Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*

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Social information is invaluable in assessing the need for antipredator behaviour. Individuals can acquire such information by observing the behaviour of others, but reliance on visual cues may be undermined by visual obstructions and social monitoring is often incompatible with foraging. Vocal communication does not require the close proximity of senders and receivers or the suspension of other activities, and there is increasing evidence that foragers can use vocalizations to inform decisions about their own vigilance. However, less work has focused on what factors influence signallers in this context. We used detailed behavioural observations and a playback experiment manipulating perceived risk to investigate the calling behaviour of dwarf mongoose sentinels. Sentinels vocalized more often in dense habitats and when foragers were further away, when visual cues were less likely to be useful. Sentinels also vocalized more in situations most advantageous to others, including when groupmates were likely to be distracted (e.g. when babysitting or foraging) and following an alarm call; sentinels may provide an 'all clear' signal. Call rate was reduced in high-risk situations, such as immediately after an alarm call. Individuals of different age, sex and dominance status varied in their likelihood of calling and their response to situations of similar risk, probably because of different cost–benefit trade-offs for separate classes. Our study offers strong evidence that dwarf mongoose sentinels are adjusting their vocal behaviour both to enhance the likelihood that groupmates are aware of their presence and to provide potentially valuable social information about current risk.

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Information reduces uncertainty and aids accurate decision making (Dall et al. 2005). In addition to interacting personally with the environment, individuals can obtain information by monitoring the signals and cues available from others (Giraldeau et al. 2002; Danchin et al. 2004; Bradbury & Vehrencamp 2012). These social sources can increase the quality and speed, and reduce the cost, of information acquisition (Giraldeau et al. 2002). Such benefits are likely to be of particular importance in antipredator contexts, when decisions are crucial to survival.

Individuals can obtain risk estimates by observing the behaviour of groupmates (Treves et al. 2001; Pays et al. 2010). However, reliance on visual cues may be undermined by environmental obstructions (Quenette 1990) or the geometric arrangement of foraging group members (Bekoff 1995). Moreover, although some species are able to scan for information and forage simultaneously, often these activities are mutually exclusive or detrimental to one another, and feeding must be suspended for efficient social

monitoring to occur (Lima & Bednekoff 1999). While the transmission of vocalizations can also be disrupted by environmental factors, such as wind speed and background noise (Quinn et al. 2006; Hollén et al. 2011), vocal communication does not rely on the same close proximity of signallers and receivers nor on the suspension of other activities. It has become increasingly apparent that assessments of risk can therefore be based, at least in part, on vocal information from others.

Alarm calls, acoustic signals that warn of imminent potential danger, are the most obvious vocal source of social information relating to predation (Caro 2005; Hollén & Radford 2009). Alarm calls often provide considerable additional information about the nature and urgency of the threat (Seyfarth et al. 1980; Evans et al. 1993; Manser 2001), and receivers have evolved to respond appropriately to the warning vocalizations of both conspecifics and heterospecifics (Manser 2001; Seyfarth & Cheney 2003). There is also mounting evidence that alarm call production is sensitive to both social and ecological contexts (Kokolakis et al. 2010; Townsend et al. 2012). However, it is not just information about immediate threats that is important. To optimize the trade-off between vigilance and foraging, and to ensure the most appropriate response to alarm calls (which can be irrelevant, inaccurate or even

deceptive), individuals should constantly update their assessment of background risk (Bell et al. 2009). Regular personal assessment of the environment may compromise foraging (Lima & Bednekoff 1999) and so social information is also valuable in this context (Bell et al. 2009; Radford et al. 2011). For example, individuals have been shown to adjust their vigilance behaviour in response to the 'close' calls of fellow foragers, which can indicate to a receiver its group size and position within it (Radford & Ridley 2007), as well as the recent vigilance activity of the caller (Townsend et al. 2011).

Sentinel behaviour, in which an individual stationed in a prominent position scans for predators and warns groupmates of danger, has evolved in a number of social bird and mammal species (McGowan & Woolfenden 1989; Rasa 1989; Clutton-Brock et al. 1999; Ridley & Raihani 2007), and is known to vary with perceived risk (Ridley et al. 2010). A key component of sentinel behaviour is efficient communication of information (Bednekoff 2001). In addition to alarm calls, sentinels in a range of taxa give soft surveillance/close calls, the so-called 'watchman's song' (Wickler 1985). While not essential to sentinel behaviour, the watchman's song provides information about sentinel presence, identity and height (Manser 1999; Hollén et al. 2008; Radford et al. 2009, 2011), and current likelihood of predatory attack (Bell et al. 2009), enhancing efficient coordination of vigilance and rotation of guards, and allowing group members to optimize the foraging–vigilance trade-off (Rasa 1986a; Manser 1999; Hollén et al. 2008; Bell et al. 2010). Studies have tended to focus on the response of receivers to the information provided by signalling sentinels, with far less work considering the sender's perspective (but see Bell et al. 2009, 2010).

To investigate the ecological, social and individual factors influencing calling in relation to risk, and particularly that of sentinels, we studied the vocal behaviour of dwarf mongooses. Dwarf mongooses are cooperatively breeding carnivores living in groups of up to 30 individuals (Rasa 1977). The dominant pair monopolizes reproduction, with subordinates (related individuals or unrelated immigrants) of both sexes helping to raise young (Keane et al. 1994). Dwarf mongooses obtain most of their food by digging and are consequently unable to forage and show vigilance behaviour simultaneously (Rasa 1989). As a result of their small size (<300 g), dwarf mongooses are at risk from a large number of avian and terrestrial predators (Rasa 1986a), and while foragers do pause to scan the surrounding area, a sentinel is posted for approximately 40% of foraging time (Sharpe et al. 2010). Most group members take part in sentinel duty, but there is variation in the investment of individual classes (Rasa 1989; Sharpe et al. 2010). Dwarf mongoose sentinels are known to give the watchman's song (Rasa 1986a), but they do not vocalize during every bout; there is also considerable variation in call rate when they do vocalize.

