



# Sentinel dwarf mongooses, *Helogale parvula*, exhibit flexible decision making in relation to predation risk



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To maximize survival, animals should adjust their behaviour flexibly in response to indicators of predation risk. Predation risk is affected by a range of ecological, social and individual variables, which can fluctuate over different timescales. In general, current risk levels are known to influence the behaviour of sentinels, individuals that adopt a raised position to scan for danger while groupmates are engaged in other activities. However, there has been little consideration of whether decisions made at different stages of a sentinel bout are affected in the same way by perceived predation risk and whether the same level of behavioural plasticity is exhibited when making these different decisions. Here we used detailed behavioural observations and a playback experiment to investigate the behavioural choices of dwarf mongoose sentinels at three different stages of a bout (before, start, during). Individuals were more likely to begin a bout, and did so sooner, following alarm calls, which are immediate, direct indicators of elevated risk. Sentinels selected an initial height from which to guard depending on factors that tended to vary in the medium term (hours), choosing higher positions in denser habitat and less windy conditions. In contrast, decisions about bout duration were made in relation to short-term (seconds/minutes) changes in information, with sentinels guarding for longer when an alarm call was given during a bout, and terminating bouts sooner when groupmates moved out of sight. Our results demonstrate that sentinel decisions are influenced by both direct and indirect indicators of likely predation risk and that sentinel behaviour is adjusted flexibly with regard to information presented on various timescales, highlighting the complexity of decision-making processes.

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Animals constantly make decisions about how to balance conflicting demands (McFarland, 1977), with the trade-off between foraging and vigilance a classic example (Lima & Dill, 1990). Information is a vital modulator of behaviour, and to facilitate appropriate decision making, animals continually monitor and assess numerous external and internal factors (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; McFarland, 1977; Trimmer et al., 2008). Behavioural flexibility is limited, however, and while animals are expected to behave optimally, they may be constrained from doing so by, for instance, evolved psychological mechanisms (Fawcett, Hamblin, & Giraldeau, 2013) or the cost of information acquisition (Dall et al., 2005). Owing to the stochastic nature of the environment and changing circumstances across time, individuals should take into account fluctuating risk, rather than behave as if the relevant threats to survival were constant (Bouskila &

Blumstein, 1992). Assessing the level of behavioural flexibility exhibited at different times is therefore also important in the investigation of decision making.

Decision making in relation to predation risk can potentially be affected by ecological, social and individual variables. Ecological conditions such as habitat type (Werner, Gilliam, Hall, & Mittlebach, 1983), heterogeneity (Hilton, Ruxton, & Cresswell, 1999; Rodríguez, Andrén, & Jansson, 2001) and quality (Sapolsky, 1986), as well as wind speed (Hilton et al., 1999; Hollén et al., 2011), are associated with changes in predator detectability, density and behaviour. Similarly, predation risk depends on such social factors as group size (Hamilton, 1971; Radford & Ridley, 2007) and composition, including the presence of young (Pangle & Holekamp, 2010; Santema & Clutton-Brock, 2013), spatial position in the foraging group (Radford & Ridley, 2007), and the activity (Pangle & Holekamp, 2010) and vigilance behaviour (Pays, Blomberg, Renaud, Favreau, & Jarman, 2010; Radford, Hollén, & Bell, 2009; ) of companions. Risk levels can also differ for individuals of different age, sex and body condition (Burger, Safina, & Gochfeld, 2000; Lea & Blumstein, 2011; Lima, 1988), while risk perception may depend

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on prior experience (Stankowich & Blumstein, 2005) and personality (Dall, Houston, & McNamara, 2004).

Decision making requires continuous acquisition of data over time (Trimmer et al., 2008). Individuals must simultaneously consider multiple processes operating at different rates and time-scales (Heath, Gilchrist, & Ydenberg, 2010), and although some decision-making rules may be fixed and unresponsive to variations in stimuli, optimal decisions can involve complex interactions among these multiscale processes (Couchoux & Cresswell, 2012; Heath et al., 2010). For example, sex usually remains constant across an animal's lifetime, with age accumulating slowly over long periods. Individuals experience variation in factors such as habitat type and weather conditions in the medium term. Simultaneous short-term variation arises as a consequence of, for instance, changes in nutritional state or information provided from the production of alarm calls by groupmates.

