

The ecological benefits of interceptive eavesdropping

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Summary

1. Eavesdropping behaviour can increase the total amount of information available to an individual and therefore has the potential to provide substantial benefits. Recent research has suggested that some species are ‘information givers’, particularly social species with cooperative vigilance systems, and that these species may consequently affect community structure by influencing the behaviour and niche utilization of other species.

2. Here, using behavioural observations and playback experiments, we compared the behavioural change in a solitary species (the scimitarbill) and a social species (the pied babbler), to the presence and alarm calls of one another.

3. Our results revealed that scimitarbills underwent significant behavioural changes in the presence of social pied babblers: they reduced their vigilance rate by over 60%, increased their foraging efficiency and expanded their niche by moving into open habitat and excavating subterranean food items. In contrast, pied babblers – who have an effective intraspecific sentinel system – did not show significant behavioural changes to the presence or alarm calls of scimitarbills.

4. These results suggest that interspecific interceptive eavesdropping can provide significant benefits, influencing the behaviour and habitat utilization of eavesdropping species.

Key-words: eavesdropping behaviour, foraging niche expansion, interspecific interactions, pied babbler, scimitarbill, sentinel behaviour

Introduction

Eavesdropping, also known as public information parasitism, occurs when an individual other than the intended receiver cues in on the information that is conveyed (Mennill, Ratcliffe & Boag 2002; Peake 2005). There are two types of eavesdropping – interceptive [where absolute information in signals intended for one receiver is intercepted by another (Peake 2005)] and social [where relative information is gathered on other individuals by attending to their interactions with conspecifics (Peake 2005)]. Here, we focus on interceptive eavesdropping. If eavesdropping increases the total amount of information available to an individual (for example, regarding predator presence), it should be a behaviour under positive selection, because animals tend to invest more in behaviours that will increase their survival (Shettleworth 1998). Recently, there has been a surge in interest regarding patterns of interspecific eavesdropping and the development of a predictive theory that explains who should invest in eavesdropping behaviour (Lea *et al.* 2008; Magrath, Pitcher & Gardner 2009; Magrath & Bennett

2012). Several studies have suggested that those species that are most vulnerable to predation – such as solitary species or those with a poorly developed alarm call repertoire – would benefit the most from cueing in on the information given by other species (that share a common predator) with more reliable alarm call behaviour (Lea *et al.* 2008; Sridhar, Beauchamp & Shanker 2009). Currently, however, there are limited empirical data to support this idea.

Eavesdropping has been hypothesized to provide the eavesdropper with numerous benefits, including greater detection of predators, less time invested in vigilance and the selection of safer breeding and foraging areas (Sullivan 1984a; Doligez, Danchin & Clobert 2002; McGraw & Bshary 2002; Schmidt, Dall & van Gils 2010; Sharpe, Joustra & Cherry 2010). A number of studies have produced convincing evidence of species eavesdropping on the alarm calls of heterospecifics by demonstrating immediate antipredatory responses (Sullivan 1984b; Cheney & Seyfarth 1990; Shriner 1998; Ramakrishnan & Coss 2000; Rainey, Zuberbühler & Slater 2004; Templeton & Greene 2007; Vitousek *et al.* 2007; Magrath & Bennett 2012). However, studies demonstrating other behavioural changes (such as habitat use and foraging behaviour) that

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result from eavesdropping are surprisingly few (but see Sullivan 1984a, 1985). In a recent review, Goodale *et al.* (2010) emphasized the current lack of data available, suggesting that the benefits of information transfer are likely to strongly influence multispecies group formation, and thus understanding how animals utilize the information produced by others could give us important insights into the organization of animal communities (recently highlighted by Parejo, Avilés & Rodríguez 2012).

Sridhar, Beauchamp & Shanker (2009) suggested that there are 'leaders' and 'followers' in many multispecies communities and that the leaders are species whose vigilance information is most likely to be intercepted through eavesdropping behaviour. The fact that these 'leaders' are often social species led Sridhar *et al.* to hypothesize that the well-organized vigilance systems described for many social species (e.g. Rasa 1987; Hailman, McGowan & Woolfenden 1994; Clutton-Brock *et al.* 1999; Ridley, Raihani & Bell 2010; Sommer 2012) may be the reason that these species become the 'leaders' in flocking communities, with 'follower' species attracted to their presence and vocalizations (Thiollay & Jullien 1998; Goodale & Kotagama 2008; Goodale *et al.* 2010). To determine the benefits of eavesdropping behaviour and its influence on community structure, it is necessary to document behaviours during heterospecific association in comparison with behaviours displayed in the absence of eavesdropping opportunities. A significant change in habitat use and foraging behaviour by eavesdropping species could indicate that eavesdropping is a behaviour of considerable ecological significance.