We used detailed observational data and a playback experiment designed to manipulate perceived risk to consider two main questions. First, how do fluctuating individual, social and ecological conditions influence production of the watchman's song? Selfish and cooperative benefits from giving this vocalization (Manser 1999; Hollén et al. 2008) must be weighed against the potential energy consumption and predator attraction costs of calling (Roulin 2001; Bell 2007; Haff & Magrath 2011). The watchman's song might therefore be expected when the benefits are particularly high (e.g. when visual communication is compromised in denser habitats or by the wider spread of foragers in larger groups) or when the costs are relatively low (e.g. when predation risk is lower). Since the cost–benefit trade-off of call production is likely to differ between individuals (Trillmich et al. 2004), we might also expect different usage of the watchman's song depending on age, sex and dominance status. Second, what factors affect the rate of calling when the watchman's song is produced? Recent evidence from pied

babblers, *Turdoides bicolor*, suggests that sentinel calling may vary depending on current risk (Bell et al. 2009). If perceived risk does play a role, then the call rate of dwarf mongoose sentinels might vary depending on relevant ecological (e.g. likely presence of predators) and social (e.g. presence of pups) conditions. Moreover, different individuals might be expected to categorize the same situation differently in terms of risk (Houston & McNamara 1988; Lea & Blumstein 2011), and so call rate is likely to vary depending on individual characteristics.

METHODS

Observational Data Collection

The study took place on Sorabi Rock Lodge Reserve, a 4 km^2 private game reserve in Limpopo Province, South Africa (24°11'S, 30°46'E), part of southern Africa's Savanna Biome. The lowveld climate is characterized by two distinct seasons: cold, dry winters (May–August) and hot, wet summers (September–April), with most rainfall occurring between October and April (mean annual rainfall 467 mm; September 1998–May 2012). Data were collected from four groups of wild dwarf mongooses (mean group size = 13.3), habituated to close observation (<5 m) on foot. Individuals were individually marked with blonde hair dye applied with an elongated paintbrush while group members were foraging (Wella UK Ltd, Surrey, U.K.) or were identifiable from natural features such as scars or facial irregularities. Group members were classified as either 'dominant' (male and female pair) or 'subordinate' (the remaining adults and yearlings). The dominant pair could be identified through observations of aggression, feeding displacement, scent marking and greeting behaviour (Rasa 1977). Adults were individuals older than 18 months that had survived two dry seasons; yearlings were individuals born during summer 2010–2011, and had survived one dry season. Individuals under 6 months of age were classified as pups and are the age class most vulnerable to predation (Rasa 1986a). This study was conducted under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013), the Ethical Review Group of the University of Bristol, U.K., and the ethical committee of Pretoria University, South Africa.

Observation sessions ($N = 182$, total 470 h) were conducted between November 2011 and May 2012, recording ad libitum occurrences of sentinel behaviour by known individuals. Sentinels were defined as individuals at least 10 cm above ground and actively scanning for predators while groupmates were engaged in other activities, primarily but not exclusively foraging (Sharpe et al. 2010). For all bouts of sentinel duty, we noted whether sentinels gave the watchman's song (at least one call heard). We excluded from analyses any cases in which distance or background noise prevented certain determination of whether an individual was vocalizing ($N = 56$), and partial bouts, in which the beginning or end was missed and thus it was not possible to determine for certain whether a seemingly silent sentinel had been so throughout ($N = 77$).

For each bout, we recorded (1) sentinel identity (and thus sex, social status and age); (2) initial post height (to the nearest 10 cm); (3) whether the sentinel was accompanied; (4) whether an alarm call was given during the bout; (5) bout duration (only bouts longer than 10 s were analysed); (6) group size; (7) horizontal distance from the sentinel to its nearest neighbour (<2 m, 2–5 m, >5 m, present but inside refuge); (8) location (refuge used for sleeping or elsewhere); (9) pup presence/absence; and (10) group activity. Activities were divided into babysitting, foraging, travelling and 'distracted' (including grooming, play and scent marking); full

descriptions of behaviours are available in Rasa (1977). We also noted wind speed (still < light breeze < strong wind) and habitat type (open, medium, dense). Open habitats (<20% ground cover) were sparsely vegetated sandy areas; medium habitats (20–60% ground cover) were characterized by low-lying shrubs, mainly *Heliotropium steudneri*; and dense habitats (>60% ground cover) were characterized by large numbers of thick shrubs such as *Abutilon angulatum* and *Pechuel-Loeschea leubnitziae*.

Vocal Recordings and Acoustic Analysis

Acoustic recordings of the watchman's song were collected in tandem with observations of sentinel behaviour from mid-November 2011 to the end of April 2012 (Fig. 1a). Vocalizations were recorded from a distance of 0.5–10 m onto a Transcend compact flash card (Transcend, Taipei, Taiwan, R.O.C), using a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ, U.S.A.) and a handheld highly directional Sennheiser ME 66 short gun microphone (Sennheiser UK, High Wycombe, Buckinghamshire, U.K.) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, U.K.). Call rate (mean calls/min) was calculated from the original sound files.

Playback Experiment

To assess the influence of elevated risk on the watchman's song, playbacks of conspecific alarm calls (and control close calls) were conducted between 28 February and 14 April 2012. Twenty-four playback tracks were constructed using six alarm calls recorded opportunistically (as per the watchman's song, above) from each of the four study groups. Each track was 5 s in length, comprising one alarm call by a known adult individual. Dwarf mongooses produce two main alarm call types (Beynon & Rasa 1989); we used only pulsed calls given to aerial predators to create playback tracks (Fig. 1b). As a contextual control treatment, close calls from the same adult individuals were used to construct six 5 s tracks per group (Fig. 1c). It is possible that any variation in behaviour following playback of the two sound treatments is caused by alarm calls being more plosive than close calls (see Hollén & Radford 2009; Rendall et al. 2009), rather than a perceived difference in risk, but this would also be true of natural calling situations. The vocalization (alarm or close call) began 2 s into the track with the remaining time comprising background noise. Tracks did not include any other dwarf mongoose vocalizations.

Each habituated group was presented with six pairs of playback trials, comprising an alarm call and a close call from the same group member. Calls were broadcast from an mp3 player (Apple Inc, Cupertino, CA, U.S.A.) connected to a single speaker (Excel Audio, Guangzhou, China) positioned on a wooden block at a height of 5 cm. Calls were played at an intensity similar to that of naturally occurring vocalizations, as assessed from the LED display of the solid-state recorder when re-recording playbacks from a distance comparable to that at which natural recordings were made (i.e. ca. 5 m). A sound pressure meter was not available, but this method was deemed to be more consistent and standardized than assessing playback intensity 'by ear'. The two treatments were separated by a minimum of 1 h and played when the entire group was foraging in the same habitat type. Playbacks took place when there had been no natural sentinel present for at least 5 min and no natural alarm call for at least 10 min. Following any major disturbances, such as an intergroup encounter or snake mobbing, a minimum of 15 min elapsed before the next playback took place. Subsequent pairs of trials were presented to each group a minimum of 36 h after the previous playback. Playbacks were balanced to ensure that each group received three trials in which an alarm call was presented first and three in which a close call was presented first, but the order of these pairs was randomized within each group. Following a playback, it was noted when a sentinel went on duty during the subsequent 10 min, whether the individual produced the watchman's song and its call rate.

