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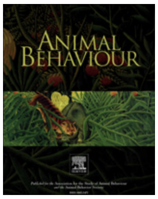

Ecological conditions influence sentinel decisions

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Ecological conditions can influence decisions relating to antipredator behaviour through impacts on the likelihood of detecting predators and the ability to hear vocalizations. Previous studies of antipredator behaviour have tended to focus on foragers, whose vigilance behaviour may be confounded by the type of food they are eating, and on receivers in vocal communication networks. We examined the impact of habitat and wind conditions on the behaviour of sentinels, individuals that suspend their own foraging to adopt a raised position to scan for danger while groupmates continue feeding, and that produce a variety of calls used by foragers to adjust their antipredator behaviour. Sentinels of the pied babbler, *Turdoides bicolor*, a cooperatively breeding bird, started guarding sooner and guarded for longer in long grass compared to more open habitats, and also initiated sentinel bouts sooner in high wind, probably because of the increased predation risk in such circumstances. Sentinels also selected positions that were both lower and closer to the foraging group when it was windy, potentially improving transmission of vocal signals that are valuable to foragers. Our results demonstrate that sentinel behaviour can be influenced by extrinsic factors, as well as the intrinsic factors previously shown, and suggest that ecological variation may affect decisions bearing both selfish and cooperative benefits.

Ecological conditions are known to affect behavioural decision making, especially choices relating to antipredator behaviour, in a variety of taxa. Predator detection, for example, can be compromised by the conditions in which an animal is foraging, leading to changes in vigilance behaviour (Arenz & Leger 1997; Hilton et al. 1999; Whittingham et al. 2004; Devereux et al. 2006; Mateo 2007; Griesser & Nystrand 2009). In particular, vegetation that might provide protective cover from predators can also obstruct a forager's view of potential danger (e.g. Lazarus & Symonds 1992; Whittingham & Evans 2004), and so foragers often change their vigilance pattern depending on the habitat. Belding's ground squirrels, *Spermophilus beldingi*, in obstructed areas stay alert for longer and show more exaggerated escape responses than individuals in open areas (Mateo 2007), thirteen-lined ground squirrels, *Spermophilus tridecemlineatus*, feeding in visually obstructed boxes spend more time vigilant in response to simulated hawk attacks than those in more open boxes (Arenz & Leger 1997), while starlings, *Sturnus vulgaris*, and chaffinches, *Fringilla coelebs*, increase their scanning rate when foraging in long grass compared to short grass (Whittingham et al. 2004; Devereux et al. 2006). Wind conditions can also influence the ability to detect predators (Hilton et al. 1999), and so individuals foraging in windy areas may change their antipredator behaviour (Woo et al. 2009; Carr & Lima 2010), although empirical work on the effect of wind is more limited than that investigating the importance of habitat.

In many species, antipredator behaviour is also influenced by various vocalizations. The most obvious of these are alarm calls, which warn of approaching danger (Klump & Shalter 1984; Hollén & Radford 2009). However, low-amplitude 'close' calls produced by many species (see Palombit 1992; Radford 2004; Hollén et al. 2008) can provide valuable information about the need for vigilance (e.g. Radford & Ridley 2007; Hollén et al. 2008; Townsend et al. 2011). As with the spotting of predators, detection of relevant vocalizations can be influenced by a variety of ecological factors (Wiley &

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Richards 1982; Johnstone 1998). Quinn et al. (2006), for example, have shown that when there are high levels of background noise, foraging chaffinches decrease the latency between vigilance bouts to compensate for the potential masking of alarm calls. The ease with which vocalizations are detected can also be affected by wind speed, and individuals that are reliant on vocal cues from others often avoid areas of high wind to increase the chance of hearing them (e.g. Dolby & Grubb 1999).

Sentinel behaviour, which has evolved in a variety of social bird and mammal species (e.g. Rasa 1986; Clutton-Brock et al. 1999; Wright et al. 2001a; Ridley & Raihani 2007), involves both antipredator vigilance and the use of various vocal signals relating to danger. Sentinels adopt a raised position to scan for predators while the rest of the group is foraging (Bednekoff 1997), and they are usually the first group members to spot danger and give warning alarm calls (Wright et al. 2001a; Ridley et al. 2010). Moreover, they often use quiet vocalizations (the 'watchman's song'; Wickler 1985) to provide continuous additional information to foragers (Rasa 1986; Manser 1999; Hollén et al. 2008); foragers are known to alter their vigilance behaviour in response to these calls (Manser 1999; Hollén et al. 2008; Bell et al. 2009; Radford et al. 2009). Sentinels might therefore be expected to alter their behaviour in response to habitat and wind conditions, but this possibility has not been previously considered.