In a number of social species, the foraging–vigilance trade-off has led to the evolution of sentinel systems (Clutton-Brock et al., 1999; Horrocks & Hunte, 1986; McGowan & Woolfenden, 1989; Rasa, 1989; Ridley & Raihani, 2007; Wright, Berg, de Kort, Khazin, & Maklakov, 2001a). Sentinels are individuals that adopt a raised position to scan the surroundings and provide information about potential threats to groupmates engaged in other activities (Bednekoff, 1997; Bell, Radford, Rose, Wade, & Ridley, 2009; McGowan & Woolfenden, 1989). Group members can benefit from the presence of a sentinel in terms of reduced predation risk and increased foraging success (Hollén, Bell, & Radford, 2008; Ridley, Raihani, & Bell, 2010). In general, sentinel behaviour is known to be affected by individual factors, such as age, sex, dominance rank and nutritional status. For instance, dominant female meerkats, *Suricata suricatta*, contribute less to sentinel duty than other adults (Clutton-Brock et al., 1999), sentinel effort in Arabian babblers, *Turdoides squamiceps*, is greater for males than females, and with increasing dominance status in both sexes (Wright et al., 2001a), and supplementary feeding resulted in meerkats, Arabian babblers and pied babblers, *Turdoides bicolor*, starting sentinel bouts sooner (Bell, Radford, Smith, Thompson, & Ridley, 2010; Clutton-Brock et al., 1999; Wright, Maklakov, & Kkazin, 2001b). Previous studies have also demonstrated that both direct indicators of greater predation risk (Clutton-Brock et al., 1999; Radford, Bell, Hollén, & Ridley, 2011; Ridley et al., 2010) and changes in risk-related factors such as habitat and wind (Hollén et al., 2011; Santema & Clutton-Brock, 2013) can lead to general increases in sentinel behaviour. However, sentinels must make a series of decisions before, at the start and during a bout. Whether and how perceived predation risk affects each of these in turn, and the level of behavioural flexibility exhibited, have received little consideration. Moreover, a true assessment of decision making requires some knowledge about the choices available to the animal (Van Moorter, Visscher, Herfindal, Basille, & Myserud, 2013). Apparent differences in behaviour between, for example, habitats may simply arise because of differences in availability of a particular resource, but potential options are rarely quantified.

Here we examined how predation risk affects the decision making of sentinels in a wild population of dwarf mongooses. These are cooperatively breeding carnivores living in groups of up to 30 individuals (Rasa, 1977). The dominant pair monopolizes reproduction with related and unrelated subordinates of both sexes helping to raise young (Keane et al., 1994). Dwarf mongooses search for their primarily invertebrate prey by digging, and so are consequently unable to forage and be fully vigilant simultaneously (Rasa, 1986). They are at risk from a large number of avian and terrestrial predators (Rasa, 1986), with sentinels often present (Kern & Radford, 2013; Sharpe, Joustra, & Cherry, 2010). Sentinels alert other group members to the approach of predators using alarm

calls which not only signify 'danger' but also indicate the type of predator and urgency of the threat (Beynon & Rasa, 1989). Although most group members take part in sentinel duty, studies have found variation in the investment of individual classes in different populations: Rasa (1989) reported subordinate males investing significantly more time in sentinel bouts than other group members, whereas no such dominance-based difference has been found at our study site (Kern, n.d.).

In the current study, we investigated how predation risk affects decisions at three different stages of a sentinel bout (before, start, during): (1) when to become a sentinel; (2) what height above ground to choose as an initial position; and (3) how long to remain as a sentinel. As it is difficult to predict exactly when a natural sentinel bout will start, a playback experiment was used for question (1), increasing perceived predation risk through the use of alarm calls. For questions (2) and (3), we analysed detailed observational data of natural behaviour and included various ecological (e.g. habitat type, wind condition) and social (e.g. presence of pups, occurrence of alarm calls) factors, while controlling for individual factors such as sex, age and dominance status. A higher predation risk might be perceived either following direct indicators of a threat (e.g. an alarm call) or in certain conditions, such as in denser habitats (Brown, 1988) or on windier days (Hilton et al., 1999). In these situations, we predicted that sentinels would start bouts sooner, choose higher initial positions and stay on guard for longer. The observational data sets also allowed a consideration of whether the same level of behavioural flexibility is exhibited at different decision stages. Specifically, are decisions made in relation to factors that alter predation risk in the medium term (e.g. changes in habitat or group size that might occur across the day) or to factors that can alter the perception of predation risk in the short term (e.g. alarm calls, group activity), and is the same level of flexibility exhibited both at the start and during sentinel bouts?

## METHODS

### Study Site and Population

The study took place on Sorabi Rock Lodge Reserve, a 4 km<sup>2</sup> private game reserve in Limpopo Province, South Africa (24°11'S, 30°46'E), part of southern Africa's Savanna Biome (see Kern & Radford, 2013 for full details). All work 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.

At the study site, potential terrestrial predators of the dwarf mongoose were the African wildcat, *Felis lybica*, black-backed jackal, *Canis mesomelas*, side-striped jackal, *Canis adustus*, African civet, *Civettictis civetta*, honey badger, *Mellivora capensis*, serval, *Felis serval*, slender mongoose, *Galerella sanguinea*, rock monitor, *Varanus exanthematicus*, African rock python, *Python sebae*, puff adder, *Bitis arietans*, Mozambique spitting cobra, *Naja mossambica*, snouted cobra, *Naja haje*, and black mamba, *Dendroaspis polylepis* (Sharpe et al., 2010). The region is home to 14 species of large diurnal raptor which prey upon mammals the size of dwarf mongooses. Eleven are resident throughout the year, the most commonly encountered of which are the African fish-eagle, *Haliaeetus vocifer*, African hawk-eagle, *Hieraaetus spilogaster*, brown snake-eagle, *Circaetus cinereus*, blackbreasted snake-eagle, *Circaetus pectoralis*, and tawny eagle, *Aquila rapax*. The rest occur here during only part of the year, most notably the steppe eagle, *Aquila nipalensis*, and Wahlberg's eagle, *Aquila wahlbergi*, which are present during the summer months.

Data were collected from four groups of wild dwarf mongooses (mean group size = 13.3; range 5–17), 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, Weybridge, 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 the previous summer and who 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, 1986).