Statistical Analysis

All analyses were performed using R version 2.15.1 (R Development Core Team 2012). All tests were two tailed and were considered significant at $P < 0.05$. We used linear mixed models (LMMs) and generalized linear mixed models (GLMMs), to take account of repeated measures from the same group, individual and/or playback pair. A GLMM with a binomial error structure and logit-link function was used to examine whether sentinels gave the watchman's song (see Table 1 for predictor variables). Following a square-root transformation, sentinel call rate was analysed using an LMM (see Table 2 for predictor variables). A GLMM with Poisson error structure and log-link function was used to examine differences in call rate before and after an alarm call in the same sentinel bout. The playback experiment was analysed using a GLMM with binomial error structure and logit-link function. GLMMs were conducted using the lmer function in package 'lme4' (Bates et al.
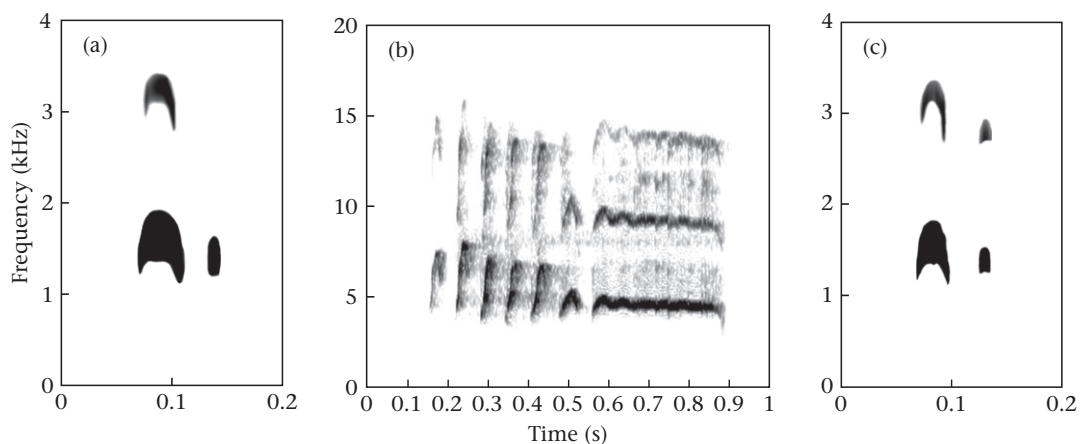

Figure 1. Spectrograms of dwarf mongoose vocalizations: (a) the watchman's song, (b) aerial alarm call and (c) close call. Spectrograms were created in Raven Pro 1.4 from vocalizations of the same subordinate adult male (Raven, Ithaca, NY, U.S.A.; FFT length 1024, Hamming window, 50% overlap).

Table 1
Generalized linear mixed model with binomial error distribution and logit-link function investigating the individual, social and ecological variables affecting when sentinels give the watchman's song

Fixed effect	Effect±SE	LRT−χ^2	df	P
Nearest-neighbour distance		21.32	3	**<0.0001**
<2 m	0±0			
2−5 m	1.297±0.405			
>5 m	0.659±0.549			
In refuge	−1.230±0.504			
Activity		19.24	3	**0.0002**
Babysitting	0±0			
Distracted	−1.669±0.755			
Foraging	−2.587±0.648			
Travelling	−3.080±0.810			
Habitat		12.40	2	**0.002**
Dense	0±0			
Medium	0.007±0.305			
Open	−3.205±1.182			
Age (yearling)	−0.925±0.363	6.50	1	**0.011**
Social status (subordinate)*group size	−0.412±0.105	18.31	1	**<0.0001**
Sex (male)*group size	−0.230±0.095	6.38	1	**0.012**
Location		3.13	1	0.077
Alarm call during bout		1.66	1	0.198
Duration		1.36	1	0.243
Height		0.76	1	0.385
Pups		0.14	1	0.705
Accompanied during bout		0.10	1	0.757
Period		0.03	1	0.875
Wind		0.01	2	0.999
Group ID	0.00			
Individual ID in group	<0.001			
Intercept	−4.533±1.373			

Individual identity nested within group was included as a random term ($N = 278$ bouts, 36 individuals, four groups), and the variance reported. Significant P values are in bold.

2012); the LMM was conducted using the lme function in package 'nlme' (Pinheiro et al. 2012).

All terms and two-way interactions of biological interest were included in the maximal model. Model simplification was then conducted using stepwise backward elimination (Crawley 2005). Likelihood ratio tests (LRT) comparing the deviance of models with and without the term of interest allowed fixed effects to be sequentially removed in order of least significance until a minimal

Table 2
Linear mixed model investigating the individual, social and ecological variables affecting sentinel decisions about call rate

Fixed effect	Effect±SE	χ^2	P
Activity		13.68	**0.003**
Babysitting	0±0		
Distracted	0.881±0.345		
Foraging	0.300±0.298		
Travelling	0.958±0.397		
Period (PM)	−0.440±0.165	7.66	**0.006**
Accompanied during bout (yes)	−0.369±0.151	6.46	**0.011**
Location (refuge)	−0.348±0.161	5.11	**0.024**
Alarm call during bout (yes)	−0.359±0.169	4.94	**0.026**
Sex (male)*social status (subordinate)	−1.598±0.371	17.70	**<0.0001**
Sex (male)*group size	−0.129±0.033	15.57	**0.0001**
Social status (subordinate)*pups (yes)	2.632±1.024	7.16	**0.008**
Wind		3.86	0.145
Age		0.47	0.493
Height		0.19	0.667
Duration		0.07	0.793
Habitat		0.44	0.801
Group ID	<0.001		
Individual ID in group	<0.001		
Intercept	3.502±0.922		

Group and individual identity were included as random terms, with identity nested within group ($N = 151$ bouts, 30 individuals, four groups), and the variance reported. Significant P values are in bold.

model containing only significant effects was reached. Removed terms were returned to the minimal model individually to confirm that they were not significant. Presented χ^2 and P values for significant terms were obtained by individually removing terms or interactions from the minimal model and comparing the entire minimal model with the reduced model, while values presented for nonsignificant terms were obtained by adding each term to the minimal model. Presented effect sizes ± SE were obtained from the minimal model. For categorical terms, differences in average effects are shown relative to one level of the factor, set to zero. For categorical variables containing more than two levels, post hoc comparisons of each pair of levels were conducted with Tukey's tests using the 'glhd' function in package 'multcomp' (Hothorn et al. 2012); Tukey's tests correct for multiple testing and thus there is no need for additional use of Bonferroni corrections (Ruxton & Beauchamp 2008). Only results of significant post hoc comparisons are presented.