Studying the impact of ecological conditions on sentinel behaviour offers the possibility of various novel insights. First, although several previous studies have demonstrated an effect of ecological factors on vigilance behaviour (see above), many of the vigilance measures used can be confounded by foraging behaviour. What type of food is being eaten, for example, may impact how much an individual can scan for predators (Whittingham et al. 2004). Sentinels do not eat during a bout and so their vigilance behaviour is removed of such confounds. Second, previous studies investigating how the masking of vocalizations might influence antipredator behaviour have focused on the receiver. By considering the behavioural decisions of vocal sentinels, we explored the importance of ecological conditions from the perspective of the sender. Finally, much of the work in this area to date has been conducted on species whose behavioural decisions are likely to be made on the basis of selfish benefits. The presence and calling of sentinels is known to bring antipredator and foraging advantages for groupmates (Hollén et al. 2008; Ridley et al. 2010), as well as immediate direct benefits to the sentinel itself (Bednekoff 1997; Clutton-Brock et al. 1999), so sentinels might be expected to adjust their behaviour in response to ecological factors to gain selfish and/or cooperative benefits (Lehmann & Rousset 2010).

The pied babbler, *Turdoides bicolor*, a cooperatively breeding bird species from southern Africa, offers an ideal opportunity to investigate how ecological variation influences sentinel decisions. Babbler groups spend approximately 95% of their foraging time on the ground, in a variety of habitats (ranging from open areas with little vegetation to sites covered with thick long grass), probing into the sand and sifting through vegetation for invertebrate prey (Radford & Ridley 2006). These methods of foraging often result in restricted vigilance (Radford & Ridley 2007), making individuals particularly vulnerable to predation from a variety of raptors (e.g. gabar goshawks, *Micronisus gabar*, and pale chanting goshawks, *Melierax canorus*), mammals (e.g. yellow mongooses, *Cynictis penicillata*) and reptiles (e.g. cape cobras, *Naja nivea*). Foraging groups frequently have a sentinel in place who often gives alarm calls (Ridley & Raihani 2007; Ridley et al. 2010) and continuously produces a low-amplitude watchman's song, which conveys information about their presence (Hollén et al. 2008) and position (Radford et al. 2009), as well as the current level of risk (Bell et al. 2009). The watchman's song is likely to be part of the short-range communication repertoire, adapted to minimize predatory attention. Sentinels select a wide range of positions from which to conduct a bout (Radford et al. 2009; see also Gaston 1977; Wright et al. 2001a), potentially affecting the magnitude of the selfish and/or cooperative benefits that arise (Radford et al. 2009); there is considerable variation in sentinel behaviour.

We used natural variation in habitat types and weather conditions to examine the impact of these ecological factors on: (1) latency between sentinel bouts; (2) bout duration; and (3) the initial position chosen by sentinels (height and distance to foragers). At a coarse scale, we predicted variation dependent on year because of differences in overall climate. Specifically, in years with greater rainfall, when vegetation is likely to be generally denser and thus foragers are potentially more vulnerable to predation, we predicted that latency between bouts would be shorter and that bouts would be longer than in drier years. At a finer scale, we predicted variation dependent on habitat type and wind condition. In denser and more visually obstructive habitats, such as long grass, individuals should initiate sentinel bouts sooner and guard for longer compared to more open areas. Likewise, sentinel bouts should be initiated sooner and last for longer in windy conditions, when predators are harder to spot and thus the predation risk is higher. Given the importance of the watchman's song, we also expected that sentinels in windy conditions would adopt lower positions and perch closer to foragers, to improve the chances of groupmates detecting their vocalizations.

