, the majority of individuals in the group (including the focal individual) had to be foraging, with the group in their own territory, and with no or only light wind. Moreover, the focal individual had to be towards the periphery of the group or isolated in instances when the group was spread over a large distance. There also had to have been no alarm calls from either conspecifics or tree squirrels for 10 min, no latrine or mobbing events for 30 min and no intergroup interactions for 3 h (adapted from Kern & Radford, 2014). If any of these latter disruptions occurred during a trial, or if an individual became isolated from the group and began lost calling, and the trial had run for less than 5 min, it was repeated (audience experiment: $N = 10$; satiation and danger experiment: $N = 15$). For the audience experiment, trials were also not started or were repeated ($N = 15$) if the individual whose close calls were being played moved within 3 m of the focal individual for longer than 10 s, to maximize the likelihood that the playback was the major stimulus.

Once the relevant general experimental trial conditions were met in the audience experiment, the focal individual received one of the two playback treatments: close calls of the opposite-sex dominant or ambient sound. The order of treatment presentation was counterbalanced between individuals. Experimental tracks were played using an iPhone 7 (Apple Inc, Cupertino, CA, U.S.A.) connected to a Bose Soundlink Micro loudspeaker (Bose Corporation, Framingham, MA, U.S.A.) via Bluetooth, with the loudspeaker anchored to the ankle of the experimenter at a height of 10 cm, the natural height at which close calls from adjacent conspecifics occur, and oriented towards the focal individual at all times. Ambient-sound tracks (40 dB at 10 m) and close-call tracks (45 dB at 1.5 m) were played at their natural amplitudes.

Once the relevant general experimental trial conditions were met in the satiation and danger experiment, the focal individual received its feeding treatment (Fed or Control-Fed). In both treatments, the relevant food (a quarter of a hard-boiled egg or a few egg crumbs, respectively) was delivered from a plastic pot by hand to the focal individual. The Control-Fed treatment controlled for potential confounding effects of the individual feeding from the pot, interacting at a close distance with the experimenter or any feedback associated with the ingestion of egg; the latter is relevant as the entire study population is habituation trained using egg for the purposes of close observation, dye marking and weighing. After completion of the feeding treatment, a 30 s ‘break’ period (to allow the focal individual to resume general foraging activity; duration determined by pre-experiment pilot tests) was followed by the playback treatment (Danger or No-Danger). Experimental tracks (tree squirrel alarm or close calls, respectively) were played using the same equipment as in the audience experiment, oriented towards the focal individual at all times, but with the loudspeaker anchored at a height of 110 cm on the belt of the experimenter; tree squirrels spend most of the time in trees, so this height was chosen to mimic the angle from which the relevant calls would naturally be heard. Both tree squirrel close and alarm calls were played back at 45 dB at 1.5 m. Whenever possible, each focal individual received all four experimental conditions (Fed × Danger, Fed × No-Danger, Control-Fed × Danger, Control-Fed × No-Danger), and these were assigned so that each individual received a unique trial order.

Data Collection

In both experiments, the sentinel behaviour of the focal individual was monitored during the trial. Trials were filmed from 2–5 m with a Canon 70D DSLR camera with a Canon 50 mm f1.8 lens (both Canon Inc, Tokyo, Japan). Audio recording was embedded in the video track via an attached RODE VideoMic Pro shotgun microphone (RØDE Microphones, Sydney, Australia). The experimenter dictated information that might not have been clear on the video/audio recordings: confirmation of any surveillance calls and commentary on any head scanning or distraction (see Table 1 and below for details). In the audience experiment, focal individuals were filmed for a 10 min observation period from the beginning of the playback. In the satiation and danger experiment, focal individuals were filmed for a 15 min observation period from the start of the playback (230 s playback period and subsequent time to total 15 min).

Videos were watched using a VLC Media Player (VideoLAN, Paris, France) to record detailed information on sentinel behaviour. A sentinel was classed as an individual that adopted a position with its feet at least 10 cm above the ground and remained vigilant for at least 10 s (as in Kern & Radford, 2013, 2018). Seven response variables were decoded from the video data in three main sentinel elements, listed in Table 1. The surveillance call and distraction responses were originally collected as frequency data within a sentinel bout, but later transformed to binary measures due to a high number of bouts where neither behaviour was presented.

Ethical Note

All work was conducted with permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013), the Ethical Committee of the University of Pretoria, South Africa and the Ethical Review Group of the University of Bristol, U.K. (University Investigator Number: UIN/17/074). Only those individuals comfortable with close presence of experimenters were included in the study. Alarm call playbacks were limited to two per group per day, far lower than the natural rate during the study period.

Statistical Analyses

Data on focal individual behaviour were analysed using R statistics build version 3.4.2 (R Core Team, 2019). Mixed models were used due to the repeated sampling of individuals and groups created by the matched design. Generalized linear mixed models (GLMMs) were generated using the ‘glmer’ function from the lme4 package (Bates, Mächler, Bolker, & Walker, 2015; v.1.1–21). Likelihood data (becoming a sentinel, giving surveillance calls, distraction) were modelled with binomial error distributions; time until first bout was modelled with a gamma error distribution; number of bouts was modelled with a Poisson error distribution; and mean bout duration was modelled with an inverse-Gaussian error distribution (full specification given in Appendix Tables A1–A4). Mean data on head scan rates were parametric and therefore analysed via a linear mixed model (LMM) generated using the ‘lmer’ function (also lme4). Continuous predictors were centred and scaled to give variables with mean = 0 and SD = 1. For all models, Individual ID was nested within Group ID as random terms to control for inter-individual and intergroup differences; group structure did not change across the course of a set of trials for any individual, and an individual was only ever found in one group. In all models except that considering the number of bouts, the ‘blmer’/‘bglmer’ wrapper functions from the package blme (Chung, Rabe-Hesketh, Dorie, Gelman, & Liu, 2013; v.1.0–4) were used to prevent singular model fit. In these instances, the default Wishart covariance prior was used to provide a weakly informative prior to aid model fitting.