RESULTS

Use of the Watchman's Song

Sentinels gave the watchman's song in 57% of bouts ($N = 383$ bouts, 38 individuals). When we controlled for a significant effect of activity (Table 1), habitat significantly influenced the likelihood of vocalizing (Table 1). Sentinels were more likely to vocalize when guarding in visually restricted habitats (Tukey's post hoc test: dense versus open: $P = 0.015$; medium versus open: $P = 0.014$; Fig. 2a). The distance to its nearest neighbour also significantly influenced the likelihood of a sentinel vocalizing (Table 1). Sentinels were more likely to vocalize when group members were 2−5 m away than when they were within 2 m ($P = 0.007$), but less likely to vocalize when group members were present but inside a refuge (in refuge versus 2−5 m: $P < 0.001$; in refuge versus >5 m: $P = 0.036$; Fig. 2b).

On an individual level, age, sex and social status all significantly influenced likelihood of vocalizing (Table 1). While yearlings were simply less likely to vocalize than adults (Fig. 2c), the effect of sex and social status depended on group size. In general, males vocalized in a greater proportion of bouts than females, but male tendency to vocalize remained unchanged with variation in group size (Fig. 2d). In contrast, females guarding in larger groups were substantially more likely to vocalize during a sentinel bout than when guarding in smaller groups (Fig. 2d). Similarly, while subordinates were more likely to vocalize than dominants overall, they were unaffected by changing group size whereas a strong positive relationship was found between group size and a dominant sentinel's likelihood of vocalizing (Fig. 2e).

Call Rate

Sentinel call rate was highly variable, ranging from 0.14 to 26.7 calls/min (mean ± SE = 5.85 ± 0.41, $N = 151$ bouts, 30 individuals). When we controlled for significant effects of period and location (Table 2), sentinels called at a significantly reduced rate when accompanied (Table 2, Fig. 3a) and when an alarm call occurred during a bout (Table 2). Moreover, call rate in the same bout dropped significantly in the first minute after an alarm call when compared with call rate the minute beforehand (GLMM: $\chi^2_1 = 17.45$, $N = 18$, $P < 0.001$; Fig. 3b). Activity also significantly affected call rate (Table 2). Sentinels called at a lower rate when group members were babysitting or foraging than when distracted (Tukey's post hoc test: babysitting versus distracted: $P = 0.033$; foraging versus distracted: $P = 0.026$), and there was a strong
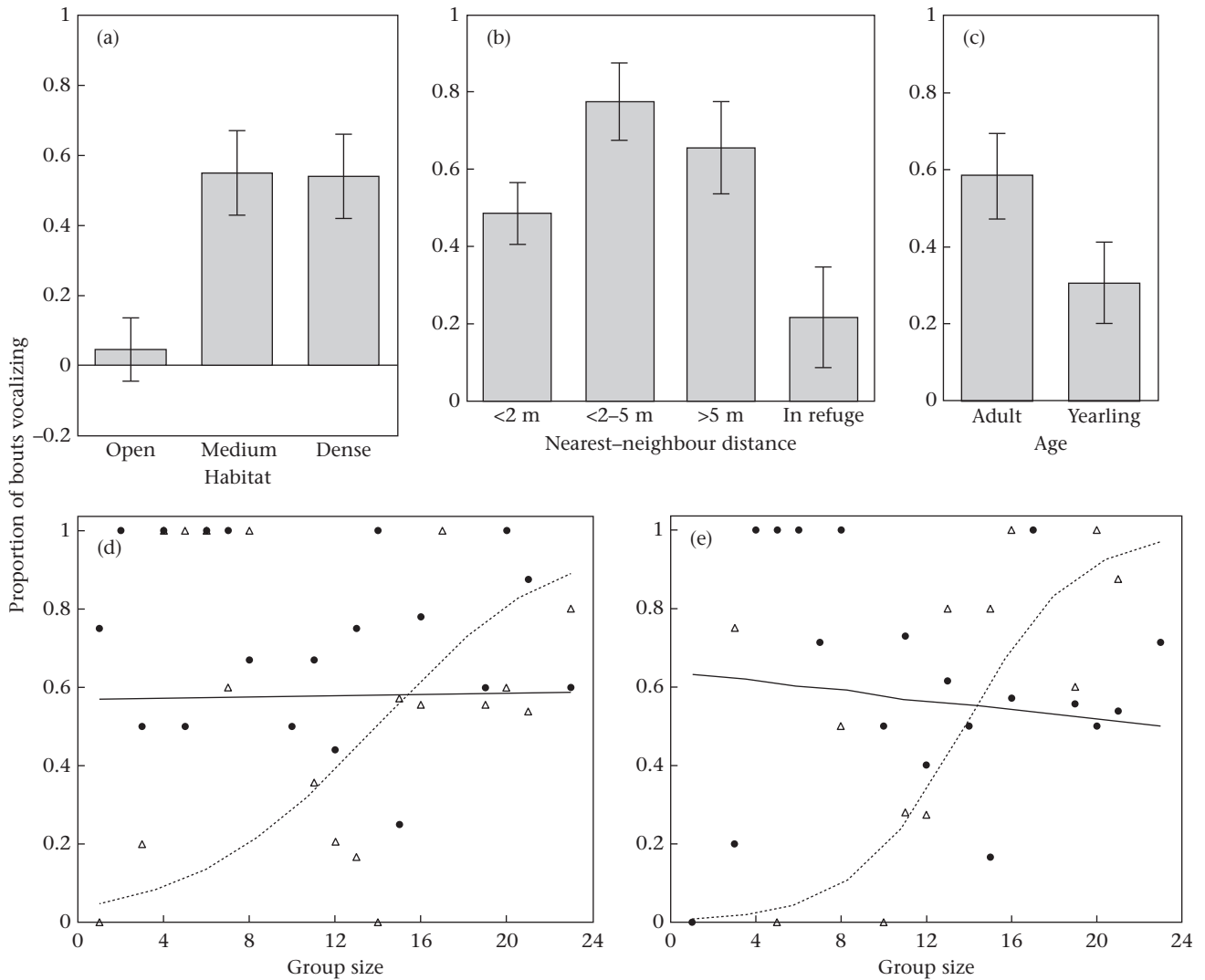
Figure 2. The influence of (a) habitat, (b) nearest-neighbour distance, (c) age, (d) the interaction between group size and sex (females: open triangles, dotted line; males: black circles, solid line), and (e) the interaction between group size and social status (dominants: open triangles, dotted line; subordinates: black circles, solid line) on the likelihood that a sentinel gave the watchman's song. Predicted means and SEs generated from the GLMM in Table 1 are shown in (a)–(c). Lines shown in (d) and (e) are plotted from predictions from the GLMM in Table 1, and points give mean values of the raw data.

tendency for sentinels to reduce call rate when the group were babysitting as opposed to travelling ($P = 0.051$; Fig. 3c).