METHODS

Study Site and Species

The study site is located on the Kuruman River Reserve in the Northern Cape province of South Africa (26°58′S, 21°49′E), and includes stretches of dry riverbed with vegetated dunes on either side. The vegetation comprises a combination of annual and perennial grasses (*Eragrostis*, *Aristida*, *Schmidtia*, *Stipagrostis*) and *Acacia* and *Boscia* trees. There are two distinct seasons: a cold–dry season from May to September and a hot–wet season from October to April. Average annual rainfall (measured daily at the study site) is 217 mm, but the amount can vary substantially between years. During the data collection period in 2008 the average ± SE daily rainfall was 6.6 ± 1.5 mm ($N = 62$ days), whereas in 2009 the average ± SE was 2.0 ± 0.8 mm ($N = 70$ days). Further details of the climate and vegetation are given in Clutton-Brock et al. (1999) and Raihani & Ridley (2007).

We studied groups of pied babblers that were colour-ringed and habituated to a level that facilitates detailed observations of sentinel and forager behaviour (see Radford & Ridley 2006; Hollén et al. 2008; Radford et al. 2011). Groups varied in size and composition throughout the study, containing varying numbers of dependent fledglings, independent fledglings and adults (mean ± SE group size during study = 4.9 ± 0.3, range 2–12, $N = 15$ groups). Fledglings were defined as independent once they obtained 95% of their food from self-feeding; prior to this they were termed dependent. Individuals over 12 months old were classified as adults and were divided into dominants (the putative breeding pair) and subordinates (all other adults); paternity analysis has confirmed that the vast majority of young (95%) are the offspring of the putative breeding pair (Nelson-Flower et al. 2011). Breeding females always incubate the eggs overnight; breeding males were identified from mid-air courtship chases and copulations with breeding females.

Pied babblers are sexually monomorphic in plumage and size, so subordinates and fledglings were sexed using a DNA test (see Griffiths et al. 1998 for details). Individuals were caught using a walk-in trap, ringed and a blood sample (ca. 50 μl) obtained by brachial venipuncture (under SAFRING licence no. 1263 issued to Amanda Ridley); see Radford & Ridley (2008) for further details. There were no adverse effects of the trapping and ringing procedure: birds were promptly released back to their group following completion of ringing and resumed normal foraging behaviour within 10 min of release; birds were not attacked by other group members on their return to the group and no bird was injured or died during the ringing process. Blood samples were kept cool in the field and then stored at 4 °C until DNA extraction and analysis in the laboratory.

Observational Data

Observations were made during the 4 h period following dawn and the 3 h period before dusk. Sentinel data were collected from 11 groups between April and July 2008 and between March and July 2009. Sentinels were defined as individuals perched >1 m above the ground and actively scanning for predators while other group members were foraging. To obtain information on sentinel bout latency and duration, and on initial sentinel height and horizontal distance to the nearest forager, we collected ad libitum data on all sentinel decisions during 1 h sessions (mean ± SE sessions per group = 24.3 ± 4.0, range 8–45). During ad libitum sessions, we recorded: (1) the start and end of every sentinel bout; (2) sentinel identity; (3) initial sentinel height; (4) initial horizontal distance from the sentinel to the nearest forager; (5) habitat; and (6) wind condition. From (1) we extracted bout duration and latency between consecutive bouts by the same or a different group member. Height was estimated to the nearest 0.5 m if <4 m and to the nearest 1 m if >4 m. Horizontal distance (from the point on the ground directly beneath the sentinel) to the nearest forager was estimated to the nearest 1 m if <15 m and to the nearest 5 m if >15 m. We defined three habitat types: grass (ground dominated by long grass where foragers and any awaiting terrestrial predators are completely covered); thickets (ground covered with small bushes and thickets with open areas in between); and open (stretches of exposed sand with little vegetation). Wind condition was defined as low (occasions when there was no vegetation movement or leaves and grass were moving slightly) or high (occasions when tree branches were clearly moving). Opportunistic focal watches were conducted during a separate 1 h session from ad libitum data collection (mean ± SE watches per individual = 9.0 ± 1.3, range 1–44, $N = 48$ individuals) as part of another study investigating the effect of calling by concluding sentinels (Hollén et al. 2011). These provided additional data on initial sentinel height and distance to the nearest forager. The order in which ad libitum and focal watch sessions were conducted was randomized between observation periods. Data were collected from all study groups in all three habitat types and both wind conditions; groups frequently moved between habitats within an observation session. All data were recorded onto a Palm TX PDA (Palm Inc., Sunnyvale, CA, U.S.A.), which automatically noted the time of each event.