To begin analysis, a maximal model was created by fitting treatments (and their interaction in the satiation and danger experiment) and trial order as fixed terms. Within the satiation and danger experiment, for models analysing the likelihood of performing a sentinel bout and the number of bouts, trial duration was included as a fixed term. For models analysing within-bout characteristics, bout duration was included as a fixed term (full maximal model specifications listed in the Appendix Tables). Stepwise backwards elimination was then used to remove nonsignificant terms (Crawley, 2005) until the minimal model remained: the model at which further removal of terms caused a significant loss in explanatory power. This was determined by running a likelihood ratio test on the model with and the model without the term in question; a significant difference between these two models indicated a loss of explanatory power. Significant terms were subsequently removed from the minimal model one at a time, with the comparison between the resulting model and the minimal model generating the reported χ^2 and P values. Similarly, nonsignificant terms were tested by individually re-adding them to the minimal model. The effect size and SE for fixed terms, the intercept values and the variance ± SE for random terms were all derived from the minimal model.

Separate models were also run replacing trial order with either number of playbacks to the focal individual or number of playbacks to the focal individual's group (to consider eavesdropping); these measures were fitted separately as they were not independent and were, in some cases, highly correlated (Pearson correlation: $r_{ab} = 0.36–0.74$). There were no qualitative differences between the models including trial order and the number of playbacks to the focal individual, while the number of playbacks to the focal individual's group had no significant effects on any response measure. Thus, we present the output of the models containing trial order in the Results.

All data and R code used to produce all models presented are available in the Supplementary material.

RESULTS

Audience Experiment

The likelihood that a sentinel bout (Fig. 1a) was performed by the focal individual was significantly affected by playback treatment (Appendix Table A1). Individuals performed bouts in 11 of the 20 control trials, but in only four of the 20 trials when there was close call playback to simulate an audience (Fig. 1b).

Owing to the low number of sentinel bouts performed (sentinel bouts occurred in 15/40 trials, $N_{\text{Bouts}} = 28$), and to the majority occurring during the control trials (11/15 trials with sentinel bouts, 19/28 total bouts), there was insufficient statistical power to examine effects of the playback treatment on response variables relating to bout quantity decisions and within-bout characteristics.

Satiation and Danger Experiment

Initial bout decisions showed some response to both satiation and danger levels. The likelihood that a focal individual performed a sentinel bout was significantly affected by both satiation level and danger level, but not the interaction between the two factors (Appendix Table A2). Individuals were more likely to become a sentinel following a Fed (bouts in 22/26 trials) than a Control-Fed (16/26 trials) treatment (Fig. 1c), and also following a Danger (24/26 trials) than a No-Danger (14/26 trials) treatment (Fig. 1d). However, the time until the first sentinel bout was not significantly affected by satiation level, danger level or their interaction (Appendix Table A2).

Bout quantity decisions showed a strong contextual response to the treatments, with number of bouts performed and mean bout duration both significantly affected by satiation level (Appendix Table A3). The provisioning of a quarter of an egg (Fed) resulted

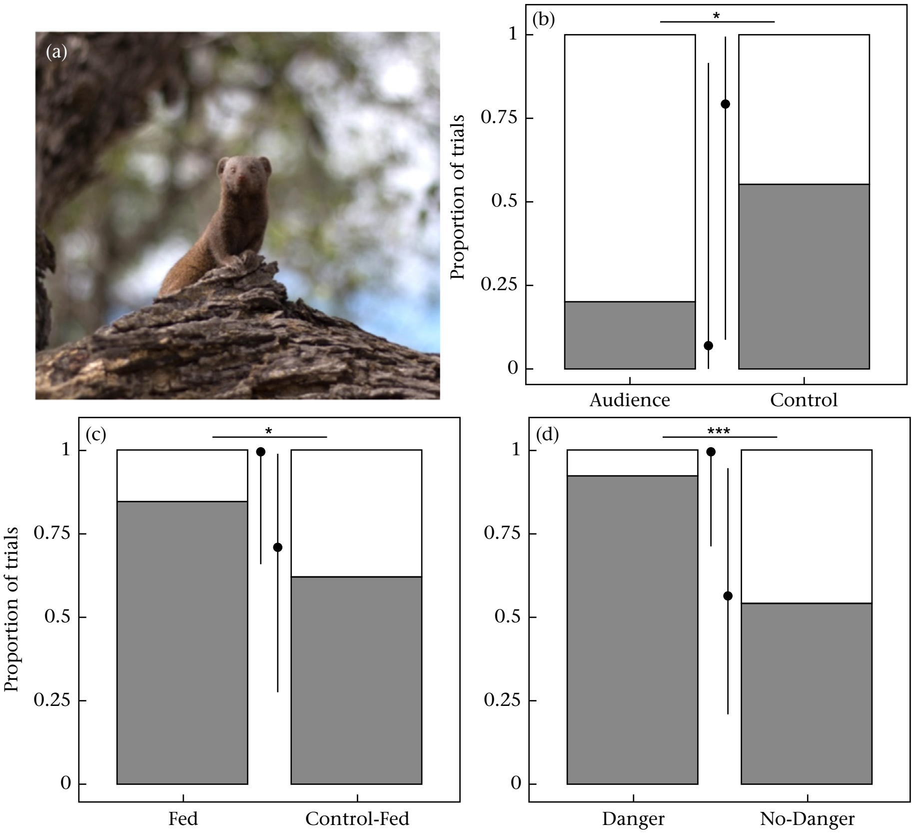

Figure 1. (a) A dwarf mongoose sentinel; (b, c, d) the effect of (b) a conspecific audience, (c) supplementary feeding and (d) playback treatments on the likelihood that an individual performed a sentinel bout. Grey bars represent trials where a sentinel bout was performed; white bars indicate trials where no sentinel bout was performed. Model predicted means and 95% confidence intervals are displayed. $^*P \leq 0.05$; $^{***}P \leq 0.001$. (b) $N_{Groups} = 5$, $N_{Individuals} = 20$, $N_{Trials} = 40$; (c, d) $N_{Groups} = 5$, $N_{Individuals} = 15$, $N_{Trials} = 52$.

in more bouts (Fig. 2a) and longer bouts (Fig. 2b) than in Control-Fed trials. There was no significant effect of danger level on mean bout duration, but danger level did have a significant effect on the number of bouts performed, with more sentinel bouts performed following alarm call playback (Danger) than control (No-Danger) playback (Appendix Table A3, Fig. 2c). There was no significant interaction between the feeding and playback treatments on the number of bouts performed or mean bout duration (Appendix Table A3).

