

SINGING FOR YOUR SUPPER: SENTINEL CALLING BY KLEPTOPARASITES CAN MITIGATE THE COST TO VICTIMS

Andrew N. Radford,^{1,2} Matthew B. V. Bell,³ Linda I. Hollén,¹ and Amanda R. Ridley^{4,5}

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

²*E-mail: andy.radford@bristol.ac.uk*

³*Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, United Kingdom*

⁴*Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, Cape Town, South Africa*

⁵*Department of Brain, Behaviour and Evolution, Macquarie University, Sydney, NSW 2109, Australia*

Received July 20, 2010

Accepted October 12, 2010

Parasitism generally imposes costs on victims, yet many victims appear to tolerate their parasites. We suggest that in some cases this may be because parasites provide victims with mitigating benefits, paradoxically giving rise to selection for advertisement rather than concealment by parasites. We investigate this possibility using the interaction between an avian kleptoparasite, the fork-tailed drongo (*Dicrurus adsimilis*), and one of its victims, the pied babbler (*Turdoides bicolor*). Combining field observations and a playback experiment, we demonstrate that a conspicuous vocal signal broadcast by drongos perched waiting to steal food from foraging babblers allows the latter to improve their own foraging efficiency, although not to the same extent as that experienced in response to conspecific sentinel calling. We argue that “sentinel” calling by drongos may originally have arisen as a means of manipulating babblers: because babblers find more food items and venture into the open more in response to these vocalizations, drongos are presented with more kleptoparasitism opportunities. However, the resulting benefit to babblers could be sufficient to reduce selection for the evolution of defenses against drongos, and the current situation may represent a rare example of an interspecific relationship in transition from a parasitism to a mutualism.

KEY WORDS: Foraging success, interspecific interaction, mutualism, parasitism, vigilance, vocal communication.

Interactions between parasites and their victims provide one of the most interesting and powerful tools for investigating the evolutionary dynamics of conflict. Parasites, by definition, impose costs and are therefore expected to exert selection pressure on victims to evolve defense mechanisms (Davies et al. 1989; Sheldon and Verhulst 1996). In many situations, however, victims appear to tolerate parasites. Such apparently paradoxical tolerance has generally been explained as the result of either evolutionary lag (Hosoi and Rothstein 2000) or a constraint imposed on victims because the costs of evolving resistance outweigh the potential benefits; the latter can arise if parasitism occurs only rarely (Hauber et al. 2004), recognition errors are costly (Davies et al.

1996) or defense is expensive (Sheldon and Verhulst 1996). An additional possibility is that the presence or behavior of a parasite provides an incidental benefit to the victim, which is therefore selected to become more, rather than less, tolerant. Although this is often suggested as a theoretical route by which mutualism might evolve from an initial parasitism (Ewald 1987; Roy and Kirchner 2000), the potentially rapid adaptive changes at this stage of a relationship mean that supporting data are scarce. Here, we provide a rare empirical example involving the sentinel behavior of kleptoparasitic fork-tailed drongos (*Dicrurus adsimilis*).

Kleptoparasitism (stealing food obtained by others) is a foraging strategy employed by a taxonomically diverse range of

species (Brockmann and Barnard 1979; Morand-Ferron et al. 2007). Many kleptoparasites use threats or physical aggression to force the victim to abandon its food (Maxson and Bernstein 1982; Tershy and Breese 1990), but some, including fork-tailed drongos, use a more subtle, deceptive strategy: they give false alarm calls to scare foragers away from prey items, which can then be stolen (Munn 1986; Ridley and Raihani 2007; Satischandra et al. 2010). When associating with target species, however, fork-tailed drongos may effectively perform the role of a sentinel: they perch in raised positions, scan the surroundings and give true alarm calls on detecting predators (Ridley and Raihani 2007). Moreover, perched drongos produce a low-amplitude call (the “twank”) every 4–5 s (Hockey et al. 2005), which announces their presence and may therefore act as a watchman’s song (sensu Wickler 1985). In response to the watchman’s song of conspecific sentinels, foragers of a number of social species alter their behavior in ways that allow them to capture more food (Manser 1999; Hollén et al. 2008). We suggest that foragers may similarly benefit from the calling of heterospecific “sentinels,” even those that are present to steal food, and we argue that this benefit may mitigate the cost of kleptoparasitism.

