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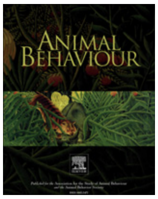

Ecological conditions influence sentinel decisions

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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 $= 4.9 \pm 0.3$, 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