#### Observational Data Collection

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 (see also Kern & Radford, 2013). Sentinels were defined as individuals whose feet were at least 10 cm above ground and who were actively scanning for predators while groupmates were engaged in other activities, primarily but not exclusively foraging (Kern & Radford, 2013; Sharpe et al., 2010). For each bout, we recorded (1) sentinel identity (and thus sex, dominance status and age); (2) initial height above ground chosen as a position from which to guard (to the nearest 10 cm); (3) whether the sentinel was accompanied (i.e. another individual also acted as a sentinel for at least some of the same period); (4) whether an alarm call was given during the bout; (5) bout duration; (6) group size; (7) horizontal distance from the sentinel to its nearest neighbour (<2 m, 2–5 m, >5 m, present but inside day or overnight refuge); (8) location (overnight refuge e.g. termite mound, hollow tree, log or rock cluster used for sleeping, or elsewhere); (9) pup presence/absence; and (10) group activity. Only bouts longer than 10 s were analysed, to ensure that an individual had adopted a fixed position (Kern & Radford, 2013). 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*.

#### Ecological Surveys

To provide an assessment of potential differences in sentinel visibility at different heights and in different habitats over the course of the study period, surveys were carried out on a weekly basis at six sites randomly chosen from each habitat type (open, medium, dense). The coordinates of each site were recorded using a Garmin etrex H handheld GPS device (Garmin Europe Ltd, Southampton, Hampshire, U.K.), to allow repeated returns to the same location. On each occasion, the observer faced north (determined with a compass) and assessed the distance at which objects just above ground level were visible from heights of 10 cm, 30 cm, 50 cm and 1 m; this analysis provides an indication of the likelihood of keeping groupmates in sight and of spotting terrestrial predators. Each sentinel bout included in the analysis of bout duration (see below) was assigned the distance visible value from

the nearest height category from the nearest survey day in the relevant habitat type.

To assess whether there are differences between habitat types in the heights available to sentinels, 12 sites in each habitat were chosen using randomly generated GPS coordinates. At each site, we measured the height of the 10 objects used by sentinels (rock, log, tree, termite mound) and higher than 10 cm (see sentinel definition above), not including refuges, closest to the GPS point. To determine whether a difference exists in height availability depending on location (overnight refuge, elsewhere), the heights of all known overnight refuges ( $N = 59$ ) were also measured for comparison with heights measured as part of the habitat assessment.

#### Playback Experiment

To assess the influence of increased predation risk on when individuals choose to start a bout, we conducted a playback experiment between 28 February and 14 April 2012 (see also Kern & Radford, 2013). The experiment involved two treatments: conspecific alarm calls and control close calls (low-amplitude vocalizations given continuously by foraging individuals). Twenty-four playback tracks were constructed using six alarm calls recorded opportunistically from each of the four study groups (see Kern & Radford, 2013 for details of recordings). 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. As a contextual control treatment, close calls from the same adult individuals were used to construct six 5 s tracks per group. It is possible that any variation in behaviour following playback of the two sound treatments is a consequence of alarm calls being naturally more alerting or 'plosive' than close calls (see Hollén & Radford, 2009; Rendall, Owren, & Ryan, 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 (as per Kern & Radford, 2013). 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. The two treatments within a trial pair 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, we noted whether any individual became a sentinel in the following 10 min, and the time until the bout started (recorded as 600 s if no group member acted as a sentinel).

#### 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 a one-way ANOVA

to investigate whether the height of available positions varied between habitat types, and a two-sample *t* test to examine whether the height of overnight refuges differed from the height of vegetation available elsewhere.

For assessments of behavioural decisions, we used mixed models to take account of repeated measures from the same group, individual and/or playback pair. Linear mixed models (LMMs) were conducted, using the *lme* function in package 'nlme' (Pinheiro, Bates, DebRoy, & Sarkar, 2012), whenever data (original or transformed) fitted the relevant assumptions of normality and constant variance; generalized linear mixed models (GLMMs) were conducted, using the *lmer* function in package 'lme4' (Bates, Maechler, & Bolker, 2012), for binomial data sets or where transformations could not improve the data fit sufficiently. Residuals for all models were examined visually to ensure homogeneity of variance, normality of error and linearity.

All likely explanatory terms were included in the full model. Model simplification was then conducted using stepwise backward elimination (Crawley, 2005) with terms sequentially removed until the minimal model contained only terms whose elimination significantly reduced the explanatory power of the model. Removed terms were returned to the minimal model individually to confirm that they were not significant. Presented  $\chi^2$  and *P* values were obtained by comparing the minimal model with models in which the term of interest had been removed (for significant terms) or added (for nonsignificant terms). Presented effect sizes  $\pm$  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 using Tukey's tests using the 'glhd' function in package 'multcomp' (Hothorn, Bretz, & Westfall, 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.

#### *When to become a sentinel*

Playback data were analysed using GLMMs. Data on whether an individual went on sentinel duty following playback were fitted to a binomial distribution with logit-link function and binary response terms (1 or 0). Latency data were log-transformed to allow analysis using a GLMM with Poisson error structure and log-link function. Both models fitted the fixed effects of treatment (alarm or control) and playback order (1–6). Playback pair (alarm call and close call from the same group member) was included as a random term, as was group identity.

#### *What height above ground to choose as an initial position*

Observational data on initial height from which to guard were analysed using an LMM following square-root transformation, fitting the fixed effects of sentinel age, sex and dominance status, habitat type, wind speed, location, period, nearest-neighbour distance, group size, group activity and pup presence/absence, with individual identity nested in group identity included as random terms.