Pied babblers (*Turdoides bicolor* Jardine) are a cooperatively breeding species with a well-described sentinel system, where one group member perches above the group and remains vigilant for predators while the rest of the group forages (Bell *et al.* 2010; Ridley, Raihani & Bell 2010; Ridley, Nelson-Flower & Thompson 2013). This sentinel system provides benefits to group members – sentinels detect predators more quickly than foraging group members (Ridley, Raihani & Bell 2010), and individuals not only gain greater biomass intake when a sentinel is present (because they spend less of their own time personally vigilant), but they also utilize more of their habitat while foraging (Hollén, Bell & Radford 2008). Considering these benefits, it seems logical that other species may try to take advantage of this sentinel system by associating closely with pied babbler groups and intercepting the information that pied babbler sentinels provide. Here, we determine the changes in pied babbler and scimitarbill (*Rhinopomastus cyanomelas* Vieillot) behaviour in response to the presence of one another. We aim to determine whether (i) there was a significant behavioural change in these species when in association with one another compared with when alone; (ii) whether there was significant responsiveness to the alarm calls of one another and (iii) whether these responses were equivalent between the two species.

Materials and methods

STUDY SITE

Data were collected from November 2011 to April 2012 at the Kuruman River Reserve in the southern Kalahari Desert, South Africa (26°58'S, 21°49'E). The study area is primarily semi-arid grassland and acacia savanna (for a description of the habitat types present, see Ridley & Thompson 2011). Both pied babblers and scimitarbills primarily used blackthorn (*Acacia mellifera* Vahl) dune habitat and open riverbed areas characterized by a low density of large camelthorn (*Acacia erioloba* Mey) trees. The study population is habituated to close observation by observers (for details of habituation, see Ridley & Raihani (2007)), allowing us to walk within 2–3 m of individuals and closely document their behaviour without causing them disturbance or alarm. The study population comprises 18 habituated groups of pied babblers, with an average group size of 3.9 ± 1.3 adults. These 18 habituated groups encompass the territories of more than 25 scimitarbill breeding pairs. All babblers at the study site are individually identifiable by a unique combination of three coloured and one metal ring. Not all scimitarbills were ringed, but we were confident that we could identify focal individuals because scimitarbills are territorial monogamous breeders that use the same roost site regularly (Hockey, Dean & Ryan 2005). We chose scimitarbill territories that were at least 1 km apart and were able to differentiate individuals within a pair because scimitarbills are sexually dichromatic (Hockey, Dean & Ryan 2005).

STUDY SPECIES

The southern pied babbler is a medium-sized (70–95 g, length 26–29 cm) cooperatively breeding passerine occupying the semi-arid acacia savannas of the Kalahari desert (Ridley & Raihani 2008). Groups are stable, comprising a dominant male and female and between 1 and 12 adult subordinates that help to raise young produced by the dominant pair (Ridley & Raihani 2008). Each group occupies a territory that they defend year-round from neighbouring groups (Golabek, Ridley & Radford 2012). Pied babblers are primarily terrestrial foragers, spending more than 95% of foraging time on the ground (Ridley & Raihani 2007). During foraging, a sentinel is often perched above the group (sentinel presence ranges between 20 and 90% of foraging time, average = 42% of observation time) and alerts group members to the presence of predators (Ridley, Raihani & Bell 2010). Previous research on pied babblers has revealed that they respond strongly to the vocal information provided by other species, and derive foraging and antipredatory benefits from doing so (Bell *et al.* 2009; Ridley & Raihani 2007; Ridley, Child & Bell 2007; Radford *et al.* 2011). For example, pied babblers are less vigilant when a drongo (*Dicrurus adsimilis* Bechstein) is following the group and flee to cover when a drongo gives alarm calls (Ridley & Raihani 2007; Radford *et al.* 2011). Research into the vocal behaviour of pied babblers has revealed that they are a highly vocal species: regularly giving alarm calls to approaching predators (Bell *et al.* 2010; Ridley, Raihani & Bell 2010), soft calls during sentinel behaviour (Hollén, Bell & Radford 2008), provisioning calls to young (Raihani & Ridley 2007) and contact calls during foraging (Radford & Ridley 2007). Pied babblers give alarm calls to both aerial and terrestrial predators (Ridley, Raihani & Bell 2010), but aerial predators are the most common alarm call given at our study site (for an alarm call spectrogram, see Fig. S1, Supporting Information). The alarm call of the pied babbler is best described as a series of harsh repetitive 'peeps', ranging in duration from 1 to 4 s (average 2.2 s). The average volume of this call at 10 m, as determined by sound level meter when a predator is approaching and <100 m away, is 69.4 dB.

The common scimitarbill is a medium-sized (24–42 g, length 24–28 cm) 'near passerine' (Order Coraciiformes, family Phoeniculidae) inhabiting semi-arid woodland in southern Africa (found as far north as Kenya), noted as particularly common in the Kalahari biome (Hockey, Dean & Ryan 2005). The scimitarbill has a highly distinctive curved bill, which it uses to probe in the bark and crevices of trees in search of food (Hockey, Dean & Ryan 2005). Because of this distinctive foraging habit, most observations of this species note that the birds primarily forage arboreally and are rarely observed coming to the ground to forage terrestrially (Hockey, Dean & Ryan 2005). Scimitarbills are not cooperative – they breed as pairs, often forage alone and do not display sentinel behaviour (Hockey, Dean & Ryan 2005). Previous vocal observations on scimitarbills have indicated that they give alarm, contact, territorial and 'nest arrival' calls (Hockey, Dean & Ryan 2005). Scimitarbills give alarm calls to both aerial and terrestrial predators, and can be observed joining with other species to mob predators (A.R. Ridley, personal observation). As for babblers, scimitarbill alarm calls to aerial predators are the most commonly observed at our study site (for an alarm call spectrogram, see Fig. S1, Supporting Information). The alarm call of the scimitarbill has previously been described as repetitive 'kw' calls, with the average alarm call length ranging between 1 and 5 s (average 2.3 s). The average volume of this call at 10 m, as determined by sound level meter when a predator is approaching and less than 100 m away, is 64.1 dB.

