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The higher the better: sentinel height influences foraging success in a social bird

Andrew N. Radford^{1,*}, Linda I. Hollén¹ and Matthew B. V. Bell²

¹*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*

²*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*

In all social species, information relevant to survival and reproduction can be obtained in two main ways: through personal interaction with the environment (i.e. ‘personal’ information) and from the performance of others (i.e. ‘public’ information). While public information is less costly to obtain than personal information, it may be inappropriate or inaccurate. When deciding how much to rely on public information, individuals should therefore assess its potential quality, but this possibility requires empirical testing in animals. Here, we use the sentinel system of cooperatively breeding pied babblers (*Turdoides bicolor*) to investigate how behavioural decisions of foragers are influenced by potential variation in the quality of anti-predator information from a vigilant groupmate. When sentinels moved to a higher position, from where their probability of detecting predators is likely to be greater, foragers reduced their vigilance, spread out more widely and were more likely to venture into the open. Consequently, they spent more time foraging and increased their foraging efficiency, resulting in a profound increase in biomass intake rate. The opposite behavioural changes, and consequent foraging outcomes, were found when sentinels moved lower. A playback experiment demonstrated that foragers can use vocal cues alone to assess sentinel height. This is the first study to link explicitly a measure of the potential quality of public information with a fitness measure from those relying on the information, and our results emphasize that a full understanding of the evolution of communication in complex societies requires consideration of the reliability of information.

Keywords: public information; reliability; anti-predator vigilance; foraging efficiency; vocalizations; cooperative breeding

1. INTRODUCTION

Individuals of all social species can acquire adaptive information of relevance to survival and reproduction in two ways. They can sample the environment themselves, thus obtaining accurate, up to date ‘personal’ information, but at a cost of time, energy and increased risk (Danchin *et al.* 2004; Valone 2007). Alternatively, they can use the performance of others, thus minimizing the conflict with other activities, but resulting in ‘public’ information that is likely to be less reliable than that acquired personally; it may be inappropriate, inaccurate or out of date (Danchin *et al.* 2004; Valone 2007). The potential quality of the personal and public information should therefore be taken into account by individuals when deciding how to balance their relative use. Although studies have considered the reliability of personal information in this regard (Coolen *et al.* 2003; van Bergen *et al.* 2004), variation in the potential quality of public information has received far less attention.

Sentinel behaviour, where an individual adopts a raised position, scans for danger and gives alarm calls to warn foraging groupmates of predatory threats, has evolved in a number of social bird and mammal species (Bednekoff 1997). In the presence of a sentinel, foragers can benefit from both a lower predation risk, because sentinels tend to detect predators more often and from further away than

do individuals on the ground (Manser 1999; Wright *et al.* 2001), and a lower starvation risk, because they can spend more time foraging and do so more efficiently (Hollén *et al.* 2008). The magnitude of these benefits is likely to vary depending on the probability of a sentinel detecting a predator; the greater the reliability of a sentinel in this regard, the less vulnerable a forager is to predation and the more attention it can devote to foraging. Although individuals are known to respond differently to alarm calls given by callers of different reliability (Hare & Atkins 2001; Blumstein *et al.* 2004a), no studies have investigated whether foragers monitor features associated with sentinel reliability and adjust their behaviour when these change.

Sentinels may differ in their likelihood of detecting a predator because of differences in such inherent characteristics as visual acuity, experience, motivation or excitation threshold, leading to consistent differences between individuals (see Blumstein *et al.* 2004a). External factors, such as the position adopted by the sentinel, may also play an important role. For example, higher perched individuals may spot predators at a greater distance (see Blumstein *et al.* 2004b; Fernández-Juricic *et al.* 2004a) and hence might be perceived as more reliable. Sentinels occupy different positions during different bouts, and they may move between trees or change their position in the same tree within a particular bout (Gaston 1977; Wright *et al.* 2001). Foragers might therefore benefit by monitoring the height of a sentinel and adjusting their behaviour accordingly.

