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# The value of constant surveillance in a risky environment

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In risky environments, where threats are unpredictable and the quality of information about threats is variable, all individuals face two fundamental challenges: balancing vigilance against other activities, and determining when to respond to warning signals. The solution to both is to obtain continuous estimates of background risk, enabling vigilance to be concentrated during the riskiest periods and informing about the likely cost of ignoring warnings. Human surveillance organizations routinely produce such estimates, frequently derived from indirect cues. Here we show that vigilant individuals in an animal society (the pied babbler, *Turdoides bicolor*) perform a similar role. We ask (i) whether, in the absence of direct predator threats, pied babbler sentinels react to indirect information associated with increased risk and whether they communicate this information to group mates; (ii) whether group mates use this information to adjust their own vigilance, and whether this influences foraging success; and (iii) whether information provided by sentinels reduces the likelihood of inappropriate responses to alarm calls. Using playback experiments, we show that: (i) sentinels reacted to indirect predator cues (in the form of heterospecific alarm calls) by giving graded surveillance calls; (ii) foragers adjusted their vigilance in reaction to changes in surveillance calls, with substantial effects on foraging success; and (iii) foragers reduced their probability of responding to alarm calls when surveillance calls indicated lowered risk. These results demonstrate that identifying attacks as they occur is only part of vigilance: equally important is continuous surveillance providing information necessary for individuals to make decisions about their own vigilance and evasive action. Moreover, they suggest that a major benefit of group living is not only the increased likelihood of detecting threats, but a marked improvement in the quality of information available to each individual.

**Keywords:** sentinel behaviour; risk sensitivity; communication; signal detection theory; cooperation; group living

## 1. INTRODUCTION

All animals foraging in the presence of predators face an acute problem: antipredator vigilance reduces foraging success (Pulliam 1973; Verdolin 2006; Hollen *et al.* 2008) yet failure to detect predators is lethal (Fitzgibbon 1989; Lind & Cresswell 2005). One solution is to concentrate vigilance during times of highest risk (Lima & Bednekoff 1999; Sih *et al.* 2000), but because predator attacks are unpredictable, doing this requires continuously updated information about attack risk (Lima & Bednekoff 1999; Sih *et al.* 2000). Obtaining this information may itself compromise foraging (Lima & Bednekoff 1999; Valone 2007), unless individuals can monitor sources of information that do not interfere with foraging—such as the conspicuous alarm call or flight behaviour of other individuals or species (Davis 1975; Beauchamp & Ruxton 2007). Such 'public information'

is abundant and considerably increases the area monitored (Valone 2007), yet it is often inaccurate, irrelevant or actively deceptive (Giraldeau *et al.* 2002; Beauchamp & Ruxton 2007; Ridley & Raihani 2007), so indiscriminate responses are costly (Lima & Dill 1990; Downes 2001; Proctor *et al.* 2001; Sirot 2006; Beauchamp & Ruxton 2007). Therefore, individuals must balance the cost of ignoring genuine alarms against the cost of inappropriate responses (Wiley 1994)—possible with access to risk estimates that inform them in advance about the likely cost of ignoring alarms. On two fundamental levels, therefore, foraging individuals stand to derive considerable benefits from a source of continuously updated, accurate information about predation risk.

In social species, foragers may be able to obtain continuous estimates of risk, without compromising foraging success, if vigilant companions evaluate and react to indirect cues associated with changes in the probability of attack, and if they transfer this information to group mates. While this is possible wherever individuals in social groups react to perceived threats in a conspicuous way, it is most likely in species with sentinel systems, where individuals stop

foraging and scan the environment for extended periods. Sentinels are well placed to detect and evaluate indirect predator cues, and in most cases produce continuous quiet surveillance calls (Gaston 1977; Rasa 1986; Manser 1999; Bednekoff *et al.* 2008; Hollen *et al.* 2008) that may carry information about changes in risk. Moreover, because sentinels also give alarms calls, some of which may be erroneous, and receivers may not be able to discriminate completely between appropriate and inappropriate alarms, foragers must make decisions about when to respond to alarm calls which balance the cost of lost foraging time against the possibility of ignoring genuine alarms. Therefore, information about risk also allows foragers to adjust their response thresholds to alarm calls in order to minimize the average cost of responding.

We investigate the information carried by surveillance calls, and its use by foraging group mates, in pied babblers (*Turdoides bicolor*), cooperatively breeding passerine birds of the Southern African Kalahari. Family groups of between 3–13 forage on the ground in open semi-desert, probing sand or prospecting through vegetation for invertebrate prey, with heads often obscured, restricting vigilance (Radford & Ridley 2007) and rendering them vulnerable to attack. Regular sentinels advertise their presence with continuous surveillance calls, and give alarm calls to warn of direct predator threats, some of which are inaccurate (see below). In addition to direct sightings, pied babblers are exposed to abundant indirect information about predator threat, most conspicuously, alarm calling by other bird species, but including heterospecific flight behaviour (bird and mammal), vegetation movement and dust clouds. Foragers are unlikely to be able to assess, or even detect, indirect predator cues without interrupting foraging, while sentinels are perfectly placed both to detect the events themselves, and to assess their relevance.