Because antipredator behaviours (such as fleeing to cover) in safe situations can be costly (Ydenberg & Dill 1986), it has been suggested that individuals should primarily eavesdrop on the alarm calls of species with whom they share common predators (Magrath, Pitcher & Gardner 2009; Carrasco & Blumstein 2012). Pied babblers and scimitarbills share a large number of predators – both are under threat of attack by several small raptors and mammals present in the study area (Hockey, Dean & Ryan 2005). The main predators for pied babblers have been described previously, with raptors comprising the bulk of observed predator attacks (see Ridley, Nelson-Flower & Thompson 2013). Although the scimitarbill has a more arboreal foraging habit than pied babblers, it is still exposed to the same suite of aerial and mammalian predators, with the main mammalian predator – the slender mongoose (*Galerella sanguinea* Rüppell), an accomplished tree climber (Skinner & Chimimba 2005).

INTERSPECIFIC INTERACTION

To determine how often scimitarbills and pied babblers associated with one another, we recorded the proportion of observation time that these two species spent foraging within 5 m of one another ($n = 15$ different babbler groups observed, average observation time at each group = 3.22 h). Scimitarbills were considered to be actively associating with babbler groups when they followed them between foraging patches (babblers were never observed to follow scimitarbills between foraging patches). Scimitarbills and babblers were only considered to be associating if they foraged within 5 m of each other for at least a minute.

FOCAL DATA COLLECTION

To determine behavioural changes in individuals according to the presence or absence of a heterospecific, we collected detailed focal data. The method of collecting time-activity focal data was identical for both species. For each individual, two 20-min foraging focals were conducted, where time spent foraging (s), location foraging in (ground or tree), type and size of food item caught and vigilance behaviour were recorded. Individuals were considered vigilant when they had paused foraging with head raised and were visually scanning the surrounding area. Food

types were defined into broad classes, such as coleoptera, orthoptera, hymenoptera, and within these classes were further defined according to life cycle stage (larvae, pupae, adult form, etc.). Food sizes were classified according to previous definitions for this population as described in Raihani & Ridley (2007). For each scimitarbill, one foraging focal was conducted when it was associating with a babbler group, and another foraging focal was conducted when it was foraging solitarily – resulting in 14 paired focals for 14 scimitarbills in 14 different babbler territories. For each focal babbler, one foraging focal was conducted when there was a scimitarbill foraging with the group, and another foraging focal conducted when a scimitarbill was absent, resulting in 15 paired focals for 15 babblers in 15 different babbler groups. Focals of babblers foraging solitarily were not possible because babblers are a highly social species and, with the exception of evicted or floating individuals, are not found foraging alone (Ridley, Raihani & Nelson-Flower 2008). Focals were not conducted if there had been a recent disturbance (such as an alarm call or border interaction). A focal was immediately paused if the focal individual went out of sight of the observer and was abandoned altogether if a major disturbance occurred during the focal period or if the individual remained out of sight for more than five minutes.

We used information from our foraging focals to calculate the proportion of observation time that each focal individual spent foraging (time observed foraging/total focal time), which locations they utilized for foraging (terrestrial or arboreal foraging), foraging efficiency (calculated as biomass ingested per unit time spent foraging) and proportion of observation time spent vigilant (time vigilant/total observation time). Because the presence of other species may affect the behavioural interactions between our two focal species, we collected data only when these two species were interacting in the absence of other heterospecifics.

EXPERIMENTAL PROTOCOL

We conducted playback experiments of alarm calls of (i) vigilant babblers to scimitarbills and (ii) vigilant scimitarbills to babblers to determine what effect this had on focal individual behaviour and to test the hypothesis that scimitarbills are more responsive to babbler alarm calls than babblers are to scimitarbill alarm calls. To conduct these playbacks, we first collected calls from our study population. All sound recordings were made using a Rode NTG-2 directional shotgun microphone coupled with a Rode blimp suspension windshield system and a Roland 24-bit digital sound recorder (Model R-05, Roland Corporation, Osaka, Japan). We chose five alarm calls from each species to use for the playback experiments. These recordings were chosen for their high signal-to-background ratio and low levels of background noise. Alarm call playbacks were taken from recordings of individuals giving a series of alarm calls when a raptor (pale chanting goshawk *Melierax canorus* Thunberg or gabar goshawk *Melierax gabar* Daudin) was flying within 100 m of the group and clearly visible. Recordings were taken from as close to 10 m from the alarm-calling individual as was possible to achieve (maximum distance = 15 m). Playback volume was adjusted to reflect the volume observed during natural calls. We used a digital sound level meter at a distance of 10 m from the focal bird (Voltcraft SL100, Voltcraft, Barking, UK) to determine the amplitude of natural alarm calls given when a predator is approaching and <100 m away (69.4 dB for babblers, 64.1 dB for scimitarbills). We tested the calls coming from the speaker at the same distance with a sound level meter to ensure that the playbacks replicated natural call volume. Each exemplar used for playback contained alarm calls that were 2.2 s long and consisted of three alarm 'peeps' to an approaching predator [average duration and content of an alarm call of this type as determined by alarm calls collected over the data collection period ($n = 79$)].