Because other studies have demonstrated that the onset of sentinel bouts can be state dependent (satiated individuals are more likely to start guarding than those that are hungry; Clutton-Brock et al. 1999; Wright et al. 2001a, b), we examined whether biomass intake rate differed between the three habitats, and thus might potentially confound any effects on latency between sentinel bouts. Data on biomass intake rate were collected between January and May 2007 from continuous focal watches (mean ± SE duration = 8.0 ± 0.5 min, range 1.3–25.7 min, $N = 228$ watches) on foraging adults (mean ± SE watches per individual = 5.4 ± 0.6, range 1–19, $N = 42$ individuals in 10 groups). Each successful foraging attempt and the size of prey captured were used to calculate the biomass intake rate of individuals per minute of observation time (see Radford & Ridley 2006 for details). Focal watches continued until an alarm call occurred, the group moved to a new habitat, or the focal individual flew off or became a sentinel. At least 1 h was left between watches on the same individual to enhance sample independence.

Data Analysis

Five separate linear mixed models (allowing the inclusion of both fixed and random terms, the latter accounting for repeated measures of the same individual and group) were fitted to analyse the different data sets. Model 1 tested the influence of year, habitat type and wind condition on latency between consecutive sentinel bouts, while controlling for foraging group size (used instead of total group size to account for individuals that were temporarily missing from the group) and rainfall (total rainfall in mm during the previous week; Table 1). To remove hunger level as a potential confounding effect on latency between bouts, model 2 tested the

Table 1

Linear mixed model examining the terms influencing sentinel decisions about the latency between consecutive bouts and bout duration

Model term	Estimate±SE	χ^2	*df*	*P*
Latency between bouts				
Habitat*wind condition		6.31	2	0.043
Grass	0±0			
Open	0.554±0.161			
Thickets	0.209±0.116			
Low wind	0±0			
High wind	−0.049±0.087			
Open:high	−0.509±0.226			
Thicket:high	−0.242±0.160			
Foraging group size		0	1	1
Year		38.70	1	<0.001
2008	0±0			
2009	0.586±0.087			
Rainfall*		0.59	1	0.440
Group ID†	0.08			
Individual ID in group†	0.06			
Residual	2.09			
Intercept	−0.017±0.113			
Bout duration				
Habitat		25.00	2	<0.001
Grass	0±0			
Open	−0.142±0.072			
Thickets	−0.247±0.051			
Wind condition		0.94	1	0.332
Foraging group size		1.46	1	0.227
Year		55.26	1	<0.001
2008	0±0			
2009	0.414±0.049			
Rainfall*		1.68	1	0.195
Sex		0.005	1	0.944
Dominance status		7.32	1	0.007
Dominant	0±0			
Subordinate	−0.182±0.056			
Group ID†	0.01			
Individual ID in group†	0.02			
Residual	0.82			
Intercept	0.783±0.062			

The *P* value for each term is based on the chi-square test for change in deviance when comparing models with or without that term. The mean effect estimates ± SE (effect sizes) are reported from the best-fitting model that included all terms that produced a significantly poorer fit when removed (minimal model). For random effects, the variance is reported.

* Total rainfall in the preceding week (mm).

† Random terms.

Table 2

Linear mixed model examining the terms affecting biomass intake rate by foragers

Model term	Estimate±SE	χ^2	*df*	*P*
Proportion of time spent foraging*rainfall*	0.066±0.027	6.28	1	0.012
Group breeding status†		0.15	1	0.702
Foraging group size		0.73	1	0.393
Habitat (grass, open, thickets)		1.85	1	0.398
Wind condition (low, high)		1.93	1	0.165
Sex		0.02	1	0.881
Dominance status		0.13	1	0.721
Age (in days)		0.20	1	0.658
Group ID‡	<0.001			
Individual ID in group‡	<0.001			
Residual	1.99			
Intercept	−3.426±0.470			

The *P* value for each term is based on the chi-square test for change in deviance when comparing models with or without that term. The mean effect estimates ± SE (effect sizes) are reported from the best-fitting model that included all terms that produced a significantly poorer fit when removed (minimal model). For random effects, the variance is reported.