We ask (i) whether, in the absence of direct predator threats, pied babbler sentinels react to indirect information associated with increased risk and whether they communicate this information to foraging group mates; (ii) whether group mates use this information to adjust their own vigilance, independent of external cues, and whether this influences foraging success; and (iii) whether information provided by sentinels modifies forager flight behaviour, reducing the likelihood of inappropriate responses to alarm calls.

## 2. MATERIAL AND METHODS
### (a) *Study site and data collection*
We carried out observations and experiments between 25 March and 15 July 2008, on the Kuruman River Reserve, in the southern Kalahari desert, South Africa (26°58′ S, 21°49′ E) (see Ridley & Raihani 2007 for habitat and climate details). We observed 10 colour-ringed groups of pied babblers habituated to close (< 5 m) observation on foot. We conducted 104 1 h observation sessions, recording *ad libitum* every instance of sentinel behaviour, every conspecific alarm call given by the focal group, every heterospecific alarm call given within 100 m of the focal group, and the response of focal groups to all alarm calls. We also conducted 473 focal watches on 47 individuals performing sentinel behaviour, recording the total number of sentinel calls per minute, which we used to calculate average call rate for each sentinel bout.

### (b) *Sentinels*
We defined sentinels as individuals who stopped foraging to perch at least 1 m above the ground, actively scanning for predators. Sentinels were present for an average of 59 per cent of observed time (range 7–100%, $n = 104$ observation sessions; median sentinel bout length = 2 min; range 1–9, $n = 473$ bouts by 47 individuals in 10 groups). Sentinels gave continuous quiet surveillance calls during every sentinel bout (median call rate = 18.3 calls min$^{-1}$; range 1–54; figure 1a), and foragers monitored the calls (Hollen *et al.* 2008; Radford *et al.* in press). Sentinels gave alarm calls during 86.5 per cent of observation sessions (median alarm call rate = 3.6 calls h$^{-1}$, range 0–17; figure 1b). Focal groups responded to sentinel alarms 88 per cent of the time, with the whole group flying to cover 33 per cent of the time.

### (c) *Indirect predator cues*
For the purposes of this investigation, we focused on heterospecific alarm calls as the most conspicuous source of indirect information about predation risk, recorded during 58 per cent of observation sessions (median heterospecific alarm call rate = 1.9 calls h$^{-1}$, range 0–9; see electronic supplementary material for full list of species to which pied babblers responded). Focal groups responded to 70.5 per cent of these calls, with whole groups flying to cover 24 per cent of the time, confirming that pied babblers do use them as a source of information about predation risk. When whole groups flew to cover, the median time before at least one individual resumed foraging was 3.8 min (range 0.4–13.6 min). Therefore, we estimate that indiscriminate responses to heterospecific alarm calls would cost 7.22 min of foraging time per hour (12%). Not all heterospecific alarm calls are likely to be appropriate to pied babblers: callers may make mistakes (as do pied babbler sentinels), and the range of stimuli they perceive as threats may differ.

### (d) *Do sentinels react to indirect information about predation risk, and do they communicate this to group mates?*

#### (i) *Natural observations*
To determine whether sentinels use indirect cues as a source of information about predation risk, we investigated whether they altered their surveillance calls in response to heterospecific alarm calls. We made two sets of 1 min recordings from 18 sentinels in six groups: (i) 'disturbed' calls, recorded immediately after a heterospecific alarm call, but when no predator was observed and no alarm calls were given by the sentinel or any other group member, and (ii) 'calm' calls, recorded at least 5 min after the last group disturbance (con- or heterospecific alarm call, group chorus, predator sighting, group move or inter-group interaction).