#### *How long to remain as a sentinel*

Observational data on bout duration were analysed using an LMM following logarithmic transformation, fitting the fixed effects of sentinel age, sex and dominance status, habitat type, visibility, wind speed, location, period, group size, group activity, pup presence/absence, whether an alarm call was given and whether the sentinel was accompanied, with individual identity nested in group identity included as random terms.

## RESULTS

### *When to Become a Sentinel*

Following playback of an alarm call, individuals were significantly more likely to become a sentinel (Table 1, Fig. 1a) and did so significantly faster (Table 2, Fig. 1b) than following a control call. Playback order (1–6) did not significantly influence whether an individual began a sentinel bout (Table 1) or latency to the start of a bout (Table 2).

### *What Height above Ground to Choose as an Initial Position*

Sentinels first positioned themselves at a height of 10–250 cm (mean  $\pm$  SE = 83.0  $\pm$  2.3 cm, *N* = 439 bouts, 40 individuals). Controlling for a significant effect of dominance status, with subordinate individuals choosing higher positions than dominants (Table 3), initial height was significantly influenced by wind condition (Table 3). Sentinels chose lower positions when guarding in a light breeze than when it was still (Table 3, Fig. 2a). Habitat also significantly affected height choice: sentinels chose higher positions in dense and medium habitats than in open areas (Table 3, Fig. 2b). This was not the consequence of a difference in available heights in the different habitats (ANOVA:  $F_{2,33} = 2.26$ , *P* = 0.12). Although location was a significant predictor of initial height in the overall model (Table 3), positions available at a refuge were significantly higher than those elsewhere (two-sample *t* test:  $t_{59} = 8.56$ , *P* < 0.0001); the use of higher positions at refuges may not represent an active choice.

### *How Long to Remain as a Sentinel*

Sentinel bouts lasted 11–38.1 min (mean  $\pm$  SE = 192.1  $\pm$  14.3 s, *N* = 342 bouts, 38 individuals). Controlling for a significant effect of age, with adults guarding for longer than yearlings (Table 4), individuals remained on guard for significantly longer if an alarm call was given during the bout (Table 4, Fig. 3a) and if there was another sentinel present during the bout rather than guarding alone throughout (Table 4, Fig. 3b). The activity of groupmates significantly affected bout duration: sentinels guarded for a shorter period of time when the group were travelling than when babysitting and foraging (Table 4, Fig. 3c). Visibility also significantly influenced bout length: sentinels guarded for longer when able to see further (Table 4, Fig. 3d).

## DISCUSSION

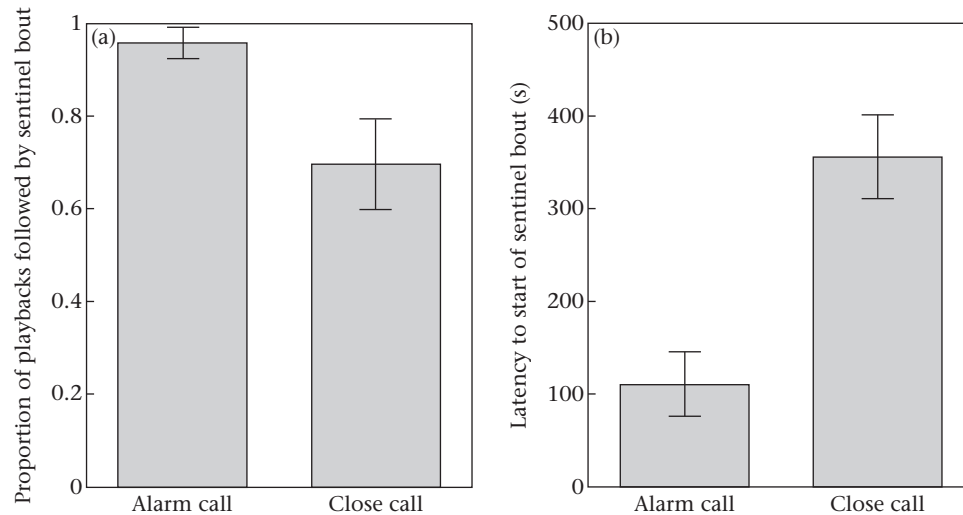
Our work provides strong evidence that the decision making of dwarf mongoose sentinels at different stages of a bout is influenced

**Table 1**  
Generalized linear mixed model on factors affecting whether to become a sentinel

	<i>df</i>	LRT $\chi^2$	<i>P</i>
Full model			
<b>Treatment</b>	<b>1</b>	<b>20.05</b>	<b>&lt;0.0001</b>
Playback order	5	0.05	0.820
Minimal model		Effect size	SE
Constant		27.57	45.67
Treatment (Control)		–15.69	47.51
Group ID		37.63	6.13
Individual ID in group		2896.60	53.82

The analysis used data from the playback experiment (*N* = 24 playback pairs, 4 groups). Data on whether an individual became a sentinel were fitted to a binomial distribution with logit-link function. Group identity and playback pair were included as random terms. The significant term is highlighted in bold.