Within-bout characteristics showed mixed responses to feeding and danger treatments. The likelihood that a focal individual produced surveillance calls during a sentinel bout was not significantly affected by feeding treatment, playback treatment or their interaction (Appendix Table A4). However, mean head scan rate was significantly affected by the interaction between the feeding and playback treatments, after controlling for a significant negative effect of sentinel bout duration (Appendix Table A4). When an individual was fed, there was no difference in scan rate between the two playback treatments, but individuals scanned at a higher rate in response to alarm call playback (Danger) than the control playback when Control-Fed (Fig. 3). Finally, there was no significant effect of feeding treatment, playback treatment or their interaction

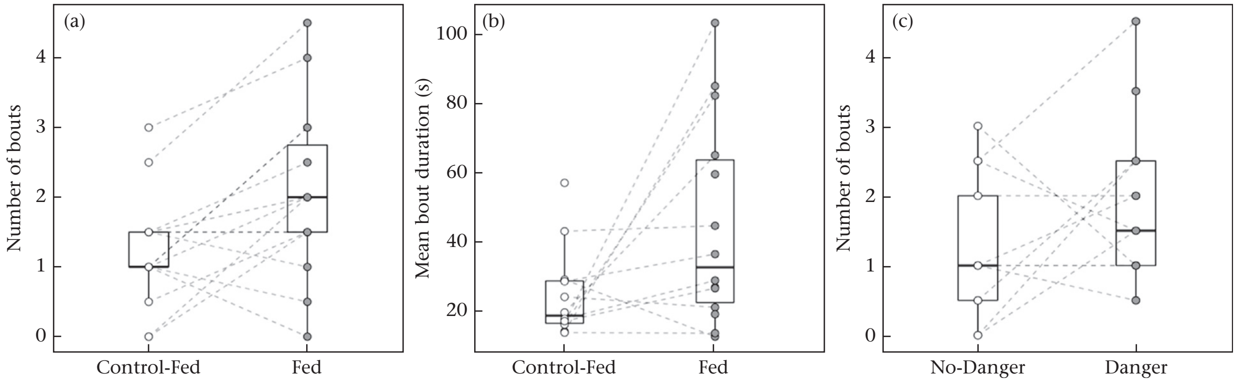

Figure 2. Effects of experimental treatments on bout quantity decisions. (a, b) Effect of feeding treatment on (a) number of bouts performed and (b) mean bout duration; (c) effect of playback treatment on number of sentinel bouts performed. Box plots display medians and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range. Points represents the mean value for each individual across both trials of the same treatment, with lines connecting individual values across treatment type. Orphan points with no corresponding partner (where an individual only performed sentinel bouts in one treatment type) are also plotted. $N_{Groups} = 5$, $N_{Individuals} = 15$, $N_{Bouts} =$ (a,c) 79 and (b) 38.

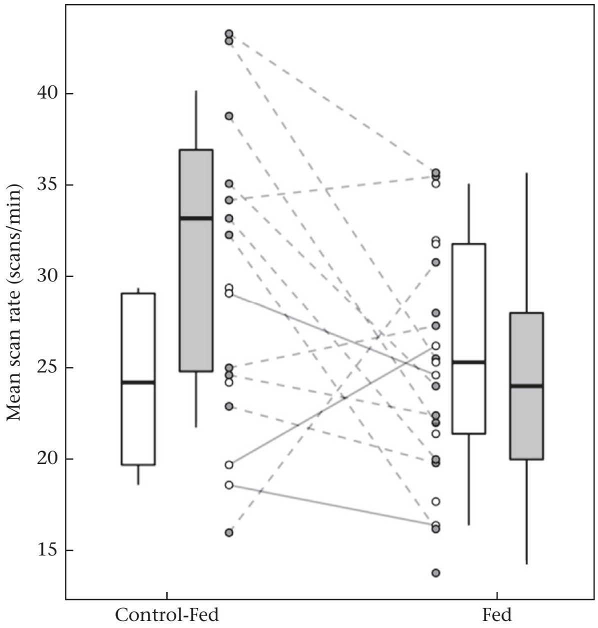

Figure 3. Effect of feeding and playback treatments on mean head scan rate during sentinel bouts. Box plots display medians and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range. White box plots/points represent No-Danger trials; grey box plots/points represent Danger trials. Each point represents the mean head scan rate for all bouts within one trial, with lines joining data from the same individual within playback treatment (solid lines for No-Danger, dashed for Danger). Orphan points with no corresponding partner are also plotted. $N_{\text{Groups}} = 5$, $N_{\text{Individuals}} = 15$, $N_{\text{Bouts}} = 79$, averaged to 38 means.

on the likelihood an individual became distracted during a sentinel bout, after controlling for a significant positive effect of bout duration (Appendix Table A4).

DISCUSSION

Dwarf mongooses altered their sentinel investment in the presence of a conspecific audience, as well as in response to changes in satiation and danger levels. Using field experiments, we found that a conspecific audience reduced the likelihood that individuals would perform sentinel bouts, while increases in both satiation and perceived danger caused individuals to increase their investment in all three main elements of sentinel behaviour to varying degrees. Initial bout and bout quantity decisions displayed responses largely in line with predictions; by also considering within-bout characteristics, we achieved fine-tuned assessment of sentinel attentiveness and found that internal and external factors interacted to influence sentinel behaviour. Overall, our results provide strong evidence for the context-dependent nature of sentinel behaviour, highlighting how individual contributions to group behaviours can vary in response to social, internal and environmental factors.