As controls, we played back (i) foraging contact calls of scimitarbills to pied babblers and (ii) foraging contact calls of pied babblers to scimitarbills. Contact calls are made consistently and regularly when foraging or moving between foraging patches, as described in Radford & Ridley (2007 – for pied babblers) and Hockey, Dean & Ryan (2005 – for scimitarbills). The control calls were played back for the same duration (2.2 s) as alarm calls, to the same focal individuals. We determined the natural amplitude of contact calls and adjusted the volume of playbacks to replicate natural calls in the same way as described previously for alarm calls. We used six exemplars of pied babbler contact calls and six scimitarbill contact call exemplars. Control calls were never played back on the same day as experimental calls: we left a 1-week gap between the playback of experimental versus control playbacks, and we alternated the order in which the different playbacks were given. Playbacks were paired such that the same individual was exposed to both the control and experimental playback, with only one replicate of the alarm and control playback conducted at each group (babblers) or within each territory (scimitarbills). For each exemplar, 1.5 s of background noise, taken from the same sound file the calls were taken from and edited in the same way, was added immediately preceding and following the alarm or contact call. Sound files were edited using CoolEdit Pro 2.0 (Syntrillium Software Corporation, Scottsdale, AZ, USA), stored as WAV audio files on an Apple iPod and played back on an Altec Lansing Orbit speaker.

Playbacks were played at a distance of 10 m from the focal individual and were only conducted when the group (or individual in the case of scimitarbills) was exhibiting normal foraging behaviour. If there was a disturbance (such as a mobbing event, predator alarm or intergroup interaction), playbacks were not conducted until 30 min after the disturbance, to ensure that individuals had resumed normal foraging behaviour. In addition, playbacks were not conducted if the species being played back was currently present (within 100 m). For example, a babbler call would not be played back to a scimitarbill if a babbler was naturally present near the scimitarbill at the time of playback. This is because in such a situation, it would be impossible to determine whether the scimitarbill was responding to the real babbler's response or the 'playback babbler'.

The experimental protocol was standardized so that all individuals were approximately the same distance from cover (between 1 and 2 m from cover) when the playback was given. Immediately after the playback, we recorded the response of the focal individual to the playback, with response categorized as: *no response* – where the focal individual's behaviour did not change, *vigilant* – where the focal individual looked up from its foraging patch and scanned its surroundings but did not move from the foraging patch, and *flee* – where the focal individual moved quickly to the cover of vegetation following playback. A response to a playback was only considered to have occurred if the focal individual responded within 2 s of the playback ending. We defined birds as having reached cover when they were completely obscured by vegetation, and their position was generally only detectable by the movement of vegetation. Areas of cover were sufficiently thick in vegetation or other material to admit babblers and scimitarbills, but not their predators (Ridley, Nelson-Flower & Thompson 2013).

STATISTICAL ANALYSIS

To investigate the relationship between scimitarbill–babbler association and babbler group size, we used a linear mixed model (LMM) with a normal error structure and an identity link function in *SPSS* (version 20.0, IBM, Armonk, NY, USA). The proportion of observation time that scimitarbills were observed foraging with babbler groups was set as the response term, with

babbler group size at the time of the association (number of adult babblers) and habitat type (dune, riverbed, blackthorn) set as potential predictor terms.

For our comparisons of the difference in behaviour when foraging alone or in association with heterospecifics, we conducted within-individual paired comparisons using paired *t*-tests. Because in some cases there was very little variation in behaviours (e.g., most scimitarbills spent 100% of their time foraging arboreally when alone), data could not always meet the assumptions of normality. This required us to use a nonparametric Wilcoxon signed-rank test instead of a paired *t*-test in some cases.

For our comparison of the difference in response to an interspecific alarm call playback and an interspecific contact call playback, we conducted within-individual paired comparisons using McNemar's related samples test (where 0 = no response, 1 = response). Paired control and alarm call playbacks were given to 11 different scimitarbills residing in 11 different territories and to 16 different babblers residing in 16 different babbler groups. To test whether the responsiveness of scimitarbills to babbler alarm calls was greater than the response of babblers to scimitarbill alarm calls, we conducted independent sample comparisons of responses to the alarm call playback using a nonparametric Fisher's test.