**Figure 1.** The effect of playback treatment on (a) whether an individual became a sentinel, and (b) latency to the start of a bout. Means and SEs are shown.

by a range of ecological and social factors relating to predation risk. Vigilance effort should increase during periods of higher risk (Lima & Bednekoff, 1999), so animals are expected to adjust their behaviour according to direct cues of predator presence (e.g. alarm calling, predator sightings and flight behaviour). In our study, playback of conspecific alarm calling (suggesting imminent threat) resulted in a greater likelihood of an individual becoming a sentinel and doing so faster. This is in line with recent experimental work in other species showing that individuals alter their sentinel behaviour in response to model predators and heterospecific alarm calls (Bell et al., 2009; Ridley et al., 2010). Animals are also expected to make vigilance decisions in relation to indirect cues of predation risk (Carr & Lima, 2010; Hollén et al., 2011; Mateo, 2007; Whittingham, Butler, Quinn, & Cresswell, 2004), and our results from the detailed observational data set demonstrate that a range of ecological and social factors, varying in the time frame over which they change, affect decisions both at the start and during a bout.

The decision about what positional height to adopt at the start of a bout was influenced predominantly by ecological factors that vary in the medium term (wind condition and habitat type), that is, factors that are likely to vary across the day, but that are reasonably stable on a short-term basis. Windy conditions are associated with increased risk, as the ability to detect predators accurately and rapidly using visual and olfactory cues is compromised (Carr & Lima, 2010; Conover, 2007; Hilton et al., 1999), while attacks may

occur more frequently owing to an increase in general energy expenditure which requires avian predators to hunt more often (Masman, Daan, & Beldhuis, 1988). The lower height chosen by sentinels in our study during windier conditions might therefore be because branches at such heights are sturdier and offer more protection from predators (see also Hollén et al., 2011). Alternatively, that decision might be made because wind lessens the likelihood of vocalizations being detected by intended receivers (Wiley & Richards, 1982). Sentinels might therefore guard closer to the ground to increase the chances of foraging groupmates hearing

**Table 3**

Linear mixed model on factors affecting above ground height of post chosen by sentinels

	$\chi^2$	df	P
Full model			
<b>Location</b>	<b>7.78</b>	<b>1</b>	<b>0.005</b>
<b>Dominance status</b>	<b>7.48</b>	<b>1</b>	<b>0.006</b>
<b>Habitat</b>	<b>7.05</b>	<b>2</b>	<b>0.029</b>
<b>Wind</b>	<b>6.27</b>	<b>2</b>	<b>0.043</b>
Nearest-neighbour distance	4.72	1	0.192
Age	1.15	1	0.282
Sex	0.89	1	0.344
Pups	0.50	1	0.476
Activity	2.17	3	0.537
Period	0.01	1	0.919
Group size	0.01	1	0.964
Minimal model	Effect size	SE	
Constant	7.96	0.38	
Location (Refuge)	0.70	0.38	
Rank (Subordinate)	1.01	0.31	
Habitat			
Dense	0	0	
Medium	−0.04	0.27	
Open	−1.76	0.68	
Wind			
Light breeze	0	0	
Still	0.86	0.33	
Strong wind	0.08	0.39	
Group ID	0.33	0.0	
Individual ID in group	0.39	0.0	

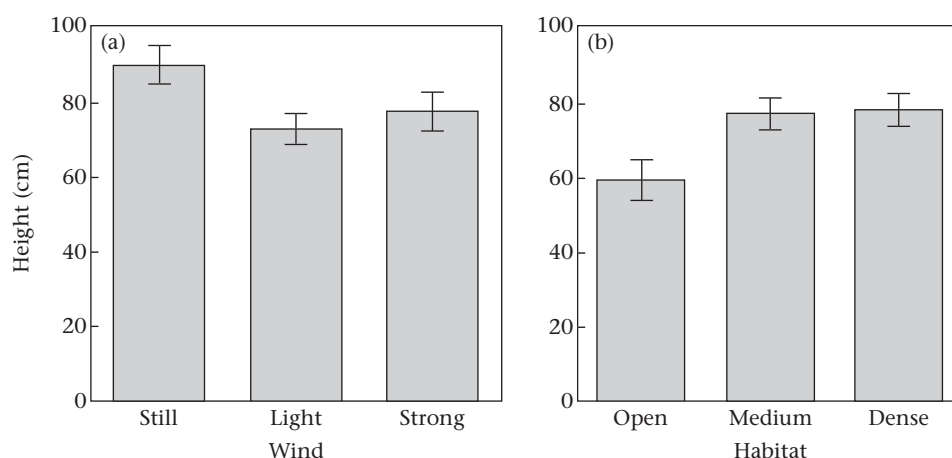
The analysis used observational data from 439 sentinel bouts by 40 individuals in four groups, with individual ID nested within group ID included as random terms. Post hoc Tukey's tests for habitat type (dense versus both other habitat categories:  $P = 0.026$ ) and wind speed (light breeze versus still:  $P = 0.008$ ). Significant terms are highlighted in bold.

**Table 2**

Generalized linear mixed model on factors affecting latency to become a sentinel

	df	LRT $\chi^2$	P
Full model			
<b>Treatment</b>	<b>1</b>	<b>4.52</b>	<b>0.033</b>
Playback order	5	0.14	0.706
Minimal model		Effect size	SE
Constant		0.45	0.17
Treatment (Control)		0.45	0.21
Group ID		0.0	0.0
Individual ID in group		0.0	0.0

The analysis used data from the playback experiment ( $N = 24$  playback pairs, 4 groups). Latency data were log-transformed and fitted to a Poisson distribution with log-link function. Group identity and playback pair were included as random terms. The significant term is highlighted in bold.