Information about a sentinel could be obtained by foragers in two ways. First, through visual monitoring,

* Author for correspondence (andy.radford@bristol.ac.uk).

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which is how social information is generally assumed to be gathered (Fernández-Juricic *et al.* 2004b, 2005). Second, from vocal cues, because while on duty sentinels of several species produce regular quiet vocalizations known as the 'watchman's song' (Wickler 1985). Experimental studies have shown that foragers use these calls to detect the presence of a sentinel (Manser 1999; Hollén *et al.* 2008), but they might also use them to gain additional information, such as the sentinel's height. Any such information transfer might arise either because sentinels actively change their calling to announce their height or because foragers have been selected to extract the information from passive changes in call structure that arise as the sound travels between sender and receiver (Bradbury & Vehrencamp 1998).

The pied babbler, *Turdoides bicolor*, a group-living passerine, provides an ideal opportunity to investigate whether foraging group members monitor sentinel height and adjust their behaviour accordingly, and whether they can use the watchman's song to obtain the relevant information. Pied babblers forage predominantly on the ground (Radford & Ridley 2006) and are preyed on by a variety of raptors, terrestrial mammals and snakes (Ridley & Raihani 2007). Foraging groups often have a sentinel in place and these individuals tend to be the first to detect a predator and give an alarm call (Ridley & Raihani 2007). During a bout, sentinels continuously produce a watchman's song to which foragers are known to respond (Hollén *et al.* 2008). Sentinel height varies both because of differences in vegetation throughout a group's territory and because individuals change position in a tree during a particular bout. It is possible to assess the impacts of a change in sentinel height on the relative positions of all foraging group members, because individuals are generally found within 20 m of one another (Radford & Ridley 2006, 2008), and on anti-predator vigilance, because foragers dig for prey in the sand and so must raise their head to look for danger (Radford & Ridley 2007). It is also possible to measure foraging success accurately, because groups can be habituated to the close presence of observers, and thus prey capture can be scored easily and reliably (Radford & Ridley 2006; Hollén *et al.* 2008).

Here we use observational data, acoustic analyses and a playback experiment to answer four main questions. First, do foragers alter their behaviour in response to changes in sentinel height? We assume that when sentinels are positioned higher, they will be more likely to detect predators and thus that foragers will be less vulnerable to predation. We therefore predict that when sentinels move higher, foragers will reduce their vigilance, spread out more widely and be more likely to venture into the open. Crucially, we also predict that foragers will make the opposite behavioural changes when sentinels move to a lower position. Second, do these alterations in behaviour result in changes in foraging success? We predict that the food intake rate of foragers will show a positive relationship with sentinel height. Third, do sentinels alter the rate or the acoustic structure of their watchman's song depending on their height? That is, do they make an active change to their calling and thus announce their position? Fourth, can foragers use vocal cues alone to assess not only the presence of a sentinel but also more detailed information about it, such as its height? If they can, foragers should reduce their vigilance, spread out

more widely and be more likely to venture into the open when the recording of a watchman's song is played back from a higher position.

2. MATERIAL AND METHODS

(a) *Study site and species*

We studied 15 colour-ringed, habituated pied babbler groups (containing a median of 7.5 adults and independent fledglings, range 3–13) at the Kuruman River Reserve (26°58' S, 21°49' E) in the southern Kalahari, South Africa (see the electronic supplementary material for additional information). Foraging pied babblers peck at prey on the surface of the sand and probe into it for buried items. Sentinels were defined as individuals perching at least 1 m above the ground and actively scanning for predators while other group members were foraging. All adults act as sentinels, with bouts lasting a median of 2 min (range 1–9 min, $n=473$ bouts by 47 individuals). Sentinels are found at a median height of 3 m (range 1–12 m, $n=473$ bouts by 47 individuals) and change height during 24 per cent of bouts. Individuals always produce the watchman's song throughout a sentinel bout (median call rate = 18.3 calls min^{-1} , range 5–54 calls min^{-1} , $n=473$ bouts by 47 individuals).

