Experimental evidence that sentinel behaviour is affected by risk

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Sentinels are a conspicuous feature of some cooperative societies and are often assumed to provide benefits in terms of increased predator detection. Similar to other cooperative behaviours, variation in investment in sentinel behaviour should reflect variation in the benefits of such behaviour. However, evidence for this is inconclusive: to date experiments have manipulated the cost of sentinel behaviour, and considerations of changes in the benefits of sentinel activity on investment patterns are lacking. Here, we experimentally manipulated the benefits of sentinel behaviour in the cooperatively breeding pied babbler (*Turdoides bicolor*) to assess whether this had any impact on sentinel activity. We simulated the presence of an unseen predator using playbacks of heterospecific alarm calls, and the presence of an actual predator using a model snake. In both cases, the increase in perceived predation risk caused an increase in sentinel activity, demonstrating that investment in sentinel activity increases when the benefits are greater.

Keywords: sentinel activity; pied babbler; predator detection; behavioural response

1. INTRODUCTION

Sentinel activity is a conspicuous behaviour where individuals adopt prominent, exposed positions while groupmates forage, and occurs in a variety of social species (Rasa 1986; McGowan & Woolfenden 1989; Zahavi 1990; Clutton-Brock *et al.* 1999). It has often been assumed that sentinel activity has a beneficial function as a predator detection system, and this has been empirically proven for some species (McGowan & Woolfenden 1989; Manser 1999). However, sentinel activity is likely to also incur a cost, such as a loss in foraging time (Bednekoff 1997, 2003), and individuals may therefore be selected to balance these costs against the benefits of such behaviour. Investment in sentinel behaviour should therefore be sensitive to short-term changes in either the costs or benefits of such activity. Previous research has investigated this by showing that

when the cost is lowered (via supplemental feeding), individuals are more likely to invest in sentinel behaviour (Clutton-Brock *et al.* 1999; Wright *et al.* 2001; Bednekoff 2003), but the effect of changes in the benefit of sentinel behaviour (e.g. according to predator presence) on investment have not been investigated.

Here, we examine the effect of variation in the potential benefit of sentinel behaviour on investment in this activity in cooperatively breeding pied babblers. We assume that the benefits vary according to predation risk, being low when predation risk is low, and increasing as predation risk increases. Most obviously, the physical presence of a predator indicates a definite threat. However, many species use indirect environmental cues (such as heterospecific alarm calls) to detect threats (Rainey *et al.* 2004; Magrath *et al.* 2007). Pied babblers respond to heterospecific alarm calls (Ridley *et al.* 2007; Bell *et al.* 2009) and may use these cues to adjust their sentinel behaviour over the short term, increasing investment at times of high predation risk and decreasing it at times of low risk. Here, we use observational data and a series of experiments to determine (i) whether sentinel activity results in greater detection of predators, and (ii) whether the changing benefits of sentinel activity (in terms of predation risk) affects the occurrence of this behaviour.

2. MATERIAL AND METHODS

(a) Study species

Pied babblers are medium-sized (70–95 g) social passerines inhabiting the semi-arid regions of southern Africa. Individuals use their bills to dig in the substrate for prey and thus cannot forage and remain vigilant simultaneously (Ridley & Raihani 2007). All adult group members participate in sentinel behaviour (defined as perching in an elevated position greater than 1 m above the foraging group and actively scanning the area, with individuals only recorded as sentinels if they remained in position for greater than 30 s (average duration of sentinel bouts 192.6 ± 17.2 s)). Sentinels give alarm calls upon sighting a predator, to which foragers respond strongly (Ridley *et al.* 2007). Sentinel behaviour in this species is best defined as 'high-level group coordination' (Bednekoff 1997), with usually one sentinel present at a time, and changes coordinated such that a retiring sentinel is swiftly replaced, providing continuous sentinel coverage.