Contrary to our prediction, the simulated presence of a nearby group member (an opposite-sex dominant) resulted in a lower sentinel investment than in control conditions. Only one-fifth of individuals performed sentinel bouts when in the presence of a simulated audience, so there is no evidence that prestige effects are driving sentinel investments (Zahavi, 1990; Zahavi & Zahavi, 1997) as individuals do not seem to be using sentinel bouts as a signal of quality. This parallels results on the provisioning of young by chestnut-crowned babblers, *Pomatostomus ruficeps* (Nomano et al., 2013). Our experiment also provides no evidence that individuals are increasing investment in sentinel behaviour to increase cooperative benefits (Kern & Radford, 2018) although this was a short-term playback and so caution is needed with such interpretations. The audience-induced lower sentinel investment might instead be explained by a localized group size effect (Clutton-Brock et al., 1999; Rasa, 1989; Ridley & Raihani, 2007). It is unlikely that dwarf mongoose individuals are able to monitor accurately complete sentinel coverage, forager spread and potential group splits in the dense habitat found at the study site. Thus, it is possible that sentinel investment could be influenced by smaller-scale feedback loops, with individuals assessing their immediate environment (i.e. number and identity of conspecifics) and contributing more to sentinel behaviour when surrounded by fewer nearby conspecifics. An alternative explanation for the lower sentinel contributions in the simulated presence of a nearby conspecific relates to the contributions of others. Previous work has shown that pied babblers, *Turdoides bicolor*, were less likely to become a sentinel when the satiated state of a conspecific was conveyed through its close call rate (Bell et al., 2010). If dwarf mongoose close calls convey information not only about identity (Rubow, Cherry, & Sharpe, 2017) but also about current state, focal individuals would be able to moderate their own contributions accordingly. A third possibility is that accompanied individuals perceive their personal danger level to be lower than those foraging in isolation, resulting in a decreased need for vigilance (Radford & Ridley, 2007). These explanations are not mutually exclusive, and it is probable that individuals are integrating some, or all, of the above information and making decisions based on their own contributions and personal risk, as well as the contributions of others. Future work might profitably explore variation in sentinel responses dependent on the identity of the audience (e.g. comparing responses to dominant versus subordinate group members or those of the same versus the other sex), while ideally tracking the proximity of other group members (although this is logistically challenging in field conditions).

Satiation level and, to a lesser extent, danger level both had a significant effect on overall sentinel behaviour. As expected, additional food affected initial bout decisions, with a greater likelihood that an individual became a sentinel, although it did not reduce the time until the first sentinel bout. Bout quantity decisions were also affected, with an increase in both the total number of bouts performed and the duration of bouts compared to control conditions, showing that satiation levels influence both decisions regarding whether to perform sentinel behaviour and the characteristics of the bouts performed. This greater sentinel contribution when fed is a similar finding to previous empirical studies on other species (Bell et al., 2010; Clutton-Brock et al., 1999; Wright, Maklakov, et al., 2001), and matches the predictions of the theoretical model on state-dependent sentinel behaviour (Bednekoff, 1997). A larger contribution when satiated is probably due to individuals having more resources to invest, allowing a shift towards vigilance in the trade-off with foraging. There was some evidence that a greater danger level also induced increased investment in initial bout and bout quantity decisions, with a positive effect on the likelihood of sentinel behaviour and number of bouts performed, but no effect on time until first bout or mean bout duration. These results could indicate that in response to heightened danger levels, dwarf mongooses perform more frequent, as opposed to longer, vigilance bouts. An effect of danger level on sentinel behaviour is a qualitatively equivalent result to that of Kern and Radford (2014) with dwarf mongooses and findings in other species (Ridley et al., 2010; Sorato et al., 2012). Such responses provide further evidence for the general theory that vigilance should increase with perceived risk (Lima & Bednekoff, 1999a).

The changes in sentinel behaviour in response to tree squirrel alarm calls (which were used to simulate an increased predation risk) provide evidence that heterospecific information affects short to mid-term decision making. Eavesdropping on heterospecific alarm calls is relatively common in animals, including many mammals, birds and even lizards (Magrath, Haff, Fallow, & Radford, 2015), but most studies focus on the immediate reaction (i.e. likelihood of fleeing) to such signals of danger. As with pied babblers (Bell et al., 2009; Ridley et al., 2010), dwarf mongooses appear to use heterospecific warning signals to assess current threat levels and alter their sentinel contributions accordingly. The lack of an effect on the time until the first sentinel bout but an influence on the number of bouts indicates that the information is being retained and used past the very short term, influencing both initial bout and bout quantity decisions; heterospecific signals could have a longer-term and wider influence than generally considered (Magrath et al., 2015).