(b) *Observational data collection*

To examine whether foraging group members adjust their behaviour in response to changes in sentinel height, we conducted group scans and focal watches of individual foragers. Group scans were used to determine the spread of individuals on the ground and the proportion of individuals foraging in the open. One scan was completed as soon as a sentinel changed its height by at least 1 m (either up or down) and then a second scan was conducted 2 min later (see the electronic supplementary material for additional information). Continuous focal watches on foraging adults and independent fledglings (median length of focal watch = 2.37 min, range 0.22–17.42 min, $n=417$ watches; median number of focal watches per individual = 8, range 1–38, $n=36$ individuals) were used to determine the proportion of time spent vigilant, proportion of time spent foraging, look-up rate (number of separate bouts of vigilance), foraging efficiency (amount of food eaten per minute of foraging time) and biomass intake rate (amount of food eaten per minute of observation time) in the 2 min period both before and after a change in sentinel height of at least 1 m (see the electronic supplementary material for additional information).

(c) *Acoustic recordings and analysis*

To assess whether sentinels change their calling depending on their height, we recorded the watchman's song of the same 10 individuals when they were acting as a sentinel between 1 and 3 m ('low') and between 4 and 6 m ('high'). We then extracted and compared the following acoustic parameters: call rate (calls per min); fundamental frequency (Hz); peak frequency (Hz); first quartile energy (Hz); and duration (s; see the electronic supplementary material for additional information).

(d) *Playback experiment*

To test whether foraging group members can use vocal cues to assess sentinel height, eight groups were each presented with two trials involving 5 min playbacks of the same watchman's