(b) Natural observations

We conducted 905 observation sessions (1800.5 h), recording ad libitum every instance of sentinel behaviour (total seconds), alarm-calling and predator presence. We confined our analysis to alarm call events and predator sightings where the cause was positively identified and less than 100 m from the focal group, since distance may affect alarm-calling behaviour (Leavesley & Magrath 2005). For each sighting, we compared the total duration of all sentinel activity for the 10 min before versus after each alarm call. We excluded cases where a second alarm call or group disturbance occurred during the 20 min period. Data collection for the post-alarm period commenced only once the group had stopped alarm-calling and resumed normal foraging (defined as more than 75% of group foraging and no alarm calls given). To account for the effect of group size on sentinel behaviour, we used a linear mixed model (LMM) with an identity link function in GENSTAT (11th edition, VSN International, UK). We set total duration of sentinel activity as the response variable with group size and observation period (before or after alarm call) as predictors and group identity as a random term (for further details of LMM analysis, see electronic supplementary material). Throughout, means are presented as $\pm$ s.e.m.

(c) Playback experiment

To determine whether sentinel activity was influenced by secondary cues indicating an increase in predation risk, we simulated the presence of an unseen predator by conducting playbacks of heterospecific mobbing calls and recorded the duration of all sentinel activity in the 10 min before versus after each playback. Mixed-species flocks aggressively mob predators, giving repeated loud calls, to which

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Table 1. LMM of total group sentinel activity in the 10 min before versus after a predator alarm. Data are based on sentinel activity during 593 predator sightings at 16 groups. Variance component: group identity 0.08 ± 0.07 .

	Wald statistic	<i>p</i> -value	average effect	s.e.
<i>minimal model</i>				
constant			3.74	0.12
predator presence	69.86	<0.001		
before predator			0	0
after predator			1.12	0.13
<i>other terms tested</i>				
group size	0.32	0.57		

pied babblers respond strongly. We recorded five mobbing events that did not involve pied babblers (three at pearl-spotted owlets, *Glaucidium perlatum*, one at a giant eagle-owl, *Bubo lacteus*, and one at a Gabar goshawk, *Melierax gabar*—all species that pied babblers are known to both mob and give alarm calls to). Using these recordings, we constructed ten 1 min playback tracks. No section of recording was used on more than one track; all tracks contained the same number of calls from the same species. As controls, we recorded the same species giving context-neutral calls (territorial or sexual) and created ten 1 min tracks with the same number of calls and same ratio of background noise to calling as the mobbing tracks. The experiment was abandoned if at any point there was a major group disturbance (e.g. pied babbler border conflict) or a genuine predator alarm (for further details, see electronic supplementary material).

(d) *Predator presentation experiment*

To determine whether predator presence affected sentinel activity, we used a model of a known local predator, the puff adder (*Bitis arietans*): a venomous terrestrial viper common at our study site. Pied babblers actively alarm at and mob all puff adders they encounter (100% of encounters, $n = 32$). We presented the model to 10 groups, recording the total duration of all sentinel bouts in the 10 min before and after presentation. Observations began after there had been no natural alarm or group disturbance in the previous 10 min and the group was foraging normally. After detecting the model, groups always alarm-called and mobbed the model ($n = 10/10$ trials). We then waited until mobbing ceased and the group resumed foraging before recording sentinel activity. As a control, we used a plastic water bottle of the same length as the snake placed on the ground. Groups showed no response to the bottle ($n = 0/10$ trials; for further details, see electronic supplementary material).

3. RESULTS

(a) *Predator detection*

Sentinels were the first individuals to give an alarm call to an approaching predator in 59.9 per cent of cases, higher than expected if the rest of the foraging group had an equal opportunity of seeing predators (binomial test: $p = 0.001$, $n = 636$ alarm calls). Sentinels were also the first member of the group to give an alarm call at the model snake in 80 per cent ($n = 8$) of presentation experiments. They were also more likely to detect predators than other group members: there were 36 cases when no group members detected an approaching predator. In 30 of these cases (83.3%), there was no sentinel present. This was higher than expected, given that sentinels were present for an average of 43 per cent of observation time (expected rate of missed detections by sentinels assuming rest of group equally likely to detect predators = 18 out of 36 cases, $\chi = 16.1$, $p = 0.001$). Overall, sentinels detected 98.4 per cent of approaching predators ($n = 438$ alarm

Figure 1. The proportion of observation time that a sentinel was present in the 10 min before versus after a predator sighting. Means $\pm$ s.e. are displayed.

calls) compared with an 88.9 per cent detection rate when no sentinel was present ($n = 198$ alarm calls).