**Figure 2.** The effect of environmental variables (a) wind and (b) habitat on sentinel height choice. Means and SEs, back-transformed from predicted means of the LMM presented in Table 3, are shown.

their alarm calls (Beynon & Rasa, 1989) and, particularly, their low-amplitude watchman's song (surveillance/close calls given during a bout; Kern & Radford, 2013). Since there is the possibility of vocal negotiation between sentinels and foragers about subsequent bouts (Bell et al., 2010), sentinels might want to maximize their own chances of hearing the close calls of foragers. As expected, sentinel dwarf mongooses also chose different heights depending on the habitat, adopting higher positions when guarding in denser vegetation; pied babbler sentinels have similarly been shown to make behavioural decisions according to habitat type (Hollén et al., 2011). Habitat type is likely to influence predation risk because terrestrial predators in particular are harder to detect in denser habitats (Lazarus & Symonds, 1992; Whittingham & Evans, 2004).

**Table 4**  
Linear mixed model on factors affecting duration of sentinel bouts

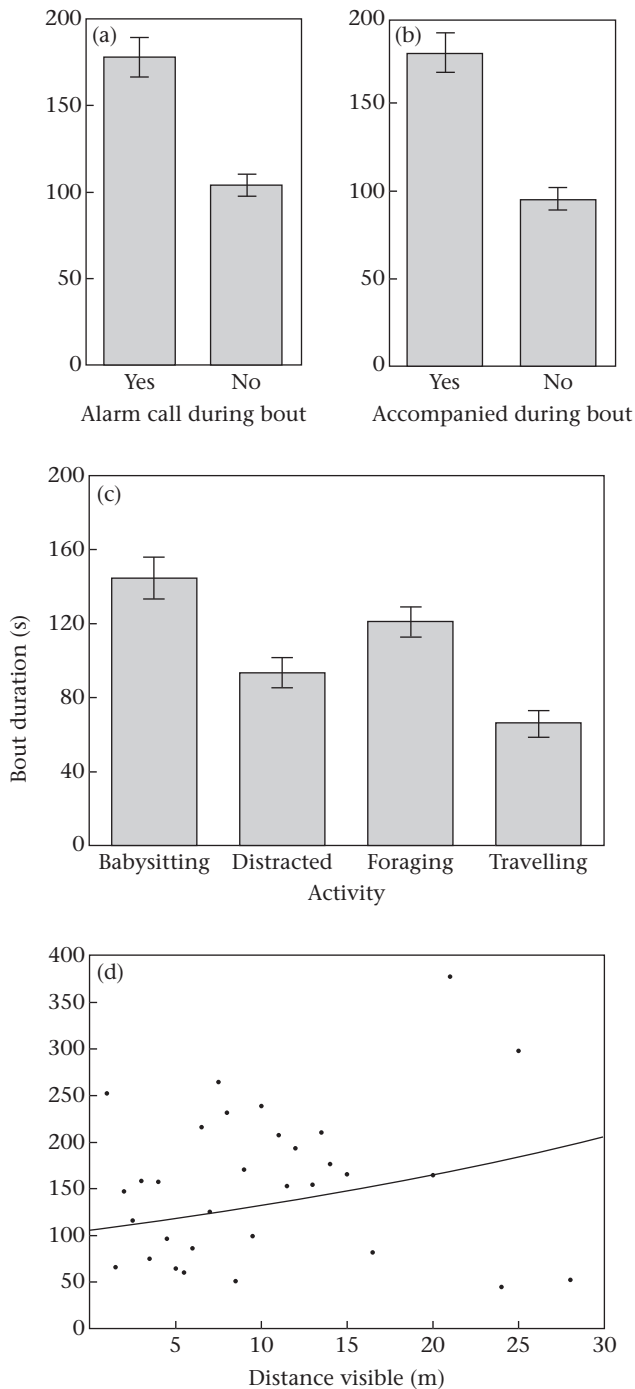
	$\chi^2$	df	P
Full model			
Alarm call during	<b>23.60</b>	<b>1</b>	<b>&lt;0.0001</b>
Accompanied during	<b>24.96</b>	<b>1</b>	<b>&lt;0.0001</b>
Activity	<b>11.90</b>	<b>3</b>	<b>0.008</b>
Visibility	<b>6.62</b>	<b>1</b>	<b>0.010</b>
Age	<b>6.66</b>	<b>1</b>	<b>0.027</b>
Location	0.01	1	0.057
Period	2.90	1	0.088
Pups	2.16	1	0.141
Habitat	3.42	2	0.181
Dominance status	1.59	1	0.208
Wind	1.61	2	0.447
Sex	0.46	1	0.500
Height	0.48	1	0.891
Group size	0.05	1	0.986
Minimal model	Effect size	SE	
Constant	1.96	0.09	
Alarm call during (Yes)	0.29	0.06	
Accompanied during (Yes)	0.25	0.05	
Visibility	0.01	0.01	
Age (Yearling)	−0.11	0.05	
Activity			
Babysitting	0	0	
Distracted	−0.18	0.09	
Foraging	−0.10	0.07	
Travelling	−0.29	0.11	
Group ID	0.00	0.00	
Individual ID in group	0.00	0.04	

The analysis used observational data from 342 full sentinel bouts by 40 individuals in four groups, with individual ID nested within group ID included as random terms. Post hoc Tukey's tests for activity (travelling versus babysitting:  $P = 0.020$ , travelling versus foraging:  $P = 0.028$ ). Significant terms are highlighted in bold.