#### (ii) *Experimental treatments*
To confirm that sentinels use heterospecific alarm calls as a source of information about risk independent of external cues, we played back both heterospecific alarm calls and context-neutral calls to 10 sentinels in eight groups. We randomized treatment order, with at least one day between alarm call and context-neutral call playbacks. We carried out playbacks at least 5 min after the last group disturbance. We recorded 1 min of surveillance calls given immediately before and immediately after the playbacks. We discarded
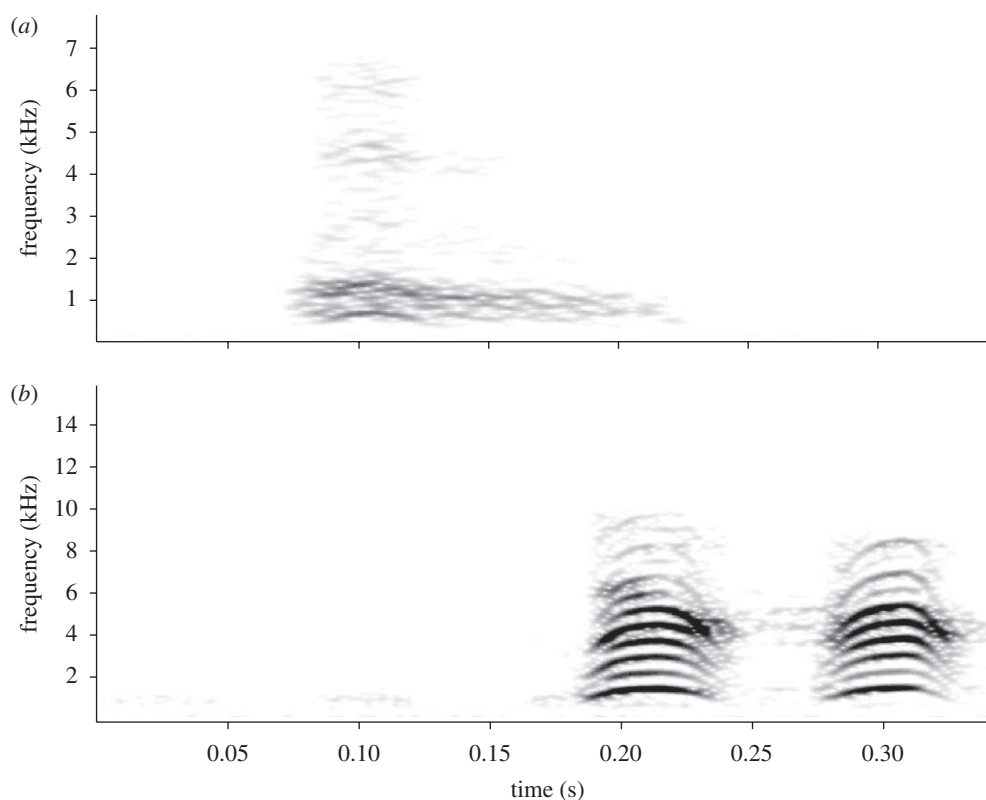
Figure 1. Example sonograms of calls given by a pied babbler sentinel: (*a*) surveillance call given throughout every sentinel bout; (*b*) alarm call; only given in presence of an aerial predator such as a gabar goshawk.

recordings if another individual became a sentinel, if groups flew away or if genuine predator alarms occurred.

For the heterospecific alarm call playback tracks, we opportunistically recorded alarm calls given by fork-tailed drongos (*Dicrurus adsimils*) and crowned lapwings (*Vanellus coronatus*) to gabar goshawks (*Micronisus gabar*), a common medium-sized raptor, known to attack pied babblers (personal observations). We constructed 10 20 s playbacks, each comprising 4 fork-tailed drongo alarm calls and 2 bouts of crowned lapwing alarm calling, with the remaining time made up using neutral background noise (figure 2*a*). This is similar to naturally observed patterns of alarm calling when a gabar goshawk is present (unpublished data). Calls were chosen at random and their order on each playback was randomized. Owing to the limited number of recordings, individual calls were used on more than one playback, but never in the same position within the playback and on no more than three playbacks. For control playbacks, we recorded calls given during territorial squabbles by white-browed sparrow weavers (*Plocepasser mahali*) (similar in amplitude and duration to the alarm calls mentioned earlier), and constructed ten 20 s playbacks with the same proportions of neutral background noise as the alarm call tracks (figure 2*b*). We did not use calls given by fork-tailed drongos or crowned lapwings in non-alarm contexts as controls because (i) fork-tailed drongos give an extremely wide variety of calls, many of which are mimicked alarm calls of other species and it is currently impossible to determine which are truly context neutral and (ii) crowned lapwings do not produce context-neutral calls when in the study area.

### (iii) *Acoustic analysis*
We analysed naturally observed and experimental recordings of surveillance calls by conducting a 512-point fast Fourier transformation (Hamming window; time step: 1 ms; overlap:

98.43%; frequency range: 8 kHz; frequency resolution: 16 kHz) of all recordings using AVISOFT-SASLab pro 4.40 (R. Specht, Berlin). We used LMA 2005 (developed by Hammerschmidt; see Schrader & Hammerschmidt 1997) to extract the following parameters from five randomly chosen calls from the disturbed and calm recordings of each individual: fundamental frequency (Hz), peak frequency (Hz), first quartile energy (Hz) and duration (s). Mean values of the five calls were used in statistical analyses. We calculated call rate (calls per minute) from the original sound files.

### (e) *Do foragers use the information contained in surveillance calls to adjust their own vigilance behaviour?*
To determine whether changes in surveillance calling influence the foraging behaviour of forging group mates, we carried out paired 5 min playbacks of calm or disturbed surveillance calls to 16 individuals in six groups, in the absence of a natural sentinel (figure 3). We used surveillance-call recordings collected as earlier from the dominant male of the focal group, or, when the focal individual was the dominant male, from the dominant female. We randomized treatment order and left at least three days between calm and disturbed playback. We started the playbacks at least 5 min after the last group disturbance, and only when there was no natural sentinel. We strapped the speakers to the observer's back-pack (approx. 1.5 m high) to ensure a constant distance (2–3 m) between speakers and focal bird.