Sentinel activity was strongly affected by predator presence (table 1). In the 10 min prior to a predator sighting, sentinel activity averaged 37.3 (± 9.1) per cent of observation time. After a predator was seen, sentinel activity increased to 48.7 (± 9.4) per cent, representing an 11.3 per cent increase (figure 1).

(b) *Experimental manipulation*

Sentinel activity increased in the 10 min following the playback of heterospecific mobbing calls compared with the 10 min prior (paired t -test: $t_9 = -3.0$, $p = 0.02$). By contrast, there was no change in sentinel activity following playback of context-neutral calls (paired t -test: $t_9 = -0.2$, $p = 0.9$; figure 2a).

There was a large increase in sentinel activity in the 10 min after the predator presentation compared with the 10 min prior (paired t -test: $t_9 = -4.9$, $p < 0.001$; figure 2b), but there was no change in sentinel activity during control presentations (paired t -test: $t_9 = -0.7$, $p = 0.5$).

4. DISCUSSION

In pied babblers, sentinels detect predators at a greater rate than other group members, suggesting that sentinel behaviour functions as an effective anti-predator activity in this species, similar to findings for both meerkats (*Suricata suricatta*) and Florida scrub-jays (*Aphelocoma coerulescens*; McGowan & Woolfenden 1989; Manser 1999). Our research also confirms that this behaviour is adjusted according to the benefits of investment: overall, groups invest more in sentinel activity when predation risk is high. This is, to our knowledge, one of the first studies to experimentally manipulate the benefits of sentinel activity according to predation risk in a cooperative species, and our results agree with those of Eggers *et al.* (2005), that facultative adjustment of behaviour can occur quickly in response to changes in predation risk, allowing species to quickly adapt to current conditions.

It is interesting to note that the increase in sentinel activity following the snake presentation was higher than that for the playback experiments, despite very similar rates of sentinel activity prior to the manipulations. This may represent a graded response to

Figure 2. The proportion of time that a sentinel was present before versus after (a) playback of heterospecific alarm calls (experimental trials, $n = 10$ groups) compared with before versus after the playback of context-neutral calls ($n = 10$), and (b) before versus after model snake presentation ($n = 10$ groups) compared with before versus after a control presentation ($n = 10$). Means $\pm$ s.e. are displayed. Filled bar, experiment; unfilled bar control.

environmental information: in the case of the model presentation, individuals were actually able to see the predator, resulting in a greater increase in sentinel behaviour when the increase in risk is more certain. Our playback results also confirm that pied babblers use cues provided by heterospecifics to provide them with information about the likely presence of a predator, as observed in other species (Rainey *et al.* 2004; Magrath *et al.* 2007), and this is, to our knowledge, the first study to show that such indirect information regarding the likely presence of a predator affects sentinel activity.

Previous work on sentinel activity has suggested that state dependency explains the patterns of behaviour observed (Wright *et al.* 2001). In Bednekoff's (1997) theoretical model, he suggested that acting as a sentinel is the safest place for an individual to be once it is satiated, and several feeding experiments have shown that individuals do guard more following satiation (Clutton-Brock *et al.* 1999; Wright *et al.* 2001; Bednekoff 2003). However, our experiments demonstrate that the immediate benefits of sentinel activity (in terms of detection and monitoring of predators) can also affect patterns of sentinel behaviour, similar

to vigilance patterns observed in non-cooperative species (Beletsky 1989, reviewed in Lima 2009). If individuals became sentinels simply because they were satiated, then we would expect changes in predation risk to have little or no effect on sentinel activity. By contrast, our results suggest a strong effect, and we suggest that further empirical research considers both the costs and benefits of sentinel activity to determine the primary factors affecting investment in this behaviour in cooperative societies.

This research was approved by the ethics committee, Department of Zoology, University of Cape Town.

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