Our ecological surveys to determine available positions in terms of height demonstrate why it is crucial to have some knowledge of potential choices when discussing decision making (Van Moorter et al., 2013). Both location and habitat were found to be significant predictors in the statistical model assessing height choice. In the former case, that could simply be because positions available at overnight refuges were higher than those elsewhere; this may not represent active choice. In contrast, positions available in the three habitat types did not differ significantly in their height, and thus the finding that sentinels adopt lower positions in the open probably reflects true decisions. We suggest that, where possible, studies on decision making should include assessment of available options.

The decision about how long to remain as a sentinel, made during a bout, was influenced predominantly by social factors that can change in the short term. For instance, if an alarm call was given by a forager, indicative of increased likelihood of predation, sentinels conducted longer bouts. These occurrences represent the most up-to-date information about current conditions. However, individuals must also consider the likely reliability and relevance of social information (Beauchamp & Ruxton, 2007; Giraldeau, Valone, & Templeton, 2002); how sentinels integrate personal and social information is an exciting topic for future studies. Bout duration was also affected by group activity and visibility, with sentinels stopping sooner when the group were travelling and lines of sight were shorter. In both cases, the rest of the group are likely to be out of sight sooner, and sentinels must balance the benefits of vigilance with the risk of losing groupmates; dwarf mongoose sentinels are particularly vulnerable when running to catch up with travelling companions (Rasa, 1987).

In general, an appreciation of how animals respond to social information is fundamental to our understanding of decision making (Giraldeau et al., 2002). Foraging groupmates would clearly benefit if information about sentinel decisions relating to starting a bout, height and duration were readily available to them. Such information could be gathered visually, but for many species this strategy disrupts foraging (Hollén et al., 2008; Manser, 1999). Use of vocal cues, such as the watchman's song (Wickler, 1985), enables group members to coordinate vigilance more efficiently. In other species, the watchman's song is known to provide information about sentinel presence (Hollén et al., 2008; Manser, 1999) and height (Radford et al., 2009), as well as estimates of current risk level (Bell et al., 2009), and to be used in negotiation with foragers about bout duration (Bell et al., 2010). Dwarf mongoose sentinels are known to produce a watchman's song, although not during every bout (Kern & Radford, 2013), and foragers appear to use it



**Figure 3.** The effect of (a) an alarm call, (b) being accompanied, (c) group activity and (d) visibility on sentinel bout duration. For (a)–(c), means and SEs, back-transformed from predicted means of the LMM presented in Table 4, are shown. For (d), the line is plotted using back-transformed predictions from the LMM presented in Table 4, and points give mean values of the raw data.

when detecting the presence of a sentinel. Whether the watchman's song provides additional information in this species and whether sentinels obtain social information about current conditions from the vocalizations of other group members are issues that remain to be tested.

Future studies might profitably consider how the payoffs to different classes of sentinel (those of different age or dominance status, for example) vary across ecological and social conditions, and how sentinels make their decisions (see Bell et al., 2010).

Moreover, the quality, as well as the quantity, of vigilance could be considered, with visual capabilities, eye and head movements and posture all potentially exerting an influence (e.g. Fernández-Juricic, Erichsen, & Kacelnik, 2004). For now, our work highlights the complexity of decision-making processes, demonstrating that sentinel choices are influenced by both direct and indirect indicators of likely predation risk and that sentinel behaviour is adjusted flexibly in relation to information available on different timescales. Such behavioural flexibility is likely to enhance survival (Blumstein & Bouskila, 1996; Couchoux & Cresswell, 2012).

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## References

- Bates, D., Maechler, M., & Bolker, B. (2012). *lme4: linear mixed-effects models using Eigen and R syntax*. R package version 0.999999-1. <http://CRAN.R-project.org/package=lme4>.
- Beauchamp, G., & Ruxton, G. D. (2007). False alarms and the evolution of anti-predator vigilance. *Animal Behaviour*, 74, 1199–1206.
- Bednekoff, P. A. (1997). Mutualism among safe, selfish sentinels: a dynamic game. *American Naturalist*, 150, 373–392.
- 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, 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: Biological Sciences*, 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.
- Blumstein, D. T., & Bouskila, A. (1996). Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos*, 77, 569–576.
- Bouskila, A., & Blumstein, D. T. (1992). Rules of thumb for predation hazard assessment: predictions from a dynamic model. *American Naturalist*, 139, 161–176.
- Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, 22, 37–47.
- 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.
- Carr, J. M., & Lima, S. L. (2010). High wind speeds decrease the responsiveness of birds to potentially threatening moving stimuli. *Animal Behaviour*, 80, 215–220.
- Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kinsky, R., Griffin, A. S., et al. (1999). Selfish sentinels in cooperative mammals. *Science*, 284, 1640–1644.
- Conover, M. R. (2007). *Predator–Prey dynamics the role of Olfaction*. Boca Raton, FL: CRC Press.
- Couchoux, C., & Cresswell, W. (2012). Personality constraints versus flexible anti-predation behaviors: how important is boldness in risk management of red-shanks (*Tringa totanus*) foraging in a natural system? *Behavioral Ecology*, 23, 290–301.
- Crawley, M. J. (2005). *Statistics: an introduction using R*. Chichester, U.K.: J. Wiley.
- Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioral ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7, 734–739.
- 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.
- Fawcett, T. W., Hamblin, S., & Giraldeau, L. A. (2013). Exposing the behavioral gambit: the evolution of learning and decision rules. *Behavioral Ecology*, 24, 2–11.
- Fernández-Juricic, E., Erichsen, J. T., & Kacelnik, A. (2004). Visual perception and social foraging in birds. *Trends in Ecology & Evolution*, 19, 25–31.
- Giraldeau, L.-A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357, 1559–1566.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295–311.