Results

INTERSPECIFIC INTERACTION

During 48.2 h of observation, pied babblers groups were accompanied by scimitarbills for 14.8 h, representing a close (<5 m) association between these two species for 30.8% of observation time. There was a strong effect of babbler group size on the amount of time that scimitarbills spent associating with babblers (LMM $F = 16.22$, $P = 0.001$, Fig. 1). Scimitarbills associated most with larger groups (averaging more than 50% of observation time) and associated with small groups the least (averaging <20% of observation time at groups of five or fewer babblers). This trend coincides directly with patterns of sentinel behaviour in babbler groups: larger babbler groups have a sentinel present for a greater proportion of

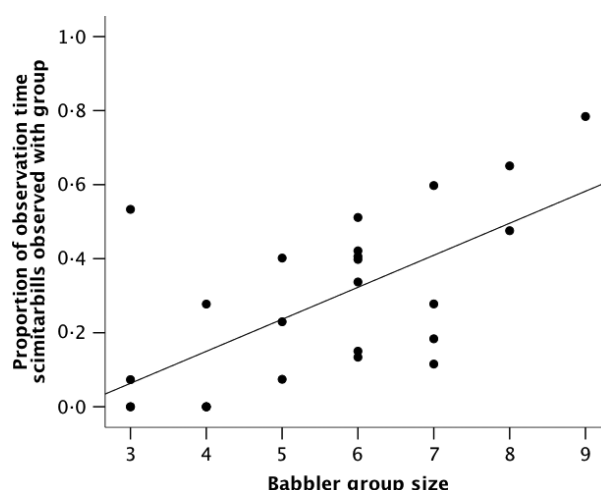


Fig. 1. The relationship between babbler group size and the proportion of observation time that scimitarbills spent associating with pied babbler groups. The line of best fit is generated from the predictions of the output of the linear mixed model analysis.

observation time than small groups (Ridley & Raihani 2007).

CHANGES IN FORAGING BEHAVIOUR

Scimitarbill behaviour changed significantly when foraging in association with babbler groups compared with when foraging alone. When associating with pied babblers, scimitarbills spent a higher proportion of observation time foraging (alone: 0.32 ± 0.05 , with group: 0.56 ± 0.03 , paired t -test, $t_{12} = 3.98$, $P = 0.002$, Fig. 2a). This could be due to individuals investing significantly less time in personal vigilance behaviour when associating with pied babblers (proportion of observation time when alone: 0.21 ± 0.03 , with group: 0.02 ± 0.01 , paired t -test, $t_{12} = -6.95$, $P = 0.001$, Fig. 2b). In addition, scimitarbill individuals experienced a significant increase in foraging efficiency when foraging with pied babblers compared with when foraging alone (alone: 0.19 ± 0.03 g min⁻¹, with group: 0.30 ± 0.03 g min⁻¹, paired t -test: $t_{12} = 2.55$, $P = 0.03$, Fig. 2c).

When alone, scimitarbills primarily foraged on the branches and trunks of trees (99% of foraging time, $n = 13$ foraging focals). In contrast, when foraging with babbler groups, scimitarbills split their time between foraging in the branches of trees and foraging terrestrially (60.1% of time foraging in trees, 39.9% of observation time spent foraging terrestrially, $n = 13$ foraging focals). Terrestrial foraging behaviour primarily involved probing into the soft sand for prey. A Wilcoxon signed-rank test of paired samples confirmed that there was a significant change in the foraging location of scimitarbills, with the proportion of time spent foraging terrestrially increasing significantly when following pied babblers groups ($n = 13$, $P = 0.003$, Fig. 2d).

Foraging on the ground allowed scimitarbills to capture different prey items compared with when they were foraging in trees. While arboreal foraging primarily involved the

extraction of small items (such as coleoptera), comprising 75.6% of biomass ingested, terrestrial foraging allowed scimitarbills to capture medium- to large-sized subterranean pupae, with medium to large items comprising 60.4% of the biomass ingested during terrestrial foraging.

Although scimitarbills showed considerable behavioural change when foraging with pied babbler groups compared with when foraging alone, pied babblers did not change their behaviour in response to the presence of a scimitarbill. The amount of time babblers spent foraging and investing in personal vigilance was unaffected by scimitarbill presence (time spent foraging: paired t -test $t_{14} = 1.03$, $P = 0.32$, vigilance: paired t -test, $t_{13} = -0.30$, $P = 0.77$, Fig. 3a,b). In addition, the location of foraging babblers and their foraging efficiency were also unchanged by the presence of a scimitarbill (foraging location: Wilcoxon signed-rank test, $n = 14$, $P = 0.40$, foraging efficiency: paired t -test, $t_{15} = 0.42$, $P = 0.68$, Fig. 3c,d).

PLAYBACK RESULTS

Our playback results were consistent with our focal observations – scimitarbill behaviour changed significantly in response to babbler alarm calls, whereas scimitarbill alarm calls did not change babbler behaviour. Scimitarbills responded strongly to babbler alarm calls – 10 of 11 focal individuals (90.9%) fled to the safety of cover within 2-s of hearing the playback of a babbler aerial alarm call (Fig. 4). This response was significantly different to the response of focal individuals to a control playback of babbler contact calls, where none of the 11 focal individuals moved to cover (McNemar's related samples test, $P = 0.002$, $n = 11$).