During each playback, an observer followed an individual at a constant distance, continuously recording its behaviour. We categorized behaviour as actively foraging (probing, digging, chasing, scraping or gleaning), moving (hopping on the ground), vigilant (stationary with head raised) or resting (allopreening, perched under cover; playing). During
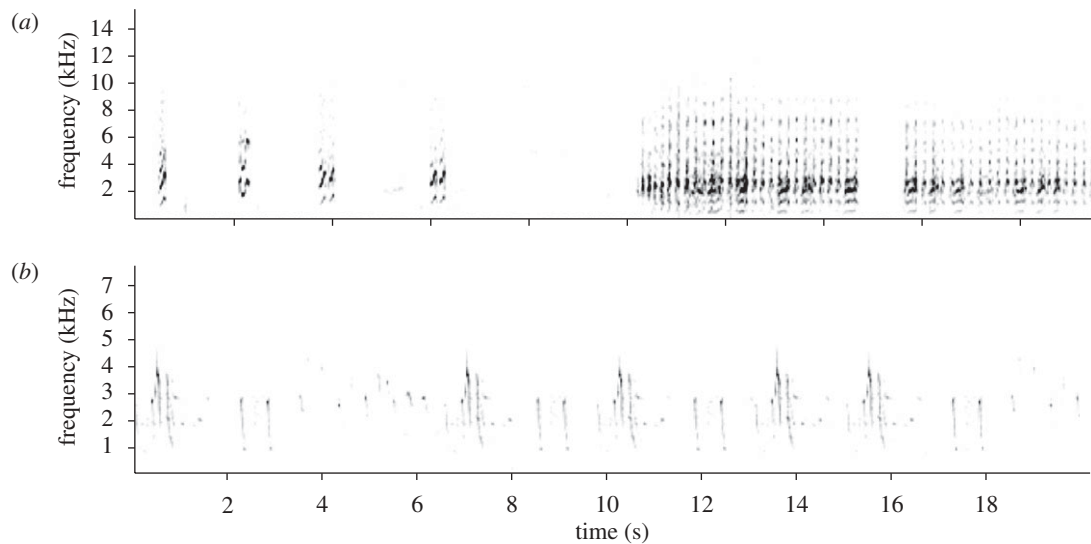
Figure 2. Example sonograms of experimental playback tracks: (*a*) heterospecific alarm calls (given by fork-tailed drongos and crowned lapwings in the presence of a gabar goshawk); (*b*) context-neutral calls (given by white-browed sparrow weavers during territorial squabbles).
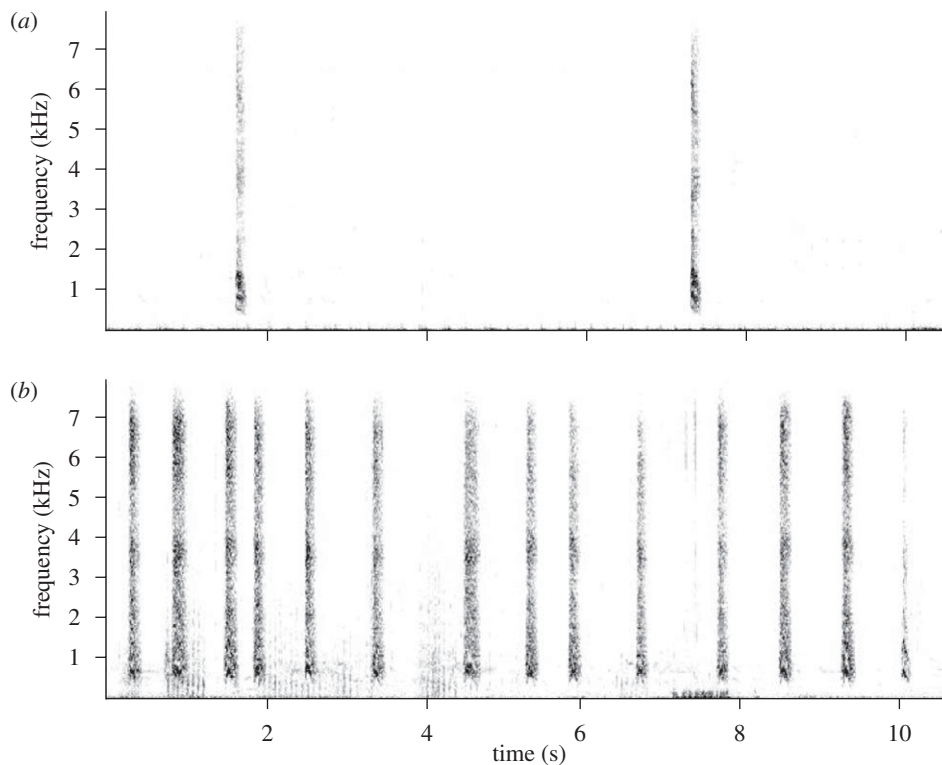


Figure 3. Sonograms of (*a*) calm surveillance calling; (*b*) disturbed surveillance calling by the same pied babbler sentinel. Calm calls followed at least 5 min without conspecific or heterospecific alarm calls, intergroup interactions or other major disturbances. Disturbed calls followed a heterospecific alarm call within 100 m of the sentinel that did not elicit an alarm call from the sentinel itself.

foraging bouts, we recorded the size of every food item captured, assigning them to the following size categories: tiny = barely visible; small = visible in the bill; medium = up to one-half of the prey hanging out of the bill; and large = one-half to three-quarters of the prey hanging out of the bill; items larger than this were scored as multiples of large. Fifty prey items representative of each size category were weighed, and prey sizes were subsequently converted to average biomass values as follows: tiny = 0.01 g, small = 0.11 g,

medium = 0.45 g and large = 0.84 g. The same observer carried out all focal watches to ensure consistency.