- Heath, J. P., Gilchrist, H. G., & Ydenberg, R. C. (2010). Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3179–3186.
- Hilton, G. M., Ruxton, G. D., & Cresswell, W. (1999). Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos*, 87, 295–302.
- 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., & 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., Wade, H. M., Rose, R., Russell, A., Niven, F., et al. (2011). Ecological conditions influence sentinel decisions. *Animal Behaviour*, 82, 1435–1441.
- Horrocks, J. A., & Hunte, W. (1986). Sentinel behaviour in vervet monkeys: who sees whom first? *Animal Behaviour*, 34, 1566–1568.
- Hothorn, T., Bretz, F., & Westfall, 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>.
- 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.
- Kern, J. M. (n.d.). [Contributions to sentinel behaviour by different classes]. Unpublished raw data.
- 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, 967–975.
- Lazarus, J., & Symonds, M. (1992). Contrasting effects of protective and obstructive cover on avian vigilance. *Animal Behaviour*, 43, 519–521.
- 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. (1988). Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. *Oikos*, 53, 3–11.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
- Lima, S. L., & Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Animal Behaviour*, 58, 537–543.
- Manser, M. B. (1999). Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. *Proceedings of the Royal Society B: Biological Sciences*, 266, 1013–1019.
- Masman, D., Daan, S., & Beldhuis, J. A. (1988). Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and double labelled water methods. *Ardea*, 76, 64–81.
- Mateo, J. M. (2007). Ecological and hormonal correlates of antipredator behaviour in adult Belding's ground squirrels (*Spermophilus beldingi*). *Behavioral Ecology and Sociobiology*, 62, 37–49.
- McFarland, D. J. (1977). Decision making in animals. *Nature*, 269, 15–21.
- McGowan, K. J., & Woolfenden, G. E. (1989). A sentinel system in the Florida scrub jay. *Animal Behaviour*, 37, 1000–1006.
- Pangle, W. M., & Holekamp, K. E. (2010). Functions of vigilance behaviour in a social carnivore, the spotted hyaena, *Crocuta crocuta*. *Animal Behaviour*, 80, 257–267.
- 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>.
- R Development Core Team. (2012). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>.
- 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: Biological Sciences*, 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.
- Radford, A. N., & Ridley, A. R. (2007). Individuals in foraging groups may use vocal cue when assessing their need for anti-predator vigilance. *Biology Letters*, 3, 249–252.
- 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. (1986). 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. (1987). Vigilance behaviour in dwarf mongooses: selfish or altruistic? *South African Journal of Science*, 83, 587–590.
- 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.
- Rodríguez, A., Andrén, H., & Jansson, G. (2001). Habitat-mediated predation risk and decision making of small making birds at forest edges. *Oikos*, 95, 383–396.
- Ruxton, G. D., & Beauchamp, G. (2008). Time for some a priori thinking about post hoc testing. *Behavioral Ecology*, 19, 690–693.
- Santema, P., & Clutton-Brock, T. (2013). Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. *Animal Behaviour*, 85, 655–661.
- Sapolsky, R. M. (1986). Endocrine and behavioral correlates of drought in wild olive baboons (*Papio anubis*). *American Journal of Primatology*, 11, 217–227.
- 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.
- Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2627–2634.
- Trimmer, P. C., Houston, A. I., Marshall, J. A., Bogacz, R., Paul, E. S., Mendl, M. T., et al. (2008). Mammalian choices: combining fast-but-inaccurate and slow-but-accurate decision-making systems. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2353–2361.
- Van Moorter, B., Visscher, D., Herfindal, I., Basille, M., & Mysterud, A. (2013). Inferring behavioural mechanisms in habitat selection studies getting the null-hypothesis right for functional and familiarity responses. *Ecography*, 36, 323–330.
- Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittlebach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64, 1540–1548.
- Whittingham, M. J., & Evans, K. L. (2004). The effect of habitat structure on predation risk of birds in agricultural landscapes. *Ibis*, 146, 210–220.
- Whittingham, M. J., Butler, S., Quinn, J. L., & Cresswell, W. (2004). The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos*, 106, 377–385.
- Wickler, W. (1985). Coordination of vigilance in bird groups. The 'watchman's song' hypothesis. *Zeitschrift für Tierpsychologie*, 69, 250–253.
- Wiley, R. H., & Richards, D. G. (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. In D. E. Kroodsma, & E. H. Miller (Eds.), *Acoustic communication in birds* (pp. 132–181). New York, NY: Academic Press.
- Wright, J., Berg, E., de Kort, S. R., Khazin, V., & Maklakov, A. A. (2001a). Safe selfish sentinels in a cooperative bird. *Journal of Animal Ecology*, 70, 1070–1079.
- Wright, J., Maklakov, A. A., & Kkazin, V. (2001b). State-dependent sentinels: an experimental study in the Arabian babbler. *Proceedings of the Royal Society B: Biological Sciences*, 268, 821–826.