Although both sexes reduced their call rate when pups were present, this was more pronounced in dominant than subordinate individuals (Table 2, Fig. 3d). In general, males called at a faster rate than females, but this was further influenced by group size and social status. Subordinate females and dominant and subordinate males called at a comparable rate, while dominant females called at a substantially lower rate (Table 2, Fig. 3e). In females, there was a weak but positive effect of group size on call rate, while in males, call rate showed a strong negative correlation with group size (Table 2, Fig. 3f).

Playback Experiment

In response to playback of an alarm call, an individual became a sentinel within 10 min in 96% of trials, as opposed to 70% of trials following a close call. Sentinels were significantly more likely to produce the watchman's song during the bout that followed playback of an alarm call than a control call (GLMM: $\chi_1^2 = 4.76$, $N = 30$, $P = 0.029$; Fig. 4). Playback order had no significant influence on

whether a sentinel vocalized ($\chi_5^2 = 5.56$, $P = 0.351$). Too few ($N = 2$) sentinels vocalized during control bouts to allow any statistical comparison of call rates between treatments.

DISCUSSION

Whether to Vocalize

Dwarf mongoose sentinels were more likely to use the watchman's song when in denser habitats and when the nearest neighbour was further away, supporting our prediction that vocalizations are employed most often when visual communication is likely to be impaired. Previous studies have shown that acoustic coordination of vigilance improves foraging efficiency and is particularly valuable to species whose choice of habitat and/or feeding strategy hinders the use of peripheral vision (Rasa 1986a, 1989; Manser 1999; Hollén et al. 2008). Our findings suggest that differences within species can be similarly explained, with individual members of a population adapting their behaviour to environmental and social conditions potentially to maximize the efficiency of information transfer. If the watchman's song is used as a vocal substitute for visual contact, then
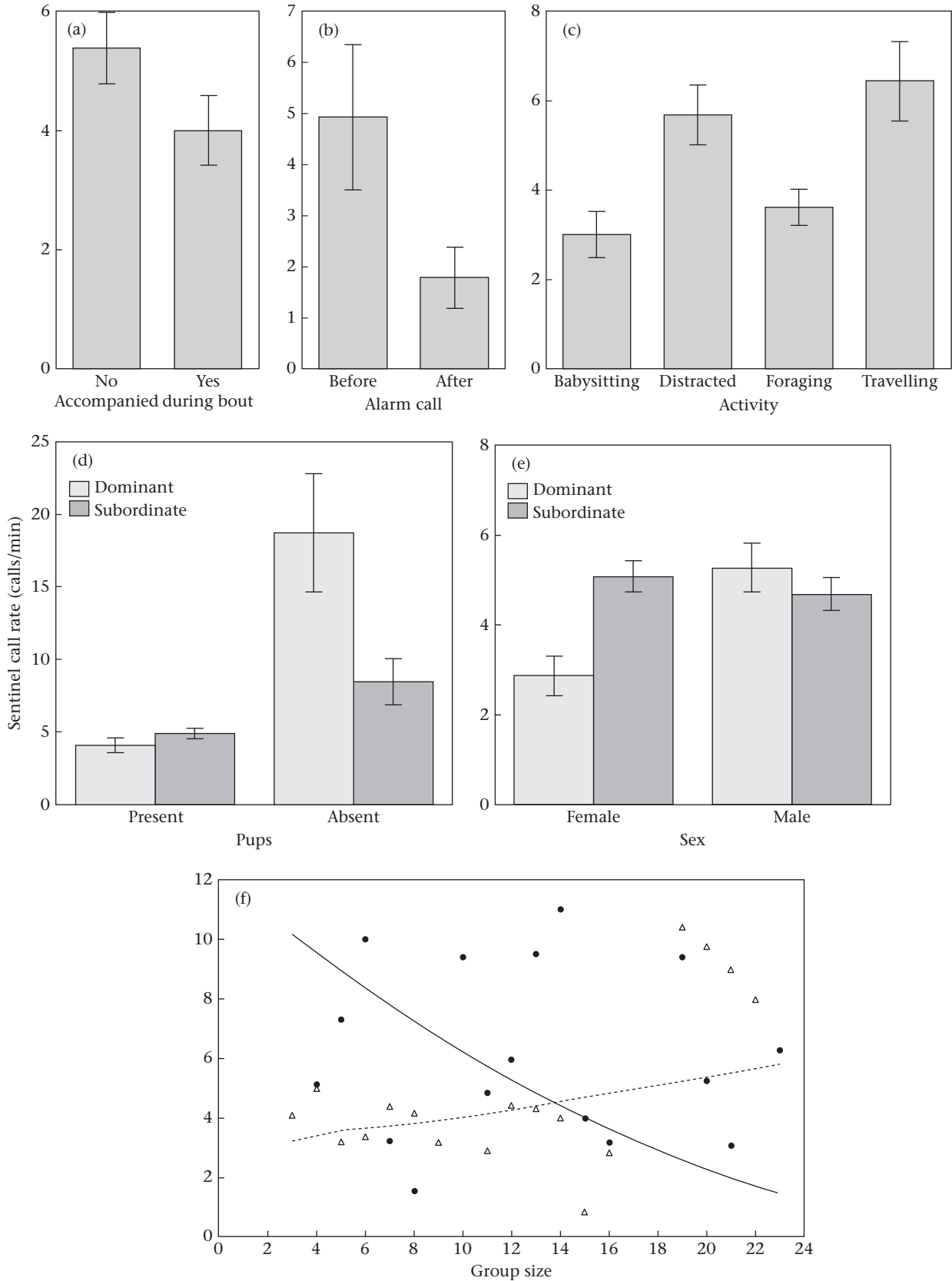
Figure 3. The influence of (a) being accompanied during a bout of sentinel duty, (b) an alarm call during a bout of sentinel duty, (c) group activity, (d) the interaction between pup presence and sentinel social status, (e) the interaction between sentinel sex and social status, and (f) the interaction between group size and sentinel sex (males: black circles, solid line; females: open triangles, dotted line). Shown are means and SEs, which were back-transformed from predicted means of the LMM in Table 2 for (a), (c), (d), (e) and (f), and a separate LMM for (b). Lines shown in (f) are plotted from predictions from the LMM in Table 2, and points give mean values of the raw data.
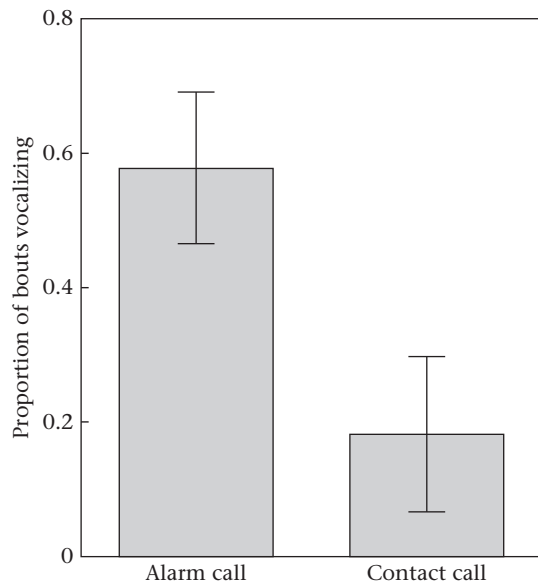
Figure 4. Proportion of sentinel bouts during which a sentinel gave the watchman's song following the playback of an alarm call or a close call. Means and SEs are shown.