The assessment of within-bout characteristics demonstrated no treatment effect on either surveillance call likelihood or distraction levels, but that head-scanning rate was affected by an interaction between feeding and playback treatments. The lack of a significant effect on vocalization and distraction likelihood could indicate that sentinel bouts are more consistent and stereotyped in dwarf mongooses than other species; it is also possible that the low frequency of observed occurrences prevented the detection of more subtle effects. In terms of head scanning, the greatest rate was found when individuals were unfed and heard alarm call playbacks. An increase in scanning when danger levels were higher was in line with predictions, but it is less intuitive why the effect was apparent only in the Control-Fed treatment. Although matching predictions of an interaction between treatments, the result was not quite what would be predicted from the risk allocation hypothesis (Lima & Bednekoff, 1999b), where both Fed treatments should have shown increased investment relative to Control-Fed × No-Danger. One possibility is that sentinels are using their elevated position to check not only for danger, but also potentially for foraging opportunities when they finish the bout. That is, they may be scanning to detect the likely presence of good feeding patches as indicated by prolonged foraging in one place by groupmates; use of such 'public' information has been shown in various other contexts (Danchin, Giraldeau, Valone, & Wagner, 2004). While it has been suggested before that sentinels may be collecting information on more than just predator presence, tests of different sentinel functions are required; it is possible that sentinels can also gain benefits by scanning for out-group threats (Morris-Drake, Christensen, Kern, & Radford, 2019), rival mating competitors (Walker, York, & Young, 2016) and potential mating opportunities (Clutton-Brock et al., 2002). While thought provoking, note that the significance of the head-scanning interaction term was marginal. In general, the scanning-rate result indicates that different factors can interact in their influence, but the likelihood of this may vary across behavioural scales. By their nature, different behavioural responses will have different outcomes for fitness (e.g. bout duration affects both predation risk and foraging efficacy, while within-bout characteristics may only directly affect the former), and as such may be differentially impacted by the interaction between factors.

Studies of sentinel contributions often frame results in relation to selfish versus cooperative arguments; our findings could be interpreted from both perspectives. The changes in sentinel behaviour exhibited by dwarf mongooses in our experiments could result from selfish decisions: for instance, individuals might have decided there is less need to contribute when others are nearby and can be vigilant, and to contribute more when their personal cost is lower (i.e. when they are satiated) or their personal benefit is higher (i.e. when they are more at risk from predation), or if sentinels are safer than foragers (Bednekoff, 1997; Wright, Berg, et al., 2001). However, they could also result from cooperative benefits: for example, the individual may be gaining indirect or direct benefits by acting as a sentinel, especially when danger levels are higher for all group members. In dwarf mongooses, it is unlikely that sentinel contributions are entirely selfish, as individuals regularly produce surveillance calls (Kern & Radford, 2013) that probably benefit other foragers (Hollén et al., 2008; Rauber & Manser, 2017), as well as receiving direct grooming benefits from groupmates (Kern & Radford, 2018). As such, further experimental work, including robust quantification of the costs and benefits to the sentinel and other group members in different circumstances, is required to disentangle individual motives.

Our field-based experimental work adds to the body of evidence that contributions to group behaviours are context dependent with both internal and external factors integrating to form individual context. Individual contributions were lower when in the proximity of others, and greater when satiated or when perceived danger was higher, largely matching our predictions of how individuals should maximize returns on their contributions. Further investigation is needed on the mechanisms that maintain context dependency and the extent to which individual context is homogeneous within groups; groupmates are unlikely to share identical experiences, with implications for assessing individual investment decisions. It would also be of interest to partition variation in contributions between fixed and contextual factors to determine their relative importance. Sentinel behaviour provides a model and tractable system for such investigations, and thus the furthering of our understanding of sociality.

Acknowledgments

We thank Henny Yeates for allowing us to conduct research on Sorabi Rock Lodge. Thanks to Sophie Manson and Jenny Linden for their invaluable contributions in the field. Further thanks to Sinead English and Joah Madden for their insightful comments on the manuscript.

Supplementary Material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.anbehav.2020.04.021.

References

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Bednekoff, P. A. (1997). Mutualism among safe, selfish sentinels: A dynamic game. *American Naturalist, 150*(3), 373–392. https://doi.org/10.1086/286070.

Bednekoff, P. A. (2015). Sentinel behavior: A review and prospectus. *Advances in the Study of Behavior, 47*, 115–145. https://doi.org/10.1016/bs.asb.2015.02.001.

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*(11), 895–903. https://doi.org/10.1046/j.0179-1613.2003.00926.x.

Bell, M. B. V., Radford, A. N., Rose, R., Wade, H. M., & Ridley, A. R. (2009). The value of constant surveillance in a risky environment. *Proceedings of the Royal Society B: Biological Sciences, 276*(1669), 2997–3005. https://doi.org/10.1098/rspb.2009.0276.

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 B: Biological Sciences, 277*(1698), 3223–3228. https://doi.org/10.1098/rspb.2010.0643.

Boesch, C. (1994). Cooperative hunting in wild chipanzees. *Animal Behaviour, 48*(3), 653–667. https://doi.org/10.1006/anbe.1994.1285.

Boland, C. R. J., Heinsohn, R., & Cockburn, A. (1997a). Deception by helpers in cooperatively breeding white-winged choughs and its experimental manipulation. *Behavioral Ecology and Sociobiology, 41*(4), 251–256. https://doi.org/10.1007/s002650050386.

Boland, C. R. J., Heinsohn, R., & Cockburn, A. (1997b). Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. *Journal of Animal Ecology, 66*(5), 683–691. https://doi.org/10.2307/5921.

Bshary, R., Hohner, A., Ait-El-Djoudi, K., & Fricke, H. (2006). Interspecific communicative and coordinated hunting between groupers and giant moray eels in the red sea. *PLoS Biology, 4*(12), 2393–2398. https://doi.org/10.1371/journal.pbio.0040431.

Canestrari, D., Vera, R., Chiarati, E., Marcos, J. M., Vila, M., & Baglione, V. (2010). False feeding: The trade-off between chick hunger and caregivers needs in cooperative crows. *Behavioral Ecology, 21*(2), 233–241. https://doi.org/10.1093/beheco/arp177.

Chung, Y., Rabe-Hesketh, S., Dorie, V., Gelman, A., & Liu, J. (2013). A nondegenerate penalized likelihood estimator for variance parameters in multilevel models. *Psychometrika, 78*(4), 685–709. https://doi.org/10.1007/s11336-013-9328-2.

Clutton-Brock, T. H. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science, 296*(5565), 69–72. https://doi.org/10.1126/science.296.5565.69.

Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M. M., Gaynor, D., Kansky, R., Griffin, A. S., et al. (1999). Selfish sentinels in cooperative mammals. *Science, 284*(5420), 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*(5579), 253–256. https://doi.org/10.1126/science.1071412.