### (f) *Do sentinels make mistakes when alarm calling, and does prior exposure to different grades of surveillance call influence the probability of foragers responding?*

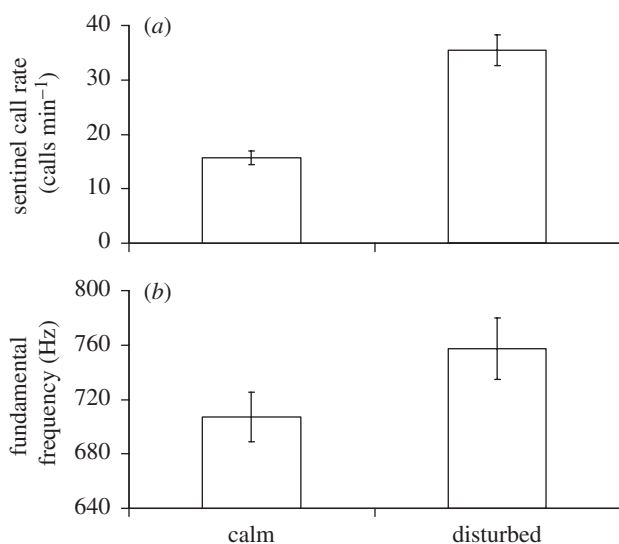To determine whether sentinels give inappropriate alarm calls, we recorded the likely cause of every sentinel alarm

Figure 4. Immediately after naturally occurring heterospecific alarm calls, sentinels (*a*) called at higher rates (paired *t*-test, $t_{18} = 6.53$, $p < 0.0001$) and (*b*) called at a higher fundamental frequency (paired *t*-test, $n = 18$, $t = 3.88$, $p = 0.001$). (Mean $\pm$ s.e.; 'calm' = at least 5 min after last disturbance, 'disturbed' = immediately after heterospecific alarm call within 100 m).
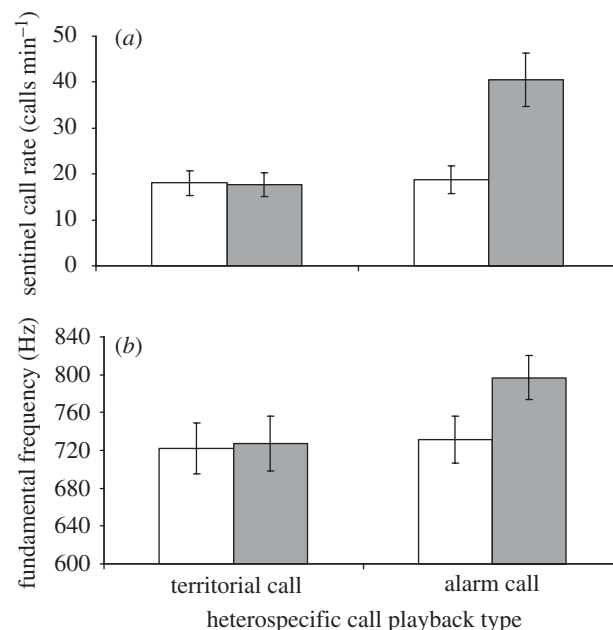


Figure 5. Immediately after experimental playbacks of heterospecific alarm calls, but not after playbacks of heterospecific territorial calls, sentinels (*a*) called at higher rates (two-way repeated measures ANOVA, interaction between experiment and treatment: $F_{1,39} = 15.45$, $p < 0.001$) and (*b*) called at higher fundamental frequencies ($F_{1,39} = 6.12$, $p = 0.02$) (mean $\pm$ s.e.; paired playbacks to 10 sentinels in eight groups). Open box, before; grey box, after.

call given during group observation sessions. We restricted further analysis to events with unambiguous causes (e.g. direct attacks by predators, or group mobbing of a hose pipe).

To determine whether prior exposure to different grades of surveillance calls influences the probability of foragers responding to sentinel alarm calls, immediately after the surveillance call playbacks, we played back an alarm call recorded from the same sentinel as the surveillance calls, noting the behaviour of the focal bird and the group as a whole. We used the same recording for both playbacks to avoid any possible effect of variations in urgency or semantic content.

### (g) Statistical analysis

We performed paired tests in Minitab 15 (all tests two tailed). To analyse the effect of calm and disturbed surveillance calls on the responsiveness of foragers to sentinel alarm calls, we used Genstat 8.1 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK) to construct generalized linear mixed models (GLMMs) with a binomial error structure and a logit link function. Because the analysis involved repeated trials with the same groups, we included random terms, which allowed the analysis to take account of repeated measures (Schall 1991), estimating the variance components using the restricted maximum likelihood method (see electronic supplementary material for more details).