it might have initially evolved as an extension of the close calling commonly employed by foragers of social species to maintain group cohesion (Radford 2004a; Radford & Ridley 2007).

Our playback experiment demonstrated that dwarf mongoose sentinels were also more likely to produce the watchman's song during bouts following an alarm call than a close call. Playback of an alarm call is likely to increase perceived risk; thus this result appears contrary to our initial prediction that sentinels should call when predation risk is lower. However, sudden silence can act as a warning in vocal species (Marler 2004), with subsequent resumption of calling indicating the passing of a threat (Sullivan 1984; Huang et al. 2011). Dwarf mongoose sentinels may be using the watchman's song to announce their presence and corresponding vigilance, signalling to group members that it is safe for them to leave cover and recommence prior behaviour. Previous studies found that other vocalizations not specific to antipredator behaviour also function as 'all clear' signals, including male song in reed buntings, *Emberiza schoeniclus* (Wingelmaier et al. 2007), the jump-yip call of black-tailed prairie dogs, *Cynomys ludovicianus* (Smith 1958), and the close calls of black-capped chickadees, *Poecile atricapillus* (Sullivan 1984) and meerkats, *Suricata suricatta* (Townsend et al. 2011).

As expected, individual classes differed in their tendency to vocalize during a sentinel bout. We found that adults, subordinates and males vocalized more than yearlings, dominants and females, respectively. Dominants and females were also more likely to vocalize with increasing group size, substantiating the hypothesis of vocal substitution for visual contact. The class differences are unlikely to be caused by varying levels of experience, as those with the most (dominant) and least (yearling) experience vocalized least. Instead, classes that had a greater tendency to vocalize as sentinels were less likely to be closely related to the dominant pair, that is, adults (because yearlings are often direct offspring of the dominant pair) and males (since they tend to emigrate to new groups while females are philopatric; Rood 1986), and so with less to gain in terms of indirect fitness benefits. These individuals might be signalling their contribution to cooperative behaviour to ensure they are allowed to remain in the group (pay-to-stay hypothesis; Mulder & Langmore 1993). Group membership is most beneficial when the predation risk is high (Heg & Taborsky 2010), so individuals least secure in their position within the group should

vocalize more at higher risk. This assumption is supported by the finding that dwarf mongoose males and subordinates vocalized irrespective of group size, maintaining high likelihood of vocalization in smaller groups in which predation risk is higher (Rasa 1986b). Since high-ranking subordinates not closely related to the dominant pair are occasionally allowed to breed in dwarf mongoose societies (Keane et al. 1994), the watchman's song may also act as an investment by helpers, increasing the likelihood of gaining a breeding opportunity.

Manipulation of Call Rate

Dwarf mongoose sentinels adjusted call rate primarily in response to social indicators of risk, reducing call rate when predation risk was high. For example, call rate within a bout was lower in the minute following an alarm call compared with the minute beforehand. Alarm calls signal an increase in immediate predation risk and thus represent 'high alert' situations. Similarly, sentinels called at a lower rate when accompanied during a bout; the need for multiple individuals on guard might also correspond to an increase in predation risk. Sentinel call rate depended on group activity and was significantly slower when groupmates were babysitting or foraging as opposed to grooming, playing or scent marking. Babysitting and foraging are arguably the activities during which an individual is least aware of potential predators, being focused on the whereabouts of vulnerable pups or digging in a head-down position, and thus most at risk. Variation in the watchman's song can potentially reduce uncertainty about risk, enabling groupmates to adjust their own vigilance accordingly and to decide how best to respond to alarm calls, thereby reducing the likelihood of an unnecessary escape response (Bell et al. 2009).

The reduction in call rate after an alarm call is in direct contrast to the finding in pied babblers, in which sentinels instead increased call rate (Bell et al. 2009). Altering call rate in either direction from the background level would presumably be sufficient to communicate a change in risk. For a small mammal such as the dwarf mongoose, calling at a rapid rate may be associated with substantial energetic costs; thus sentinels decrease rather than increase call rate. Alternatively, the reduction in call rate may represent an attempt to decrease the likelihood of detection and location by predators and under high-risk conditions it may be simply too risky for a sentinel to call rapidly.

Risk fluctuates on an individual level as a result of intrinsic biological factors such as age and body condition (e.g. Houston & McNamara 1988; Burger et al. 2000; Lea & Blumstein 2011), but perception of risk also differs between individuals. We found that dominant female sentinels called at a much slower rate than other classes of individual. In dwarf mongoose society, baseline glucocorticoid levels are highest in dominant females (Creel 2001), and as a result they may always be more 'concerned', perceive risk to be higher and call at a slower rate. Individuals also vary in their motivation for performing a particular behaviour. For example, although all sentinels reduced call rate when pups were present, the difference was more pronounced in dominant individuals. DNA fingerprinting in a different population of dwarf mongooses assigned 75% of paternities to the dominant male and 85% of maternities to the dominant female (Keane et al. 1994). Thus, if a reduction in call rate caused group members to increase vigilance effort, it may be advantageous for dominants to overestimate risk to maximize the chance of predator detection and consequently offspring protection.