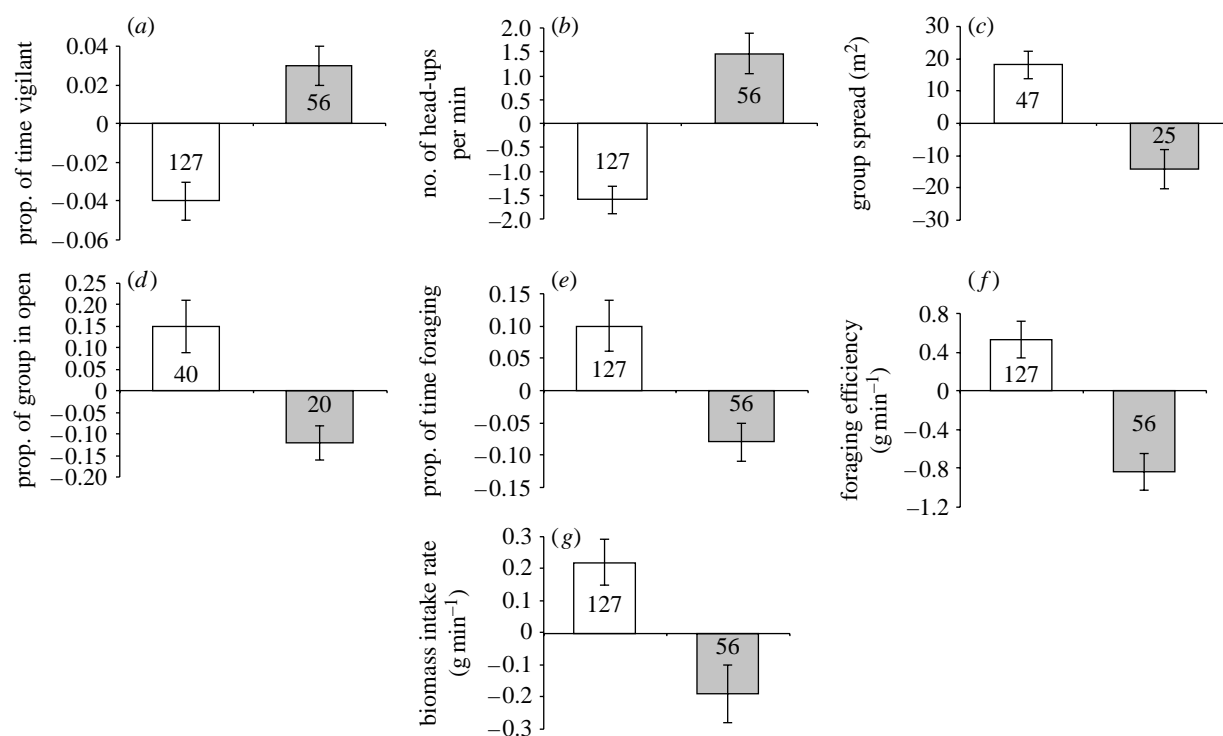


Figure 1. Mean \pm s.e.m. changes in the behaviour of foraging pied babbler group members following movement by a sentinel to a position at least 1 m higher (white bars) or lower (grey bars). In (a), (b) and (e–g), the change is that by one group member from the 2 min period before to the 2 min period after the change in sentinel height. Sample sizes refer to the number of paired focal periods. In (c) and (d), the change is that of the whole group from 0 to 2 min after the change in sentinel height. Sample sizes refer to the number of paired scans.

song from the same group member. In one trial, playback was from a speaker positioned 2.5 m above the ground; in the other trial, the same speaker was positioned 5 m above the ground (see the electronic supplementary material for additional information). Group scans were conducted at the end of each minute of the trial to record the group spread and the proportion of individuals foraging in the open. A continuous focal watch of the same randomly chosen adult group member was made throughout both trials to record its vigilance and foraging behaviour.

(e) Statistical analysis

All statistical analyses were conducted in GENSTAT (10th edition; Lawes Agricultural Trust, Rothampstead, Harpenden, UK). Acoustic variables and experimental data were analysed using paired *t*-tests; observational data were analysed with mixed models (see the electronic supplementary material for additional information). To assess the influence of a change in sentinel height on group spread and the proportion of individuals foraging in the open, we conducted separate models on paired scans conducted 0 and 2 min after either an increase or a decrease in sentinel height. We included group identity and scan pair as random terms. To assess the influence of a change in sentinel height on the proportion of time spent vigilant, proportion of time spent foraging, look-up rate, foraging efficiency and biomass intake rate of individual foragers, we conducted separate models on paired focal-watch data from the 2 min period before and after either an increase or a decrease in sentinel height. We included group identity, individual identity and focal-watch pair as random terms.

3. RESULTS

(a) Response to changes in sentinel height

After a sentinel moved to a higher position, foraging group members spent a smaller proportion of time vigilant (linear mixed model (LMM): Wald statistic=27.38, d.f.=1, $p < 0.001$; figure 1a), looked up less often (Wald statistic=22.74, d.f.=1, $p < 0.001$; figure 1b), spread out more widely (Wald statistic=24.05, d.f.=1, $p < 0.001$; figure 1c) and were more likely to forage in the open (generalized linear mixed model (GLMM): Wald statistic=9.60, d.f.=1, $p = 0.004$; figure 1d). Foragers also spent a greater proportion of time foraging (LMM: Wald statistic=9.63, d.f.=1, $p = 0.002$; figure 1e) and had a higher foraging efficiency (Wald statistic=9.46, d.f.=1, $p = 0.003$; figure 1f) following an increase in sentinel height. The increase in foraging efficiency was the consequence of an increase in the number of prey items found (mean \pm s.e.m. items per min, before = 1.38 ± 0.10 , after = 2.02 ± 0.15 ; Wald statistic=6.39, d.f.=1, $p = 0.013$), rather than a change in the average size of prey items (Wald statistic=2.23, d.f.=1, $p = 0.138$). The increases in foraging time and efficiency after a sentinel moved higher resulted in an increase in the biomass intake rate of foragers (Wald statistic=9.11, d.f.=1, $p = 0.003$; figure 1g).