Pied babblers were never observed to move to cover following the playback of a scimitarbill alarm (0 of 16 focal individuals, Fig. 4). The primary response of pied babblers was to look up briefly from foraging to scan their

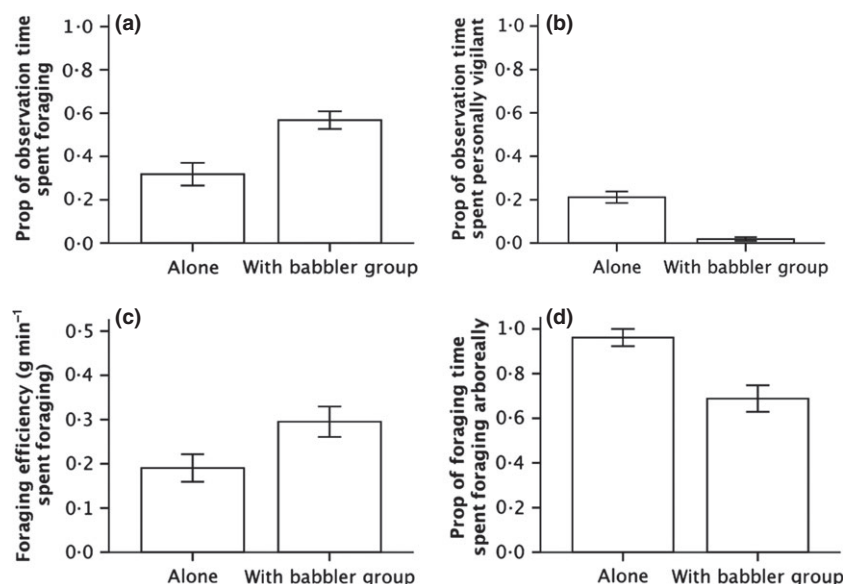


Fig. 2. Paired comparisons of the difference in (a) the proportion of observation time spent foraging, (b) the proportion of time spent vigilant (c) foraging efficiency and (d) proportion of time spent foraging arboreally by scimitarbill individuals when foraging alone compared with when they were foraging in association with pied babbler groups. Means are presented with standard errors.

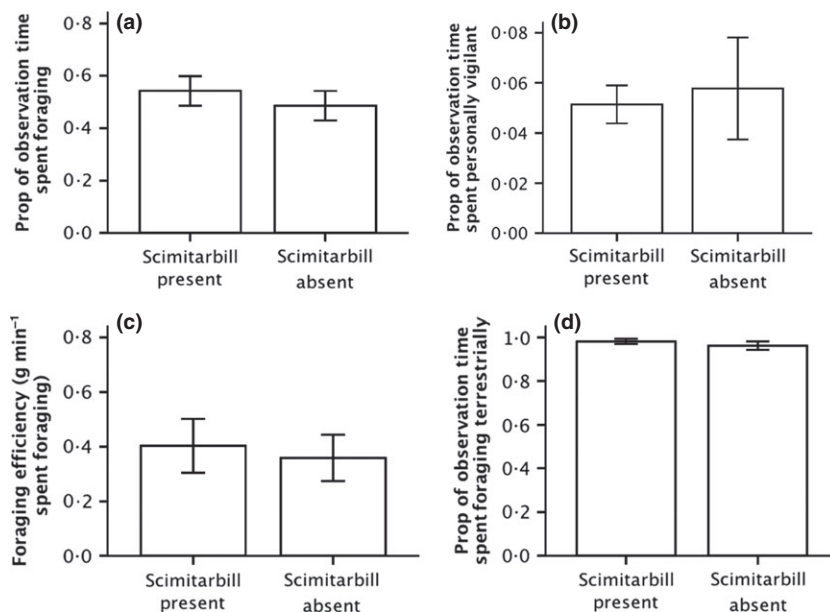


Fig. 3. Paired comparisons of the difference in (a) the proportion of observation time spent foraging, (b) the proportion of time spent vigilant (c) foraging efficiency and (d) the proportion of time spent foraging terrestrially by pied babbler individuals when a scimitarbill was associating with the group compared with when a scimitarbill was absent. Means are presented with standard errors.