Conclusions

Our study offers strong evidence that dwarf mongoose sentinels are adjusting their vocal behaviour (in terms of the decision

to call and the rate of calling) both to enhance the likelihood that groupmates are aware of their presence and to provide potentially valuable social information about current risk. Consistent variation in frequency or temporal acoustic characteristics of similar close calls of other species has been shown to provide additional information about, for example, the sex, age, dominance status and group membership of the caller (e.g. Radford 2004b; Townsend et al. 2010), but this possibility remains to be investigated in dwarf mongooses. Further work is also needed to examine precisely how the demonstrated variation in vocal behaviour of dwarf mongoose sentinels influences groupmates (see Bell et al. 2009). However, individuals who alter their behaviour appropriately to information about risk estimates are likely to improve their survival chances and selection would favour receivers who could interpret calling with reference to risk. Signallers are also likely to gain both short-term selfish benefits and cooperative benefits from their actions. Since vocalizations can aid coordination of sentinel bouts by different individuals (Rasa 1986a; Manser 1999; Bell et al. 2010), callers may be more likely to forage at the end of their bout in the presence of another sentinel (Manser 1999). Cooperative benefits might arise through either indirect fitness, because group members are close relatives (Hamilton 1964; Creel & Waser 1994), and/or group augmentation, which can result in reduced mortality rates (Creel & Creel 1991) and an increased likelihood of repelling rival groups in territorial disputes (Radford & du Plessis 2004).

The differences in vocal behaviour depending on prevailing social and ecological conditions suggest that dwarf mongooses have a level of voluntary control over their vocal production. The traditional view is that, in contrast to human language, the calling of nonhuman animals is rigid, unintentional and reflexive (see Tomasello 2008). However, there is growing evidence that nonhuman animals are highly flexible when vocalizing, adjusting their production in real time depending on external stimuli such as the current audience (see Radford & Ridley 2006; Townsend & Zuberbühler 2009; Townsend et al. 2012). Our work lends support to this view, and to the idea that it is not just our close primate relatives that have this capability, but future studies should test the degree of vocal flexibility in more detail.

Acknowledgments

References

Bates, D., Maechler, M. & Bolker, B. 2012. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-1. http://CRAN.R-project.org/package=lme4.

Bednekoff, P. A. 2001. Coordination of safe, selfish sentinels based on mutual benefits. Annales Zoologici Fennici, 38, 5–14.

Bekoff, M. 1995. Vigilance, flock size, and flock geometry: information gathering by western evening grosbeaks (Aves, Fringillidae). Ethology, 99, 150–161.

Bell, M. B. V. 2007. Cooperative begging in banded mongoose pups. Current Biology, 17, 717–721.

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, 276, 2997–3005.

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, 277, 3223–3228.

Beynon, P. & Rasa, O. A. E. 1989. Do dwarf mongooses have a language? Warning vocalisations transmit complex information. South African Journal of Science, 85, 447–450.

Bradbury, J. W. & Vehrencamp, S. L. 2012. Principles of Animal Communication. 2nd edn. Sunderland, Massachusetts: Sinauer Associates.

Burger, J., Safina, C. & Gochfeld, M. 2000. Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. Acta Ethologica, 2, 97–104.

Caro, T. M. 2005. Antipredator Defenses in Birds and Mammals. Chicago: The University of Chicago Press.

Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S. & Manser, M. B. 1999. Selfish sentinels in cooperative mammals. Science, 284, 1640–1644.

Crawley, M. J. 2005. Statistics: An Introduction using R. Chichester: J. Wiley.

Creel, S. 2001. Social dominance and stress hormones. Trends in Ecology & Evolution, 16, 491–497.

Creel, S. R. & Creel, N. M. 1991. Energetics, reproductive suppression and obligate breeding in carnivores. Behavioral Ecology and Sociobiology, 28, 263–270.

Creel, S. R. & Waser, P. M. 1994. Inclusive fitness and reproductive strategies in dwarf mongooses. Behavioral Ecology, 5, 339–348.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology & Evolution, 20, 187–193.

Danchin, E., Giraldeau, L.-A., Valone, T. J. & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. Science, 305, 487–491.

Evans, C. S., Evans, L. & Marler, P. 1993. On the meaning of alarm calls: functional reference in an avian vocal system. Animal Behaviour, 46, 23–38.

Giraldeau, L.-A., Valone, T. J. & Templeton, J. J. 2002. Potential disadvantages of using socially acquired information. Philosophical Transactions of the Royal Society B, 357, 1559–1566.

Haff, T. H. & Magrath, R. D. 2011. Calling at a cost: elevated nestling calling attracts predators to active nests. Biology Letters, 7, 493–495.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. Journal of Theoretical Biology, 7, 1–52.

Heg, D. & Taborsky, M. 2010. Helper response to experimentally manipulated predation risk in the cooperatively breeding cichlid Neolamprologus pulcher. PLoS One, 5, e10784.

Hollén, L. I. & Radford, A. N. 2009. The development of alarm call behaviour in mammals and birds. Animal Behaviour, 78, 791–800.

Hollén, L. I., Bell, M. B. V. & Radford, A. N. 2008. Cooperative sentinel calling? Foragers gain increased biomass intake. Current Biology, 18, 576–579.

Hollén, L. I., Bell, M. B. V., Wade, H. M., Rose, R., Russell, A., Niven, F., Ridley, A. R. & Radford, A. N. 2011. Ecological conditions influence sentinel decisions. Animal Behaviour, 82, 1435–1441.

Hothorn, T., Bretz, F. & Westfal, P. 2012. multcomp: Simultaneous tests and confidence intervals for general linear hypotheses in parametric models. R package version 1.2-13. http://CRAN.R-project.org/package=multcomp.

Houston, A. I. & McNamara, J. M. 1988. Fighting for food: a dynamic version of the Hawk–Dove game. Evolutionary Ecology, 2, 51–64.

Huang, P., Sieving, K. E. & Mary, C. M. S. 2011. Heterospecific information about predation risk influences exploratory behavior. Behavioral Ecology, 23, 463–472.

Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliott, L. F. & Minchella, D. J. 1994. Subordinate reproduction in dwarf mongooses. Animal Behaviour, 47, 65–75.