* Total rainfall in the preceding week (mm).

† Presence or absence of dependent fledglings.

‡ Random terms.

Table 3

Linear mixed model examining the terms influencing sentinel decisions about initial height and horizontal distance to the nearest forager

Model term	Estimate±SE	χ^2	*df*	*P*
Initial height				
Habitat		40.93	2	<0.001
Grass	0±0			
Open	−0.062±0.039			
Thickets	−0.179±0.028			
Wind condition		17.71	1	<0.001
Low	0±0			
High	−0.114±0.027			
Foraging group size	0.025±0.008	10.42	1	0.001
Year		9.28	1	0.002
2008	0±0			
2009	0.096±0.032			
Sex		2.52	1	0.113
Dominance status		9.88	1	0.002
Dominant	0±0			
Subordinate	−0.150±0.044			
Group ID*	0.009			
Individual ID in group*	0.014			
Residual	0.315			
Intercept	0.962±0.062			
Distance to foragers				
Habitat		5.52	2	0.063
Grass	0±0			
Open	−0.003±0.050			
Thickets	−0.083±0.036			
Wind condition		42.08	1	<0.001
Low	0±0			
High	−0.225±0.034			
Foraging group size	0.041±0.009	17.67	1	<0.001
Year		187.07	1	<0.001
2008	0±0			
2009	0.573±0.037			
Sex		0.02	1	0.896
Dominance status		0	1	1
Group ID*	0.040			
Individual ID in group*	0.003			
Residual	0.525			
Intercept	2.089±0.083			

The *P* value for each term is based on the chi-square test for change in deviance when comparing models with or without that term. The mean effect estimates ± SE (effect sizes) are reported from the best-fitting model that included all terms that produced a significantly poorer fit when removed. For random effects, the variance is reported.

* Random terms.

influence of habitat type on biomass intake rate, while controlling for wind condition, individual sex, status and age (in days), foraging group size, group breeding status (presence or absence of dependent fledglings), rainfall and proportion of time spent foraging (Table 2). For this analysis, we used only data from focal watches when no sentinel was in position, because we have previously shown that the presence of a sentinel influences biomass intake (Hollén et al. 2008). Model 3 tested the influence of year, habitat type and wind condition on sentinel bout duration, while controlling for foraging group size, rainfall, and individual sex and status (dominant or subordinate; Table 1). Models 4 and 5 tested the influence of wind condition on initial sentinel height and horizontal distance to the nearest forager, respectively. These models controlled for foraging group size, individual sex and status, year and habitat type (because tree height and distance between trees may vary depending on habitat; Table 3). Prior to analysis, latency between sentinel bouts, bout duration, initial height and biomass intake rate were log transformed, while distance to the nearest forager was square-root transformed. Models applied to transformed values were better fitting than models applied to nontransformed values, as assessed by residual deviance and visual inspection of normality plots.

All data were analysed in R for Microsoft Windows 2.12.1 (R Development Core Team 2010, http://www.r-project.org). LMMs were fitted using the lme4 package (Bates & Maechler 2010) and the 'lmer' function (REML fit). Individual identity nested within group identity was included as a random term in all models. Significance of each explanatory term within the models was examined using a classical model simplification approach with chi-square tests (log-likelihood ratio tests) measuring the change in deviance (Δdeviance). By removing each term in turn from a full model including all terms (including interactions), we established a minimal model with only significant terms remaining. The significance of these latter terms was established by removing each of them in turn from the minimal model and comparing the reduced model to the complete minimal model. The *P* value of nonsignificant terms was established by adding each term in turn to the minimal model. Since habitat type consists of three levels (grass, open, thickets), the significance between each pair was tested using the package 'languageR' and the function 'pvals.fnc' (which uses Markov Chain Monte Carlo simulations; Baayen 2010). Terms (main effects and interactions) were judged as adding significant explanatory value if their removal resulted in a change in deviance producing a *P* value <0.05. Effect sizes (mean difference ± SE) for significant variables are presented in the tables; *P* values only are reported for nonsignificant terms.