Collier, K., Radford, A. N., Townsend, S. W., & Manser, M. B. (2017). Wild dwarf mongooses produce general alert and predator-specific alarm calls. *Behavioral Ecology, 28*(5), 1293–1301. https://doi.org/10.1093/beheco/arx091.

Crawley, M. J. (2005). *Statistics: An Introduction using R.* Chichester, U.K.: J. Wiley.

Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour, 50*(5), 1325–1339. https://doi.org/10.1016/0003-3472(95)80048-4.

Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbours to cultural evolution. *American Association for the Advancement of Science, 305*(5683), 487–491. https://doi.org/10.1126/science.1098254.

Desjardins, J. K., Stiver, K. A., Fitzpatrick, J. L., & Balshine, S. (2008). Differential responses to territory intrusions in cooperatively breeding fish. *Animal Behaviour, 75*(2), 595–604. https://doi.org/10.1016/j.anbehav.2007.05.025.

Graw, B., & Manser, M. B. (2007). The function of mobbing in cooperative meerkats. *Animal Behaviour, 74*(3), 507–517. https://doi.org/10.1016/j.anbehav.2006.11.021.

Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*. https://doi.org/10.1007/s00265-004-0865-7.

Hollén, L. I., Bell, M. B. V., & Radford, A. N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology, 18*(8), 576–579. https://doi.org/10.1016/j.cub.2008.02.078.

Jennions, M. D., & Macdonald, D. W. (1994). Cooperative breeding in mammals. *Trends in Ecology & Evolution, 9*(3), 89–93. https://doi.org/10.1016/0169-5347(94)90202-X.

Kern, J. M., Laker, P. R., & Radford, A. N. (2017). Contextual variation in the alarm call responses of dwarf mongooses, *Helogale parvula*. *Animal Behaviour, 127*, 43–51. https://doi.org/10.1016/j.anbehav.2017.03.002.

Kern, J. M., & Radford, A. N. (2013). Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*. *Animal Behaviour, 85*(5), 967–975. https://doi.org/10.1016/j.anbehav.2013.02.020.

Kern, J. M., & Radford, A. N. (2014). Sentinel dwarf mongooses, *Helogale parvula*, exhibit flexible decision making in relation to predation risk. *Animal Behaviour, 98*, 185–192. https://doi.org/10.1016/j.anbehav.2014.10.012.

Kern, J. M., & Radford, A. N. (2017). Reduced social-information provision by immigrants and use by residents following dispersal. *Current Biology, 27*(23), R1266–R1267. https://doi.org/10.1016/j.cub.2017.10.045.

Kern, J. M., & Radford, A. N. (2018). Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. *Proceedings of the National Academy of Sciences of the United States of America, 115*(24), 6255–6260. https://doi.org/10.1073/pnas.1801000115.

Kern, J. M., & Radford, A. N. (2020). *Strongly bonded individuals prefer to forage together in cooperatively breeding dwarf mongoose groups.* Submitted manuscript.

Kern, J. M., Sumner, S., & Radford, A. N. (2016). Sentinel dominance status influences forager use of social information. *Behavioral Ecology, 27*(4), 1053–1060. https://doi.org/10.1093/beheco/arv240.

Koenig, W., & Dickinson, J. (2004). *Ecology and evolution of cooperative breeding in birds.* Cambridge, U.K.: Cambridge University Press.

Koenig, W., Mumme, R., & Pitelka, F. (1983). Female roles in cooperatively breeding acorn woodpeckers. In S. Wasser (Ed.), *Social behaviour of female vertebrates* (pp. 235–261). New York, NY: Academic Press.

Lima, S. L., & Bednekoff, P. A. (1999a). Back to the basics of antipredatory vigilance: Can nonvigilant animals detect attack? *Animal Behaviour, 58*(3), 537–543. https://doi.org/10.1006/anbe.1999.1182.

Lima, S. L., & Bednekoff, P. A. (1999b). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *American Naturalist, 153*(6), 649–659. https://doi.org/10.1086/303202.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews, 90*(2), 560–586. https://doi.org/10.1111/brv.12122.

McGowan, K. J., & Woolfenden, G. E. (1989). A sentinel system in the Florida scrub jay. *Animal Behaviour, 37*(6), 1000–1006. https://doi.org/10.1016/0003-3472(89)90144-9.

Morris-Drake, A., Bracken, A. M., Kern, J. M., & Radford, A. N. (2017). Anthropogenic noise alters dwarf mongoose responses to heterospecific alarm calls. *Environmental Pollution, 223*, 476–483. https://doi.org/10.1016/j.envpol.2017.01.049.

Morris-Drake, A., Christensen, C., Kern, J. M., & Radford, A. N. (2019). Experimental field evidence that out-group threats influence within-group behavior. *Behavioral Ecology, 30*(5), 1425–1435. https://doi.org/10.1093/beheco/arz095.

Morris-Drake, A., Kern, J. M., & Radford, A. N. (2016). Cross-modal impacts of anthropogenic noise on information use. *Current Biology, 26*(20), R911–R912. https://doi.org/10.1016/j.cub.2016.08.064.

Nomano, F. Y., Browning, L. E., Rollins, L. A., Nakagawa, S., Griffith, S. C., & Russell, A. F. (2013). Feeding nestlings does not function as a signal of social prestige in cooperatively breeding chestnut-crowned babblers. *Animal Behaviour, 86*(2), 277–289. https://doi.org/10.1016/j.anbehav.2013.05.015.

Novaro, A. J., Moraga, C. A., Briceño, C., Funes, M. C., & Marino, A. (2009). First records of culpeo (*Lycalopex culpaeus*) attacks and cooperative defense by guanacos (*Lama guanicoe*). *Mammalia, 73*(2), 148–150. https://doi.org/10.1515/MAMM.2009.016.