These results might have arisen simply because a sentinel had been present for longer (see Hollén *et al.* 2008), rather than because it changed its height. Crucially, however, foraging individuals also altered their behaviour as predicted when a sentinel moved to a lower position. That is, foragers spent a greater proportion of time vigilant (LMM: Wald statistic=11.66, d.f.=1, $p = 0.001$; figure 1a), looked up more often (Wald statistic=11.54,

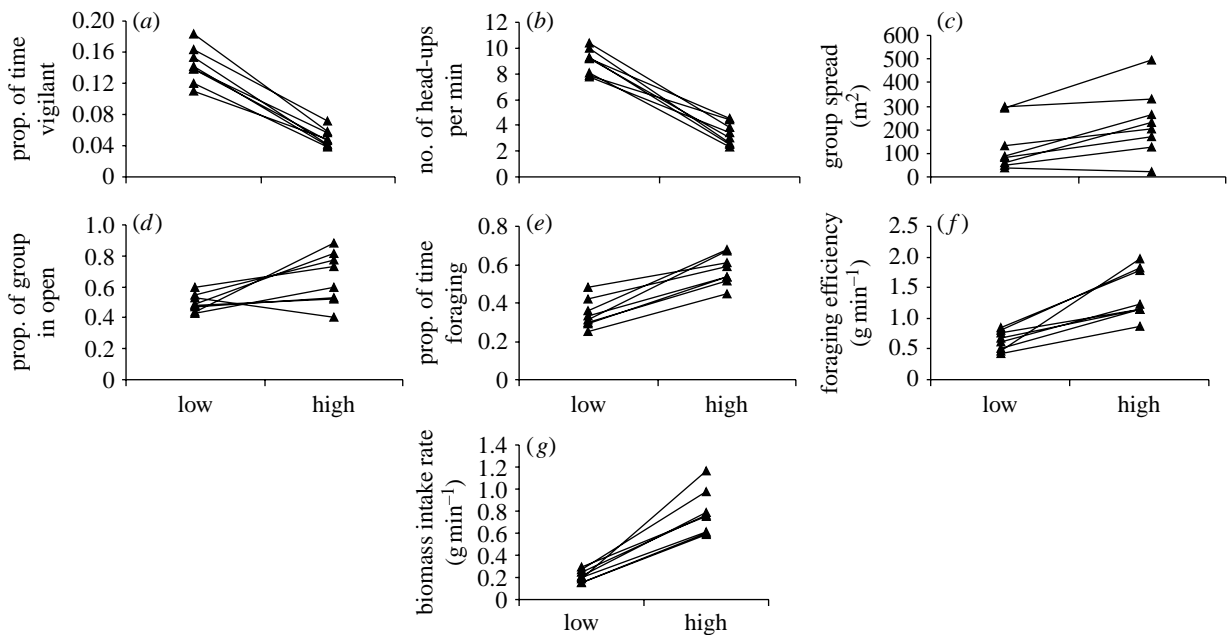


Figure 2. Response of foraging pied babblers to 5 min playback of the same watchman's song of a group member from two different heights (low = 2.5 m, high = 5 m). In (a), (b) and (e–g), results are presented for one individual in eight different groups; in (c) and (d), results are presented for eight different groups.

d.f. = 1, $p = 0.001$; figure 1b), moved closer together (Wald statistic = 17.38, d.f. = 1, $p < 0.001$; figure 1c) and were less likely to forage in the open (GLMM: Wald statistic = 6.50, d.f. = 1, $p = 0.020$; figure 1d) following a decrease in sentinel height. Foragers also spent a smaller proportion of time foraging (LMM: Wald statistic = 5.95, d.f. = 1, $p = 0.018$; figure 1e) and were less efficient when foraging (Wald statistic = 21.46, d.f. = 1, $p < 0.001$; figure 1f), thus suffering a reduction in biomass intake rate (Wald statistic = 5.35, d.f. = 1, $p = 0.024$; figure 1g) after a sentinel moved lower.