RESULTS

Latency between consecutive sentinel bouts (Model 1) was highly variable and ranged from 0.1 to 54.5 min (mean ± SE = 3.5 ± 0.1 min, $N = 2016$ bouts, 81 individuals). Year had a significant influence on latency (removing year from the model resulted in a significantly poorer fit; Table 1), with latencies being on average shorter in 2008 than 2009 (Fig. 1a). The interaction between habitat type and wind condition also added significant explanatory value (Table 1). In high wind, when bouts were generally initiated sooner, there was no significant difference between habitats ($P > 0.50$ for all comparisons; Fig. 1a), whereas in low wind, new bouts were initiated sooner in grass compared to open areas ($P = 0.001$), and there was a nonsignificant tendency towards shorter latencies in grass versus thickets ($P = 0.09$) and thickets versus open areas ($P = 0.07$; Fig. 1a). The effect of habitat

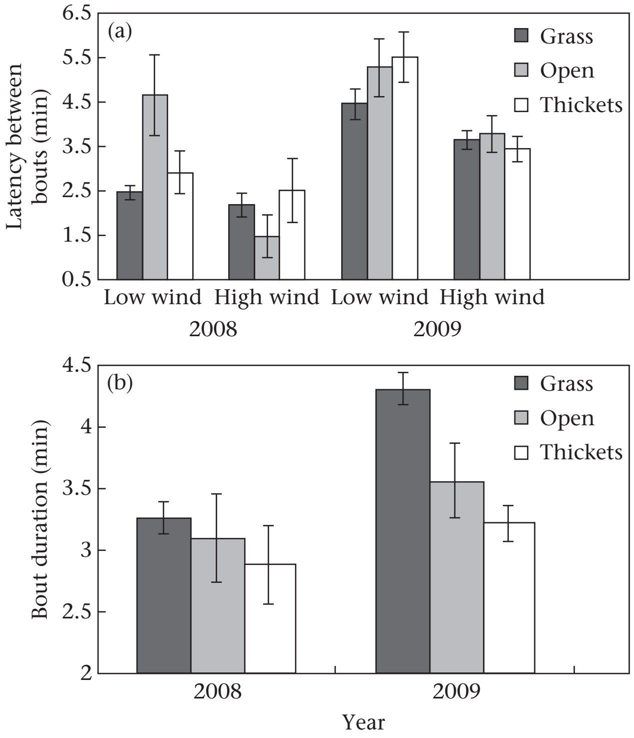

Figure 1. The effect of (a) year, habitat type and wind condition on the latency between consecutive sentinel bouts, and (b) year and habitat type on sentinel bout duration. Means ± SE are shown.

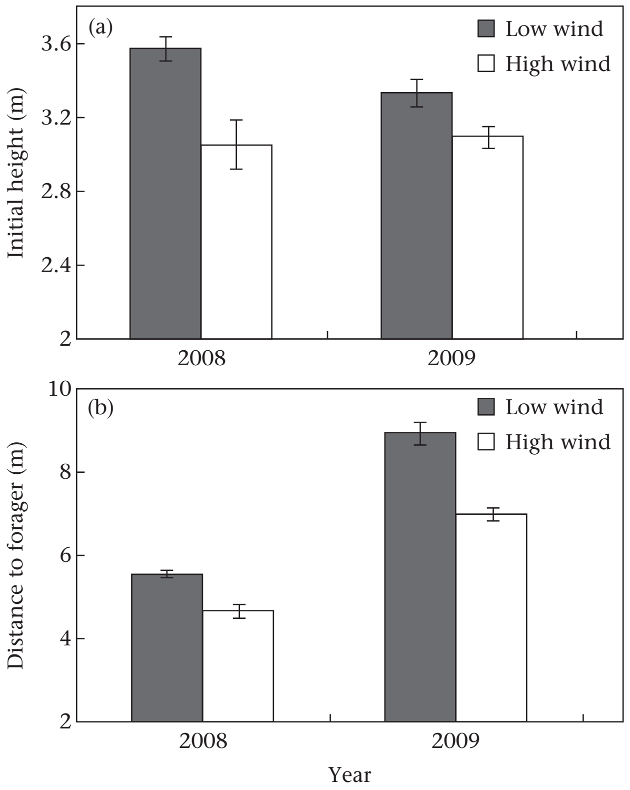

Figure 2. The effect of wind condition on initial (a) sentinel height, and (b) horizontal distance to the nearest forager. Means ± SE are shown.

on the latency between sentinel bouts seems unlikely to stem from any confounding effects of hunger on decisions to start guarding because Model 2 showed that biomass intake rate did not differ between grass, thickets and open areas (Table 2).