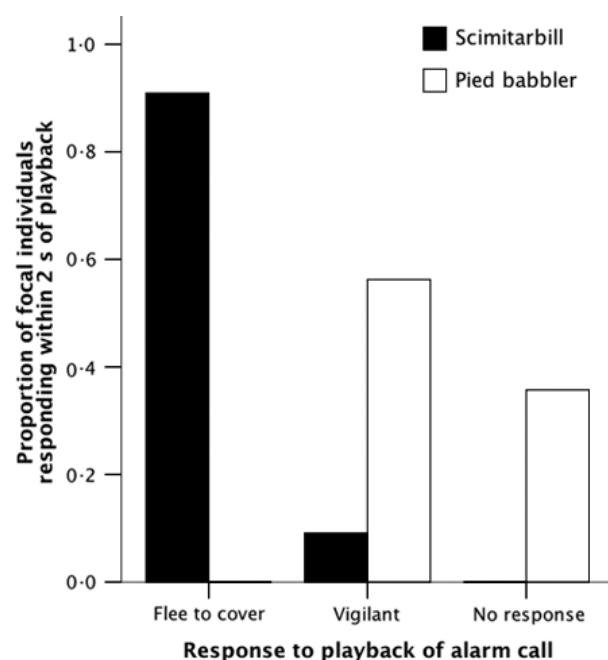


Fig. 4. The response of scimitarbills and babblers to the playback of heterospecific alarm calls. Behavioural responses were defined as the proportion of focal individuals that fled to cover, became vigilant (but did not flee to cover), and those that showed no behavioural response to the playback.

surroundings ($n = 9$ focal individuals – 56%), while the remaining focal individuals did not change their foraging behaviour at all ($n = 7$ focal individuals, 44%, Fig. 4). The ‘head up’ response of some babblers to scimitarbill alarm calls meant that the response to the alarm playback was significantly different to the response to the control playback, where none of the babblers changed their foraging behaviour (McNemar’s related samples test, $P = 0.04$, $n = 15$).

Scimitarbills responded significantly more strongly to babbler alarm calls than babblers did to scimitarbill alarm calls. Although 90.9% of scimitarbills fled to cover immediately following playback of a babbler alarm, 0% of babblers fled to cover upon hearing a playback of a scimitarbill alarm (Fisher’s test, $P < 0.001$, $n = 26$).

Discussion

While there is an increasing amount of evidence that some species eavesdrop on the alarm calls of other species (Sullivan 1984b; Peake 2005; Vitousek *et al.* 2007; Ito & Mori 2010), little is known about the ecological significance of this eavesdropping behaviour (aside from the immediate avoidance of predators). Our research revealed a significant behavioural change in a solitary forager when associating with a social species, with no reciprocal change in the behaviour of the social species. Scimitarbills became less vigilant, foraged more successfully and utilized a wider diversity of foraging patches when associating with pied babblers. Interestingly, our research revealed that the scimitarbill, widely regarded as primarily an arboreal forager (Hockey, Dean & Ryan 2005), spent an extensive amount of time foraging terrestrially when associating with pied babblers. It is unlikely that this change in foraging behaviour occurred simply because scimitarbills had to forage terrestrially in order to stay with a pied babbler group, because babblers often forage close to the cover of trees (Hollén, Bell & Radford 2008; Thiele, Jeltsch & Blaum 2008; Ridley, Nelson-Flower & Thompson 2013). Rather, terrestrial foraging allowed scimitarbills to exploit more foraging patches and access prey items not available to them during arboreal foraging. Our experiments suggested that this behavioural change was facilitated by the predator information that pied babbler groups provided – scimitar-

bills were strongly responsive to alarm calls given by pied babblers. These results suggest that interspecific interceptive eavesdropping facilitates niche expansion in the scimitarbill.

There are, however, alternative explanations for the greater amount of time scimitarbills spent foraging terrestrially when associating with babblers. Scimitarbills could be trying to kleptoparasitize food, they could be watching babblers in order to gain access to good foraging sites, or they could be 'hiding' among babblers. We reject these alternative explanations because (i) we never observed any attempts at kleptoparasitism nor (ii) any incidence where scimitarbills paused their foraging to observe foraging babblers and (iii) if scimitarbills were 'hiding' among babblers, we would expect to see them forage with other terrestrially foraging social bird species that do not have a sentinel system (e.g. wattled starlings, *Creptophora cinerea* Lesson). However, we did not observe such terrestrial foraging behaviour when scimitarbills interacted with other social species and conclude therefore that scimitarbills are expanding their niche by eavesdropping on the information provided by pied babbler sentinels.

Animals often face a trade-off between the amount of time they invest in vigilance behaviour and the amount of time available to forage (Brown, Laundré & Gurung 1999; Dall, Kotler & Bouskila 2001; Kotler, Brown & Bouskila 2004; Pays *et al.* 2012; reviewed in Beauchamp 2009). By associating with pied babbler groups, scimitarbills gain significant benefits by investing more time foraging and less time vigilant. Previous research on pied babblers has revealed that individuals that leave a group lose significant body mass as a direct result of the increase in the amount of time they invest in antipredator vigilance (Ridley, Raihani & Nelson-Flower 2008). If the same effect is occurring in scimitarbills, they could gain significant long-term benefits from associating with pied babblers, such as better body condition and higher reproductive success. This could explain the strong effect of group size on pied babbler–scimitarbill associations. Large babbler groups were accompanied by scimitarbills more often than small babbler groups, directly reflecting the increase in babbler sentinel activity with increasing group size (Ridley & Raihani 2007). This behavioural adjustment suggests that scimitarbills are aware of the benefits of following pied babbler groups and behave in a way that maximizes those benefits. We cannot rule out the possibility that the reduction in vigilance with group size was also due to scimitarbills gaining a dilution benefit of joining large groups (*sensu* Roberts 1996). However, the strong response of scimitarbills to babbler alarm calls confirms that scimitarbills are eavesdropping on vocal information produced by pied babblers.