## 3. RESULTS

### (a) Do sentinels react to indirect information about predation risk, and do they communicate this to group mates?

We found that immediately after naturally occurring heterospecific alarm calls, sentinels called at faster rates (paired *t*-test, $t_{18} = 6.53$, $p < 0.0001$; figure 4*a*) and at higher fundamental frequencies (paired *t*-test,

$n = 18$, $t = 3.88$, $p = 0.001$; figure 4*b*), compared with when there had been no disturbance. Playbacks of heterospecific alarm calls confirmed that sentinels used heterospecific alarm calls as a source of information about predation risk, in the absence of external stimuli: immediately after playbacks of heterospecific alarm calls (but not after control playbacks of heterospecific territorial calls), sentinels called at faster rates (two-way repeated measures ANOVA, interaction between experiment and treatment: $F_{1,39} = 15.45$, $p < 0.001$; figure 5*a*), and at a higher fundamental frequency ($F_{1,39} = 6.12$, $p = 0.02$; figure 5*b*).

### (b) Do foragers use the information contained in surveillance calls to adjust their own vigilance behaviour?

During calm surveillance call playbacks, focal foragers looked up less often (paired *t*-test, $t_{16} = 20.53$, $p < 0.0001$; figure 6*a*), and spent a smaller proportion of time vigilant (paired *t*-test, $t_{16} = 19.68$, $p < 0.0001$; figure 6*b*) than during disturbed surveillance call playbacks. Consequently, foragers had a higher foraging efficiency (Wilcoxon, $W_{16} = 136$, $p < 0.0001$; figure 6*c*) and spent a greater proportion of time actively foraging (paired *t*-test, $t_{16} = 5.42$, $p < 0.0001$; figure 6*d*) during calm surveillance call playbacks than during disturbed surveillance call playbacks. These changes in foraging meant that total biomass intake rate was considerably greater during calm surveillance call playbacks than during disturbed surveillance call playbacks (Wilcoxon, $W_{16} = 136.0$, $p < 0.0001$; figure 6*e*).
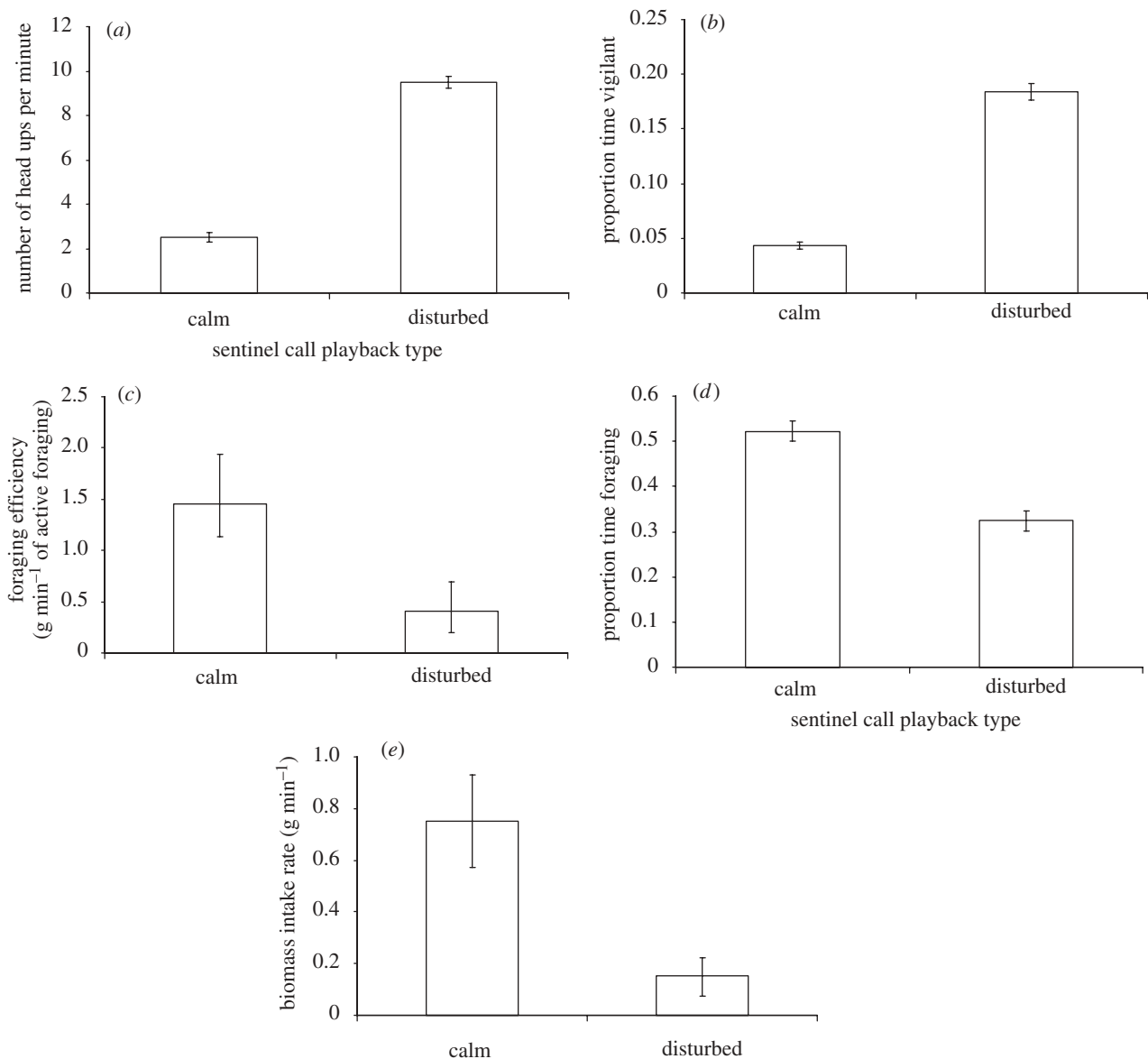
Figure 6. Behaviour of focal foragers during 5 min playbacks of either calm or disturbed sentinel calls (mean $\pm$ s.e., $n = 16$ individuals from six groups). Focal foragers (a) looked up less often (paired *t*-test, $t_{16} = 20.53$, $p < 0.0001$; (b) spent a smaller proportion of time vigilant (paired *t*-test, $t_{16} = 19.68$, $p < 0.0001$; (c) had a higher foraging efficiency (Wilcoxon, $W_{16} = 136$, $p < 0.0001$); (d) spent a greater proportion of time actively foraging (paired *t*-test, $t_{16} = 5.42$, $p < 0.0001$); and (e) had a higher biomass intake rate (Wilcoxon, $W_{16} = 136.0$, $p < 0.0001$) during playbacks of calm sentinel calling than during playbacks of disturbed sentinel calling.