As with latency between bouts, the duration of individual sentinel bouts (Model 3) was highly variable and ranged from 0.5 to 38.1 min (mean ± SE = 3.7 ± 0.1 min, $N = 2029$ bouts, 67 individuals). After we controlled for a significant effect of dominance status, where dominants guarded for slightly longer than subordinates, individual bout duration was significantly affected by year and habitat type (Table 1). Bouts were shorter in 2008 than 2009 (Fig. 1b), and were longer in grass compared to both open areas ($P = 0.044$) and thickets ($P < 0.001$); there was no difference between thickets and open areas ($P = 0.30$; Fig. 1b). Wind condition did not add any significant explanatory value above and beyond dominance status, year and habitat type (Table 1).

The height at which sentinels initially positioned themselves (Model 4) ranged from 1 to 14 m (mean ± SE = 3.4 ± 0.1 m, $N = 2583$ bouts, 69 individuals). After we controlled for significant effects of year, habitat type, foraging group size and individual status, wind condition had a significant effect on the height chosen by sentinels (Table 3, Fig. 2a). Sentinels chose lower positions in high wind than low wind, and no individuals perched above 10 m in high wind (range low: 1–14; high: 1–10).

When a sentinel bout was initiated, the horizontal distance to the nearest forager (Model 5) ranged from 0 to 50 m (mean ± SE = 6.6 ± 0.1 m, $N = 2583$ bouts, 69 individuals). Again, when we controlled for significant effects of year, habitat type and foraging group size, wind condition significantly influenced the positioning of sentinels (Table 3). Sentinels initially perched closer to the nearest forager in high wind than in low wind (Fig. 2b), and no individuals perched further than 30 m from their groupmates in high wind (range low: 0–50; high: 0–30).

DISCUSSION

Our results provide strong evidence that sentinel decisions are influenced by the prevailing ecological conditions. As predicted, latency between pied babbler sentinel bouts was shorter in the wetter of the 2 study years, when vegetation was likely to be denser. Moreover, group members initiated new bouts sooner in habitats covered with grass compared to open areas; latencies were of intermediate duration in thickets, which have both covered and open patches. However, these habitat differences were only apparent during periods of low wind; in high wind, latencies were generally much shorter in all habitats. The duration of individual guarding bouts also varied with habitat type: sentinels remained in position for longer in grassy habitat than in either thickets or open areas. As expected, wind condition influenced decisions about the initial position adopted by sentinels: during periods of high wind, sentinels perched lower and in closer proximity to the foraging individuals than in periods of low wind.

Recent experimental work has demonstrated that individuals alter their sentinel behaviour in response to direct cues of predation, specifically model predators and heterospecific alarm calls (Bell et al. 2009; Ridley et al. 2010). Our results indicate that pied babbler sentinels may also alter their behaviour in response to indirect indicators of potential predation risk. Predation risk is likely to vary depending on habitat type (Metcalfe 1984; Griesser & Nystrand 2009), so the decreased latency between sentinel bouts in wetter years and in grassy habitats, and the increased bout duration in the latter, may be the consequence of predators being harder to detect: lines-of-sight are probably more restricted and terrestrial predators may be able to hide more easily in such conditions (e.g. Lazarus & Symonds 1992; Whittingham & Evans 2004). Similarly, latency between bouts may be reduced in high wind because aerial predators in particular are harder to detect against moving vegetation (Hilton et al. 1999) and are more active in windy conditions (personal observation). Several previous studies of foraging individuals have indicated an influence of ecological conditions on antipredator vigilance behaviour (Whittingham & Evans 2004; Whittingham et al. 2004; Devereux et al. 2006; Quinn et al. 2006; Carr & Lima 2010), but our results on nonforaging sentinels remove any potential confounds of, for example, the type of food being eaten (Whittingham et al. 2004).