Kokolakis, A., Smith, C. L. & Evans, C. S. 2010. Aerial alarm calling by male fowl (Gallus gallus) reveals subtle new mechanisms of risk management. Animal Behaviour, 79, 1373–1380.

Lea, A. J. & Blumstein, D. T. 2011. Age and sex influence marmot antipredator behavior during periods of heightened risk. Behavioral Ecology and Sociobiology, 65, 1525–1533.

Lima, S. L. & Bednekoff, P. A. 1999. Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? Animal Behaviour, 58, 537–543.

McGowan, K. J. & Woolfenden, G. E. 1989. A sentinel system in the Florida scrub jay. Animal Behaviour, 37, 1000–1006.

Manser, M. B. 1999. Response of foraging group members to sentinel calls in suricates, Suricata suricatta. Proceedings of the Royal Society B, 266, 1013–1019.

Manser, M. B. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. Proceedings of the Royal Society B, 268, 2315–2324.

Marler, P. 2004. Bird calls: a cornucopia for communication. In: The Science of Birdsong (Ed. by P. Marler & H. Slabbekoorn), pp. 132–177. San Diego, California: Elsevier.

Mulder, R. A. & Langmore, N. E. 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. Animal Behaviour, 45, 830–833.

Pays, O., Blomberg, S. P., Renaud, P. C., Favreau, F. R. & Jarman, P. J. 2010. How unpredictable is the individual scanning process in socially foraging mammals? Behavioral Ecology and Sociobiology, 64, 443–454.

Pinheiro, J., Bates, B., DebRoy, S. & Sarkar, D. 2012. nlme: Fit and compare Gaussian linear and nonlinear mixed-effects models. R package version 3.1-104. http://CRAN.R-project.org/package=nlme.

Quenette, P. Y. 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecologica, 11, 801–818.

Quinn, J. L., Whittingham, M. J., Butler, S. J. & Cresswell, W. 2006. Noise, predation risk compensation and vigilance in the chaffinch Fringilla coelebs. Journal of Avian Biology, 37, 601–608.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. http://www.R-project.org.

Radford, A. N. 2004a. Vocal mediation of foraging competition in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. *Behavioral Ecology and Sociobiology*, **56**, 279–285.

Radford, A. N. 2004b. Voice breaking in males results in sexual dimorphism of green woodhoopoe calls. *Behaviour*, **141**, 555–569.

Radford, A. N. & du Plessis, M. A. 2004. Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. *Animal Behaviour*, **68**, 803–810.

Radford, A. N. & Ridley, A. R. 2006. Recruitment calling: a novel form of extended parental care in an altricial species. *Current Biology*, **16**, 1700–1704.

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**, 249–252.

Radford, A. N., Hollén, L. I. & Bell, M. B. V. 2009. The higher the better: sentinel height influences foraging success in a social bird. *Proceedings of the Royal Society B*, **276**, 2437–2442.

Radford, A. N., Bell, M. B. V., Hollén, L. I. & Ridley, A. R. 2011. Singing for your supper: sentinel calling by kleptoparasites can mitigate the cost to victims. *Evolution*, **65**, 900–906.

Rasa, O. A. E. 1977. The ethology and sociology of the dwarf mongoose (*Helogale undulata rufula*). *Zeitschrift für Tierpsychologie*, **43**, 337–406.

Rasa, O. A. E. 1986a. Coordinated vigilance in dwarf mongoose family groups: the 'watchman's song' hypothesis and the costs of guarding. *Ethology*, **71**, 340–344.

Rasa, O. A. E. 1986b. Ecological factors and their relationship to group size, mortality and behaviour in the dwarf mongoose. *Cimbebasia*, **8**, 15–20.

Rasa, O. A. E. 1989. Behavioural parameters of vigilance in the dwarf mongoose: social acquisition of a sex-biased role. *Behaviour*, **110**, 125–145.

Rendall, D., Owren, M. J. & Ryan, M. J. 2009. What do animal signals mean? *Animal Behaviour*, **78**, 233–240.

Ridley, A. R. & Raihani, N. J. 2007. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology*, **18**, 324–330.

Ridley, A. R., Raihani, N. J. & Bell, M. B. V. 2010. Experimental evidence that sentinel behaviour is affected by risk. *Biology Letters*, **6**, 445–448.

Rood, J. P. 1986. Ecology and social evolution in mongooses. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 131–152. Princeton, New Jersey: Princeton University Press.

Roulin, A. 2001. On the cost of begging vocalization: implications of vigilance. *Behavioral Ecology*, **12**, 506–511.

Ruxton, G. D. & Beauchamp, G. 2008. Time for some a priori thinking about post hoc testing. *Behavioral Ecology*, **19**, 690–693.

Seyfarth, R. M. & Cheney, D. L. 2003. Signalers and receivers in animal communication. *Annual Review of Psychology*, **54**, 145–173.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science*, **210**, 801–803.

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**, 475–477.

Smith, R. E. 1958. Natural history of the prairie dog in Kansas. *Miscellaneous Publications of the Museum of Natural History of the University of Kansas*, **16**, 1–35.

Sullivan, K. A. 1984. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*, **91**, 294–311.

Tomasello, M. 2008. *Origins of Human Communication. Cambridge*. Massachusetts. MIT Press.

Townsend, S. W. & Zuberbühler, K. 2009. Audience effects in chimpanzee copulation calls. *Communicative and Integrative Biology*, **2**, 282–284.

Townsend, S. W., Hollén, L. I. & Manser, M. B. 2010. Meerkat close calls encode group-specific signatures, but receivers fail to discriminate. *Animal Behaviour*, **80**, 133–138.

Townsend, S. W., Zöttl, M. & Manser, M. B. 2011. All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behavioral Ecology and Sociobiology*, **65**, 1927–1934.

Townsend, S. W., Rasmussen, M., Clutton-Brock, T. & Manser, M. B. 2012. Flexible alarm calling in meerkats: the role of the social environment and predation urgency. *Behavioral Ecology*, **23**, 1360–1364.

Treves, A., Drescher, A. & Ingrisano, N. 2001. Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology*, **50**, 90–95.

Trillmich, J., Fichtel, C. & Kappeler, P. M. 2004. Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*). *Behaviour*, **141**, 1103–1120.

Wickler, W. 1985. Coordination of vigilance in bird groups. The 'watchman's song' hypothesis. *Zeitschrift für Tierpsychologie*, **69**, 250–253.

Wingelmaier, K., Winkler, H. & Nemeth, E. 2007. Reed bunting (*Emberiza schoeniclus*) males sing an 'all-clear' signal to their incubating females. *Behaviour*, **144**, 195–206.