## (c) *Do sentinels make mistakes when alarm calling, and does prior exposure to different grades of surveillance call influence the probability of foragers responding?*

We observed that 27.5 per cent of sentinel alarm calls (128 out of 466) were given when the only visible stimulus was innocuous (most commonly non-predatory birds flying past rapidly; see electronic supplementary material for full list). Moreover, foragers were unable to completely discriminate between appropriate and inappropriate sentinel alarms, flying to cover after 25.4 per cent of the apparently inappropriate alarms. Considering that median time to resume foraging after flying to cover in response to a sentinel alarm is 4.3 min (range 0.3–15.1 min), foragers stand to lose an estimated 15.5 min of foraging time per hour (25.8%) if they respond indiscriminately to all sentinel alarm calls.

Playbacks of sentinel alarm calls immediately after the surveillance call playbacks revealed that focal foragers were more likely to fly to cover (GLMM, $\chi^2_{1,27} = 11.46$, $p < 0.001$, effect = 3.78, $\pm 1.12$ s.e.; figure 7a) and a greater proportion of each group flew to cover (GLMM $\chi^2_{1,27} = 42.56$, $p < 0.001$, effect = 2.96, $\pm 0.45$ s.e.; figure 7b) in response to a sentinel alarm call playback if this followed a playback of disturbed surveillance calls rather than calm surveillance calls.

## 4. DISCUSSION

In risky environments, with limited resources and imperfect information, obtaining continuous estimates of risk is crucial to success and survival: it allows vigilance to be concentrated during the riskiest periods (Lima & Bednekoff 1999) and it informs about the likely cost of
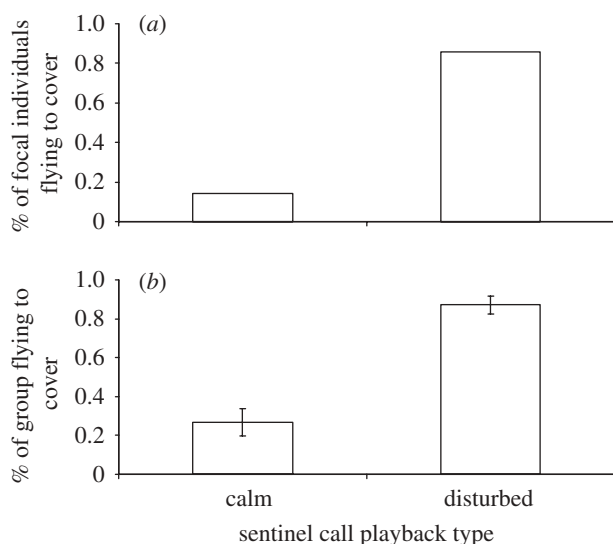
Figure 7. Responses to a sentinel alarm call playback immediately after a 5 min playback of either calm or disturbed sentinel calls: (*a*) Focal foragers were more likely to fly to cover (GLMM, $\chi^2_{1,27} = 11.46$, $p < 0.001$, effect = 3.78, $\pm 1.12$ s.e.); and (*b*) a greater proportion of the group flew to cover (GLMM $\chi^2_{1,27} = 42.56$, $p < 0.001$, effect = 2.96, $\pm 0.45$ s.e.) when a sentinel alarm was played back after 5 min of disturbed sentinel calling than after 5 min of calm sentinel calling. ($n = 14$ pairs of playbacks to six groups).

ignoring warnings (Wiley 1994). Our experiments demonstrated that pied babbler sentinels reacted to indirect predator cues by altering their surveillance calls, providing foraging group mates with the information required to adjust their vigilance appropriate to the level of risk, with substantial effects on foraging success. Critically, we showed that surveillance calls informed foragers about *reduced* risk, which is probably more difficult for foragers to assess than increased risk, (Sih 1992; Sih *et al.* 2000), allowing them to increase foraging effort when risk was low.