Ecological conditions are expected to influence behavioural decisions that have immediate selfish payoffs, with individuals known to act out of self-interest in situations of increased predation risk (Lima & Dill 1990): to enhance their own survival, solitary birds often aggregate (e.g. Elliot 1985; Gotmark & Andersson 2005), while many plural breeders become more vigilant in riskier environments (e.g. Metcalfe 1984; Devereux et al. 2006). Our findings in a permanently social, cooperatively breeding species can potentially be explained in similar fashion, with individuals adopting a raised position sooner and for longer in more risky situations because doing so is a safer option than continuing to forage on the ground (Bednekoff 1997). However, if individual group members are more likely to spot predators from a raised position (see Blumstein et al. 2004) and thus be able to warn foragers of danger, then sentinel behaviour may also result in cooperative benefits (Hollén et al. 2008; Lehmann & Rousset 2010). Any enhanced survival of groupmates as a result of sentinel warnings could lead to indirect benefits through kin selection (Hamilton 1964), because group members in cooperative societies are often close kin (Emlen 1995), and/or delayed direct benefits arising from group augmentation (Kokko et al. 2001), because group size is a key determinant of predation risk (Krause & Ruxton 2004) and successful territory defence (Radford & du Plessis 2004).

Our finding that wind condition influences the initial position chosen by sentinels might also arise because of both selfish and cooperative benefits. Decisions made by songbirds about perch height are likely to be driven by direct payoffs to the signaller (Mathevon et al. 1996), which may also be the case for pied babbler sentinels: lower positions might be chosen in high wind if branches at such heights are sturdier and offer more protection from predators; positions closer to foragers may be preferred if this reduces personal predation risk through, for example, selfish-herd effects (Hamilton 1971). However, benefits arising to individuals in social species are often dependent on efficient communication, and so signallers are expected to alter their behaviour to enhance the likelihood of successful signal transmission in different ecological conditions (Lengagne & Slater 2002). Although forager food consumption increases when pied babbler sentinels perch higher (Radford et al. 2009), foragers also obtain valuable information from the low-amplitude watchman's song about the presence (Hollén et al. 2008) and height (Radford et al. 2009) of sentinels, as well as an assessment of current risk (Bell et al. 2009). Therefore, foragers that cannot hear these calls would have to waste valuable foraging time to check visually for information; suspension of foraging may be a particular issue for species, such as babblers, that dig for mobile subterranean prey that can escape by burrowing. Since wind can reduce the effective range of a vocal signal (Wiley & Richards 1982), sentinels might be adjusting their position accordingly: by choosing perches that are both lower and closer to foragers when there is high wind, sentinels may be maximizing the chances that groupmates detect these vital calls.

An obvious question to examine in the future is how sentinels make their decisions. For example, how do they decide the optimum distance to foragers? It is intriguing to speculate that there may be some dialogue between the two parties: in pied babblers, the close calls of foragers and the watchman's song of sentinels are very similar, and recent work has demonstrated that these vocalizations mediate negotiation over sentinel bout duration (Bell et al. 2010). Further studies should also investigate how payoff distributions to different classes of sentinels (for example dominants versus subordinates) vary across ecological conditions and how this might shape cooperative decisions. It is yet to be established with certainty the evolutionary forces behind the behavioural changes shown in the current study, but it is clear from our work and that of others (e.g. Clutton-Brock et al. 1999; Wright et al. 2001b) that not all group members contribute equally to sentinel behaviour: there is considerable variation in investment depending on both sex and dominance status. Finally, there is an ongoing shift in the literature towards understanding the quality as well as the quantity of vigilance. For example, head and eye movement, posture and species-specific visual constraints and capabilities can all influence vigilance behaviour (e.g. Fernández-Juricic et al. 2004), and should be considered in the future. For now, however, our results highlight the trade-offs faced by sentinels and provide strong evidence that sentinel decisions can be affected, not only by intrinsic factors (Clutton-Brock et al. 1999; Wright et al. 2001a, b), but also by both small-scale (habitat type and wind) and large-scale (year) extrinsic factors. More generally, although many studies have demonstrated that individuals might increase their investment because of an increased benefit to recipients (e.g. parents delivering more food to offspring in greater need; Kilner & Johnstone 1997), the novelty of our work lies in showing that ecological variation can influence decisions with potential cooperative benefits.

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