In this study, we documented a behavioural change in an 'information taker' that allowed individuals to expand

their foraging niche. Several previous studies have noted that an association with other species in mixed-species flocks can enable the expansion of a foraging niche (Sridhar, Beauchamp & Shanker 2009; Zou *et al.* 2011; reviewed in Harrison & Whitehouse 2011), and several have noted that these associations tend to revolve around a nuclear, often cooperative, species or set of species that provide reliable, loud alarm calls (Dolby & Grubb 1998; Thiollay & Jullien 1998; Goodale & Kotagama 2005; Sridhar, Beauchamp & Shanker 2009). This has led to speculation that community structure may be affected by 'information givers' and the benefits of association with such species (Goodale *et al.* 2010; Harrison & Whitehouse 2011). Here, we have provided empirical evidence for this 'benefits of association' idea, originally suggested in Sullivan's research on interactions between satellite and dominant species in mixed-species flocks (Sullivan 1984a, 1985). In so doing, we have added evidence to the argument that by eavesdropping on the alarm calls of social species whose vigilance they are able to exploit, 'follower' species such as the scimitarbill can significantly expand their niche and receive foraging benefits.

An important idea put forward by Lea *et al.* 2008 is supported by our study. Lea *et al.* suggested that solitary foragers stand to gain more from eavesdropping on others, because they tend to be more vulnerable to predation. Our results support this idea, with a strong response to babbler alarm calls by scimitarbills, but a very weak response to scimitarbill alarm calls by babblers. While learning to respond appropriately to heterospecific alarm calls requires flexible associative learning abilities (Vitousek *et al.* 2007), the benefits of this to solitary species may be sufficiently high for them to be more likely to invest in this behaviour (Lea *et al.* 2008; Sridhar, Beauchamp & Shanker 2009). Although we do not have direct evidence of different predation levels in babblers compared with scimitarbills to help explain the difference in behavioural response between the two species (because predation is very difficult to observe), we make the general assumption suggested by Pulliam (1973), Lima (1995) & Lea *et al.* (2008) that solitary individuals tend to be more vulnerable.

The low level of response by pied babblers suggests that they are not utilizing the information provided by scimitarbills. This could occur for several reasons: (i) the scimitarbill may not be a reliable indicator of predator presence, (ii) the babbler sentinel system may be sufficiently effective at detecting predators such that there is no selective pressure for individuals to learn to respond to the alarm calls given by scimitarbills, or (iii) the higher communicative complexity in the calls of social species may provide more detailed information regarding the type and urgency of a predator threat (Freeberg, Dunbar & Ord 2012; Pollard & Blumstein 2012). Options (ii) and (iii) are less likely because pied babblers have been observed responding strongly to the alarm calls of other species (Ridley & Raihani 2007; Bell *et al.* 2009; Radford *et al.* 2011). A lower reliability of scimitarbill alarm calls and a

high effectiveness of the babbler sentinel system and alarm calls probably combine to create the minimal response from the pied babblers that we observed. Although the level of response was low (with no individuals fleeing to cover), a number of pied babblers paused foraging to become vigilant in response to scimitarbill alarm calls, suggesting that they are gaining at least some information from the presence of this satellite species.

By comparing the behavioural responses of a solitary species and a social species, we found evidence for unequal information transfer during interspecific interaction, suggesting that the behaviour and habitat utilization of some species may be strongly influenced by the information produced by other species. This agrees with the hypothesis put forward by Goodale *et al.* (2010) – that interspecific information transfer can influence the structure of animal communities. By following babblers between foraging patches and using the information produced by babbler sentinels, scimitarbills expanded their foraging niche and changed their foraging and vigilance behaviours. Similar behavioural changes have been reported in other eavesdropping species (Sullivan 1984a; Dolby & Grubb 1998; Lea *et al.* 2008; Magrath, Pitcher & Gardner 2009), and the direct comparative and experimental information provided here between an information ‘giver’ and an information ‘taker’ provides important information regarding patterns of information transfer within animal communities. Longer-term research on the benefits of this behaviour (in terms of body mass, mate acquisition and reproductive success for example) will provide important evolutionary insights into the adaptive benefits of interceptive eavesdropping behaviour.

Acknowledgements

We are grateful to the Kuruman Reserve Trust, Mr & Mrs de Bruins and Mr & Mrs de Kotze for land access. We thank all researchers onsite for their support and for their company at such a remote research station. We thank the editor and two reviewers for constructive comments on an earlier version of this manuscript. The Northern Cape Conservation Authority kindly granted us a research permit for this research, SAFRING provided a ringer's licence to ARR, and our research was approved by the Science Faculty Animal Ethics Committee, University of Cape Town (Ethics number R2012/2006/V15/AR). The Percy FitzPatrick Institute of African Ornithology provided logistical support for this research, and ARR was supported by an ARC Future Fellowship.

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Received 22 February 2013; accepted 3 July 2013

Handling Editor: Sara Lewis

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Spectrogram of a scimitarbill alarm call.