We also show that surveillance calls provide a solution to one of the most intractable problems facing social animals—that of deciding when to react to predator alarms when a proportion of alarms are inappropriate (Giraldeau *et al.* 2002; Beauchamp & Ruxton 2007). Since pied babbler foragers are unable to completely discriminate between appropriate and inappropriate alarms, their decisions about when to respond must balance the cost of lost foraging time against the possibility of ignoring genuine alarm calls. We argue that changes in surveillance calling allow foragers to facultatively shift their response threshold to alarm calls, reducing time lost through inappropriate responses when risk is low, but reducing the likelihood of ignoring genuine alarms when risk is high. These results indicate that sentinels may perform an additional vital role, acting to limit the probability of whole groups taking flight when single individuals panic. Sentinels may effectively act as brakes on information cascades within groups—a common problem where group members rely on public information about predation risk (Giraldeau *et al.* 2002; Sirot 2006).

An obvious question raised by these results is why sentinels should be selected to provide such valuable information to group mates. It is possible that changes in sentinel calling are unselected expressions of

anxiety—though even then, if they reliably correlate with changes in risk, foragers will be selected to attend to the changes (cf. Premack 1975). However, given that the majority of group members are close kin (Radford & Ridley 2007; Ridley & Raihani 2007), sentinels stand to gain substantial inclusive fitness benefits by improving the foraging success and survival of close relatives at relatively low cost to themselves. More intriguingly, it is possible that they communicate the need for replacement once sentinel bouts end: as risk increases, periods without a sentinel become increasingly dangerous for foragers, so retiring sentinels should benefit by ensuring swift replacement (Bednekoff 1997). Since the motivation of group mates to replace sentinels may also be influenced by nutritional state (Clutton-Brock *et al.* 1999; Wright *et al.* 2001), sentinel calling may express negotiation between sentinels and group mates over sentinel bout duration, raising the possibility that sentinels nearing the end of bouts might on occasion exaggerate risk in order to guarantee replacement (see Bednekoff *et al.* 2008 for a possible example in Florida scrub-jays, *Aphelocoma coerulescens*).

More generally, individuals in many social species that lack a sentinel system also produce continuous quiet vocalizations (reviewed in Radford 2004; Radford & Ridley 2008), the exact function of which is unclear (though see Radford & Ridley 2007, 2008 for possible explanations). In light of our current findings, we suggest that these vocalizations may represent information sharing about perceived risk: relying on public information about predators renders information cascades inevitable (Bikhchandani *et al.* 1992; Giraldeau *et al.* 2002), and unnecessary anti-predator behaviour will generally be costly (Lima & Dill 1990; Beauchamp & Ruxton 2007). However, selection may act against overly stringent acceptance thresholds for the use of public information, since this raises the probability of an individual behaving out of synchrony with its group, which will often be dangerous (Sumpter 2006). Individual group members may therefore be selected to actively contribute their own information to a public pool, since this may act to reduce the probability of group panics. Contact calls may therefore represent a form of quorum sensing regarding risk, reducing the probability of more nervous individuals or individuals with poorer information from triggering unnecessary flight.

Our results raise several further issues. First, they emphasize that individuals are selected to exploit any available information sources when making risk-sensitive decisions, whether incidental features of companions and the environment (Blumstein *et al.* 2004; Monclus *et al.* 2005), or actively broadcast signals, either conspecific (Manser *et al.* 2002) or heterospecific (Rainey *et al.* 2004; Magrath *et al.* 2007; Muller & Manser 2008). Second, they highlight an important reinterpretation of vigilance in social groups: increased vigilance by companions, rather than allowing a relaxation of personal vigilance (Pulliam 1973; Bahr & Bekoff 1999), instead may often indicate that risk has *increased*, which should select for increased personal vigilance (Sirot 2006; Beauchamp 2008). Finally, they complement recent work, revealing considerable subtlety in the information passed between group mates across a wide diversity of taxa (Zuberbuhler 2000; Manser *et al.* 2002; Templeton *et al.* 2005; Griesser 2008). Taken together, these suggest that a major benefit of group living is not

only the increased likelihood of detecting threats, but a marked improvement in the quality of information available to each individual.

To conclude, we demonstrate that pied babbler sentinels use surveillance calls to provide a continuous estimate of risk, enabling group mates not only to optimize the trade-off between foraging and vigilance, but also to alter their threshold of response to antipredator information. Identifying sporadic and unpredictable attacks as they occur is obviously important (Lind & Creswell 2005), but a continuous supply of information is necessary if individuals are to make efficient decisions about their own vigilance and evasive action—something long appreciated by human surveillance organizations, who usually invest considerably more resources into obtaining estimates of risk than into spotting attacks in progress (Handel 1989; Bernstein 1996; Keegan 2003).

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