Owings, D. H., & Coss, R. G. (1977). Snake mobbing by California ground squirrels: Adaptive variation and ontogeny. *Behaviour, 50–69*. https://doi.org/10.1163/156853977x00045.

R Core Team. (2019). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Radford, A. N. (2003). Territorial vocal rallying in the green woodhoopoe: Influence of rival group size and composition. *Animal Behaviour, 66*(6), 1035–1044. https://doi.org/10.1006/anbe.2003.2292.

Radford, A. N., & Ridley, A. R. (2007). Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance. *Biology Letters, 3*(3), 249–252. https://doi.org/10.1098/rsbl.2007.0110.

Rasa, O. A. E. (1986). Coordinated vigilance in dwarf mongoose family groups: The ‘watchman's song’ hypothesis and the costs of guarding. *Ethology, 71*(4), 340–344. https://doi.org/10.1111/j.1439-0310.1986.tb00598.x.

Rasa, O. A. E. (1989). The costs and effectiveness of vigilance behaviour in the dwarf mongoose: Implications for fitness and optimal group size. *Ethology Ecology and Evolution, 1*(3), 265–282. https://doi.org/10.1080/08927014.1989.9525516.

Rauber, R., & Manser, M. B. (2017). Discrete call types referring to predation risk enhance the efficiency of the meerkat sentinel system. *Scientific Reports, 7*, 44436. https://doi.org/10.1038/srep44436.

Ridley, A. R., & Raihani, N. J. (2007). Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology, 18*(2), 324–330. https://doi.org/10.1093/beheco/arl092.

Ridley, A. R., Raihani, N. J., & Bell, M. B. V. (2010). Experimental evidence that sentinel behaviour is affected by risk. *Biology Letters, 6*(4), 445–448. https://doi.org/10.1098/rsbl.2010.0023.

Rubow, J., Cherry, M. I., & Sharpe, L. L. (2017). Dwarf mongooses use sex and identity cues in isolation calls to discriminate between callers. *Animal Behaviour, 127*, 23–31. https://doi.org/10.1016/j.anbehav.2017.02.019.

Santema, P., & Clutton-Brock, T. H. (2013). Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Animal Behaviour, 85*(3), 655–661. https://doi.org/10.1016/j.anbehav.2012.12.029.

Seddon, N., & Tobias, J. A. (2003). Communal singing in the cooperatively breeding subdesert mesite *Monias benschi*: Evidence of numerical assessment? *Journal of Avian Biology, 34*(1), 72–80. https://doi.org/10.1034/j.1600-048X.2003.03067.x.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour, 28*(4), 1070–1094. https://doi.org/10.1016/S0003-3472(80)80097-2.

Shah, S. S., Greig, E. I., MacLean, S. A., & Bonter, D. N. (2015). Risk-based alarm calling in a nonpasserine bird. *Animal Behaviour, 106*, 129–136. https://doi.org/10.1016/j.anbehav.2015.05.011.

Sharpe, L. L., Joustra, A. S., & Cherry, M. I. (2010). The presence of an avian co-forager reduces vigilance in a cooperative mammal. *Biology Letters, 6*(4), 475–477. https://doi.org/10.1098/rsbl.2009.1016.

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., et al. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology, 64*(12), 1959–1966. https://doi.org/10.1007/s00265-010-1006-0.

Sorato, E., Gullett, P. R., Griffith, S. C., & Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species. *Animal Behaviour, 84*(4), 823–834. https://doi.org/10.1016/j.anbehav.2012.07.003.

Taborsky, M. (1984). Broodcare helpers in the cichlid fish *Lamprologus brichardi*: Their costs and benefits. *Animal Behaviour, 32*(4), 1236–1252. https://doi.org/10.1016/S0003-3472(84)80241-9.

Templeton, C. N., & Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences, 104*(13), 5479–5482. https://doi.org/10.1073/pnas.0605183104.

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*(5), 1461–1470. https://doi.org/10.1093/beheco/arw064.

Wright, J., Berg, E., De Kort, S. R., Khazin, V., & Maklakov, A. A. (2001). Safe selfish sentinels in a cooperative bird. *Journal of Animal Ecology, 70*(6), 1070–1079. https://doi.org/10.1046/j.0021-8790.2001.00565.x.

Wright, J., & Dingemanse, N. J. (1999). Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Animal Behaviour, 58*(2), 345–350. https://doi.org/10.1006/anbe.1999.1152.

Wright, J., Maklakov, A. A., & Khazin, V. (2001). State-dependent sentinels: An experimental study in the Arabian babbler. *Proceedings of the Royal Society B: Biological Sciences, 268*(1469), 821–826. https://doi.org/10.1098/rspb.2000.1574.

Zaccaroni, M., Binazzi, R., Massolo, A., & Dessì-Fulgheri, F. (2013). Audience effect on aerial alarm calls in the monogamous red-legged partridge. *Ethology Ecology and Evolution, 25*(4), 366–376. https://doi.org/10.1080/03949370.2013.798352.

Zahavi, A. (1990). Arabian babblers: The quest for social status in a cooperative breeder. In P. Stacey, & W. 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.

Zöttl, M., Vullioud, P., Mendonça, R., Ticó, M. T., Gaynor, D., Mitchell, A., et al. (2016). Differences in cooperative behavior among Damaraland mole rats are consequences of an age-related polyethism. *Proceedings of the National Academy of Sciences, 113*(37), 10382–10387. https://doi.org/10.1073/pnas.1607885113.

Zuberbühler, K. (2008). Audience effects. *Current Biology, 18*(5), R189–R190. https://doi.org/10.1016/j.cub.2007.12.041.

Appendix

Table A1

Audience experiment: factors affecting whether an individual performed a sentinel bout

Effect	χ^2	*df*	*P*	Effect ± SE
Treatment	4.65	1	**0.031**	**−3.97 ± 2.95**
Trial Order	3.74	1	0.085	
Intercept				1.34 ± 1.90
Group ID				8.73 ± 2.96
Individual ID				8.13 ± 2.85

GLMM fitted with binomial error using a logit link function, with Wishart covariance prior specified ($N_{\text{Individuals}} = 20$, $N_{\text{Groups}} = 5$, $N_{\text{Trials}} = 40$). Maximal model: Bout_Y/N ~ Treatment + Trial Order + (1|Group_ID/Individual_ID). Bold term was retained in the minimal model; random effects (variance ± SE) are italicized.