(b) Importance of vocalizations

The watchman's songs of the same individual produced at different heights did not differ significantly in their fundamental frequency (paired t -test: $t = 0.72$, $n = 10$, $p = 0.490$), peak frequency ($t = 0.28$, $n = 10$, $p = 0.784$), first quartile energy ($t = 0.26$, $n = 10$, $p = 0.803$) or duration ($t = 0.63$, $n = 10$, $p = 0.544$). Moreover, there was no significant difference in the call rate of the same individual when acting as a sentinel at different heights ($t = 0.66$, $n = 10$, $p = 0.525$).

Despite the lack of height-related variation in the watchman's song itself, foraging individuals still appeared capable of assessing sentinel height from vocal cues alone. In response to the playback of the watchman's song from a higher position, foragers spent a smaller proportion of time vigilant (paired t -test: $t = 13.14$, $n = 8$, $p < 0.001$; figure 2a), looked up less often ($t = 11.62$, $n = 8$, $p < 0.001$; figure 2b), spread out more widely ($t = 3.62$, $n = 8$, $p = 0.008$; figure 2c) and were more likely to forage in the open ($t = 2.54$, $n = 8$, $p = 0.039$; figure 2d). Foragers also spent a greater proportion of time foraging ($t = 8.66$, $n = 8$, $p < 0.001$; figure 2e) and were more efficient when foraging ($t = 5.51$, $n = 8$, $p = 0.001$; figure 2f), leading to a higher biomass intake rate ($t = 8.45$, $n = 8$, $p < 0.001$; figure 2g), in response to playback of the watchman's song from 5 m compared to 2.5 m.

4. DISCUSSION

(a) Response to changes in sentinel height

Foraging pied babblers adjusted their behaviour depending on the height of a sentinel, benefiting from an increased biomass intake rate when sentinels were positioned higher. This increase in food consumption is likely to have profound consequences for survival and reproduction in such an arid environment. Previous studies have shown that foraging group members alter their behaviour in the presence of a sentinel (Manser 1999; Hollén *et al.* 2008). Our results are the first to demonstrate that foragers take into account more detailed information about sentinels, such as their position. They also raise the possibility that foragers may adjust their behaviour in the light of the potential reliability of a sentinel.

The finding that foragers modified their vigilance and space use as predicted when sentinels moved lower, as well as higher, indicates that the behavioural alterations are the result of a change in sentinel height *per se* and not just because a sentinel has been on duty for longer (see Hollén *et al.* 2008). Sentinels positioned higher in a tree may be able to see further and/or have a wider field of view, and thus be more likely to spot predators sooner (Blumstein *et al.* 2004b; Fernández-Juricic *et al.* 2004a). The detection of terrestrial predators in particular could be enhanced by a higher position; height may be less likely to make a difference when scanning for aerial predators (Blumstein *et al.* 2004b). Because pied babblers are preyed on by a variety of terrestrial mammals and snakes (Ridley & Raihani 2007), the movement of a sentinel to a higher perch would potentially reduce the vulnerability of foraging group members, and thus explain their increased spread and use of open areas, as well as their reduced vigilance.

By decreasing the amount of time spent vigilant when a sentinel was positioned higher, foragers increased their time spent foraging. They also increased their foraging efficiency in the presence of higher sentinels, probably as the result of three changes in behaviour. First, by

spreading out more widely, individuals may have been less likely to encounter foraging areas already depleted by other group members. Second, by venturing into the open more, individuals would have had a wider choice of foraging areas and potentially access to those of higher quality. Third, by looking up less often, there would have been less disruption to foraging bouts and hence a reduced likelihood of mobile prey escaping. These possibilities are not mutually exclusive and could all have contributed to the increased rate of prey capture when individuals were foraging in the presence of a higher sentinel.