Table A2

Feeding/Danger experiment: factors affecting initial bout decisions

Effect	χ^2	*df*	*P*	Effect ± SE
Likelihood of becoming a sentinel				
Feeding	5.65	1	**0.017**	**1.43 ± 0.62**
Playback	11.91	1	**<0.001**	**2.22 ± 0.85**
Feeding*Playback	0.24	1	0.62	
Trial Order	0.01	1	0.90	
Trial Duration	0.32	1	0.57	
Intercept				−0.90 ± 0.73
Group ID				1.08 ± 1.04
Individual ID				0.56 ± 0.75
Time until first bout				
Feeding	3.72	1	0.054	
Playback	0.009	1	0.98	
Feeding*Playback	0.175	1	0.19	
Trial Order	1.91	1	0.16	
Intercept				5.10 ± 0.26
Group ID				0.076 ± 0.028
Individual ID				0.089 ± 0.030

Likelihood of becoming a sentinel: GLMM fitted with binomial error using a cloglog link function, with Wishart covariance prior specified ($N_{\text{Individuals}} = 15$, $N_{\text{Groups}} = 5$, $N_{\text{Trials}} = 52$); time until first bout was performed: GLMM fitted with gamma error using a log link function, with Wishart covariance prior specified ($N_{\text{Individuals}} = 15$, $N_{\text{Groups}} = 5$, $N_{\text{Bouts}} = 38$). Maximal model: Response ~ Feeding + Playback + Feeding:Playback + Trial Duration ('likelihood of becoming a sentinel' only) + Trial Order. Bold terms were retained in the minimal model; random effects (variance ± SE) are italicized.

Table A3

Feeding/Danger experiment: factors affecting bout quantity decisions

Effect	χ^2	*df*	*P*	Effect ± SE
Number of bouts				
Feeding	5.26	1	**0.022**	**0.33 ± 0.14**
Playback	4.93	1	**0.026**	**0.31 ± 0.14**
Feeding*Playback	1.64	1	0.20	
Trial Order	4.27	1	**0.039**	**−0.14 ± 0.07**
Trial Duration	0.33	1	0.57	
Intercept				1.22 ± 0.22
Group ID				0.025 ± 0.16
Individual ID				0.003 ± 0.056
Mean bout duration				
Feeding	7.64	1	**0.006**	**0.59 ± 0.21**
Playback	2.09	1	0.15	
Feeding*Playback	2.23	1	0.33	
Trial Order	3.60	1	0.058	
Intercept				−1.47 ± 0.19
Group ID				0.064 ± 0.25
Individual ID				0.061 ± 0.25

Number of sentinel bouts performed: GLMM fitted with Poisson error using a sqrt link function ($N_{\text{Individuals}} = 15$, $N_{\text{Groups}} = 5$, $N_{\text{Bouts}} = 81$); mean bout duration: GLMM fitted with inverse-Gaussian error using a log link function, with Wishart covariance prior specified ($N_{\text{Individuals}} = 15$, $N_{\text{Groups}} = 5$, $N_{\text{Means}} = 38$). Mean bout duration data were scaled down by a factor of 100 to aid model convergence. Maximal model: Response ~ Feeding + Playback + Feeding:Playback + Trial Duration ('number of bouts' only) + Trial order. Bold terms were retained in the minimal model; random effects (variance ± SE) are italicized.

Table A4

Feeding/Danger experiment: factors affecting within-bout characteristics

Effect	χ^2	*df*	*P*	Effect ± SE
Vocalization				
Feeding	0.045	1	0.83	
Playback	0.12	1	0.73	
Feeding*Playback	0.16	1	0.98	
Trial Order	1.59	1	0.21	
Bout Duration	0.83	1	0.36	
Intercept				−1.29 ± 0.46
Group ID				0.40 ± 0.63
Individual ID				0.34 ± 0.59
Mean scan rate				
Feeding				
Playback				
Feeding*Playback	4.0	1	**0.046**	**−8.95 ± 4.38**
Trial Order	<0.01	1	0.99	
Mean Bout Duration	8.13	1	**0.004**	**−11.38 ± 4.08**
Intercept				27.67 ± 3.40
Group ID				8.43 ± 2.91
Individual ID				8.44 ± 2.91
Distraction				
Feeding	1.18	1	0.28	
Playback	2.51	1	**0.11**	
Feeding*Playback	6.31	1	0.098	
Trial Order	0.11	1	0.74	
Bout Duration	18.34	1	**<0.001**	**0.03 ± 0.01**
Intercept				−2.25 ± 0.64
Group ID				0.38 ± 0.62
Individual ID				0.70 ± 0.84

Whether a sentinel vocalized during a bout: GLMM fitted with binomial error using a logit link function, with Wishart covariance prior specified ($N_{\text{Individuals}} = 15$, $N_{\text{Groups}} = 5$, $N_{\text{Bouts}} = 79$); mean scanning rate: LMM fitted, with Wishart covariance prior specified ($N_{\text{Individuals}} = 15$, $N_{\text{Groups}} = 5$, $N_{\text{Means}} = 38$); whether a sentinel became distracted during a bout: GLMM fitted with binomial error using a logit link function, with Wishart covariance prior specified ($N_{\text{Individuals}} = 15$, $N_{\text{Groups}} = 5$, $N_{\text{Bouts}} = 79$). Maximal model: Response ~ Feeding + Playback + Feeding:Playback + Bout Duration + Trial order + (1|Group_ID/Individual_ID). Bold terms were retained in the minimal model; random effects (variance ± SE) are italicized.