(b) Importance of vocalizations

The traditional assumption is that foragers gather information about the presence, position and behaviour of groupmates through visual monitoring (Fernández-Juricic *et al.* 2004b, 2005). Our playback results, demonstrating that pied babbler foragers can assess the height of a sentinel from the watchman's song alone, lend support to the growing body of evidence that vocal cues can be just as important as visual information in certain circumstances (Manser 1999; Radford & Ridley 2007; Hollén *et al.* 2008). By obtaining valuable information from sentinel calls, foragers do not need to suspend their digging activity and can thus increase their foraging time and reduce the starvation risk. If foragers are to adjust their behaviour continually in response to vocal cues about sentinel position, sentinel calls must be produced regularly throughout a bout, as is the case with pied babblers (Hollén *et al.* 2008; this study), meerkats (*Suricata suricatta*; Manser 1999) and dwarf mongooses (*Helogale undulata*; Rasa 1986); sentinel calls produced only rarely during a bout (see Bednekoff *et al.* 2008) or simply at the end of it (see Gaston 1977) are unlikely to play such a key role in this regard.

Alterations in call type or structure, arising either because of an active change by signallers or as a consequence of a change in their internal state, often convey information about the environment to receivers (Seyfarth *et al.* 1980; Leavesley & Magrath 2005). However, there were no discernible differences in the watchman's songs of the same pied babblers when acting as sentinels at different heights. There might be differences in acoustic parameters that we did not measure here, but foragers behaved differently in the two playback trials that differed only in height. That is, because the same watchman's song was used in both trials to a particular group, there could be no indicator of height from the inherent characteristics of the calls themselves. Instead, foragers may have been selected to obtain the relevant information passively; they might locate the position of a sentinel by using changes in the sound spectrum as it passes from sender to receiver (Bradbury & Vehrencamp 1998). For example, sound attenuates over distance and this change can be used as a ranging cue by species involved in long-distance communication (Naguib & Wiley 2001). It is perhaps unlikely that differences in sentinel height are sufficiently large to result in discernible differences in sound amplitude, so alterations of the sound on reaching the receiver may therefore be important. In humans, for example, sound is reflected by the convolutions of the ear pinnae before reaching the tympanic membrane and particular spectral features tend to vary in frequency according to the elevation of the sound source

(Middlebrooks & Green 1991). It remains to be investigated whether a similar process assists pied babbler foragers in assessing sentinel height.

5. CONCLUSION

Correct decision-making by foragers allows them to maximize foraging success and minimize predation risk (Lima & Bednekoff 1999). Group-living animals can make decisions on the basis of their own personal information or that from other group members (i.e. public information; Danchin *et al.* 2004; Valone 2007), and it has previously been suggested that foragers should take account of the quality of information provided by other foragers when assessing their need for personal vigilance (Jackson & Ruxton 2006). Our study provides the first evidence that foragers may similarly assess the potential quality of the information provided by sentinels, and then adjust their behaviour accordingly. As a sentinel moves higher, its ability to detect potential danger is likely to improve. Hence, foragers rely more heavily on this public information and focus more on foraging. When a sentinel moves to a lower position, its likelihood of spotting a predator is probably reduced, so foragers increase their investment in the acquisition of personal information. Our empirical results therefore lend support to the theoretical idea that signal reliability plays an important role in determining the balance between the use of personal and public information (McLinn & Stephens 2006; Hall & Kramer 2008). We suggest that future studies considering the value of information should therefore include an assessment about its potential reliability if we are to understand fully the evolution of communication in complex societies.

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This study complies with the current laws in the country in which it was conducted.

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