Pied babblers (*Turdoides bicolor*) are one of several avian and mammalian species kleptoparasitized by fork-tailed drongos (Ridley and Raihani 2007). They are cooperatively breeding birds that forage predominantly on the ground, probing in sand and prospecting through vegetation for invertebrate prey (Radford and Ridley 2006). When foraging in these ways, their vigilance is limited (Radford and Ridley 2007) and thus they rely on alarm calls given by others to warn them about predatory raptors, mongooses, and snakes (Ridley and Raihani 2007). Fork-tailed drongos frequently associate with foraging babbler groups, using false alarm calls to kleptoparasitize large prey items, but also apparently acting as sentinels (Ridley and Raihani 2007; Ridley et al. 2007; Ridley and Child 2009).

Here, we ask four main questions. First, do foraging pied babblers alter their behavior in the presence of fork-tailed drongo sentinels, as they do in response to conspecific sentinels (Hollén et al. 2008)? Second, do these changes in behavior result in increased foraging success for the babblers, and thus a benefit that mitigates the presence of kleptoparasitic drongos? Third, can babbler foragers detect the presence of drongo sentinels from their watchman’s song alone? Finally, do foraging pied babblers respond as strongly to heterospecific sentinel calling as they do to conspecific sentinel calling?

Materials and Methods

STUDY SITE AND SPECIES

Fieldwork was carried out on the Kuruman River Reserve in the southern Kalahari, South Africa (26°58’S, 21°49’E) (see Raihani

and Ridley [2007] for additional details about the study site). We studied 11 color-ringed groups of pied babblers (containing 3–12 individuals; mean \pm SD = 5.2 \pm 2.0). Individuals older than 12 months were classified as adults and were divided into dominants (the putative breeding pair) and subordinates (the remainder of the adults). Breeding females always incubate the eggs overnight; breeding males were identified from midair courtship chases and copulations with breeding females. Fledglings were deemed independent once they obtained 95% of their food from self-feeding; prior to this they were termed dependent. Pied babblers are sexually monomorphic in plumage, so subordinates and fledglings were sexed with a DNA test (for details of capture, bleeding, and DNA extraction and analysis, see Radford and Ridley 2006, 2008). The habituated nature of the study population means it is possible to observe individuals from approximately 2–3 m away (Ridley and Raihani 2007), and thus to collect accurate measures of vigilance and foraging behavior and to conduct controlled playback experiments (Radford and Ridley 2006, 2008; Hollén et al. 2008; Bell et al. 2010).

OBSERVATIONAL DATA COLLECTION

Observational data were collected for 4 h after dawn and for 2–3 h before dusk from November 2006 to June 2007 and from March to June 2008. To ascertain how the presence of a fork-tailed drongo sentinel influences the spread of a foraging babbler group and the proportion of babbler individuals foraging in the open (clearly visible) as opposed to under cover (e.g., foraging at the base of a bush), we conducted scans both at the start of a drongo sentinel bout and 2 min later in the same bout. Data were collected opportunistically from sentinel bouts throughout an observation session. A drongo was classified as a sentinel if it was perched in an elevated position (greater than 1 m from the ground) either above the foraging babblers or within 5 m of the most peripheral forager (Ridley and Raihani 2007). Group spread was calculated as the estimated distance between the two foragers furthest apart multiplied by the estimated distance between the two foragers furthest apart on a perpendicular axis (Hollén et al. 2008; Radford et al. 2009). At the start of a drongo sentinel bout, and as long as there was no babbler sentinel and had not been for the previous 5 min, we immediately recorded group spread and the exposure (open or cover) of each foraging babbler; we collected the same data 2 min later, as long as the drongo had remained in position during that time and no babbler sentinel had also started a bout. We discarded any paired scans in which the habitat type (open, grass, thicket) or foraging group size changed within the 2-min period; analyzed scan pairs were matched for potential confounding variables. Scans were not conducted if there had been an alarm call in the previous 5 min; babblers generally return to foraging within 2 min of an alarm call (A.N.R., unpubl. data).

We also conducted continuous focal watches on foraging babbler adults and independent fledglings (mean \pm 1 SEM length of focal watch = 4.64 ± 0.19 min, range 0.1–25.8 min, $n = 57$ individuals; mean \pm 1 SEM focal watches per individual = 13.6 ± 1.1 , range 1–35, $n = 759$ watches). Focal watches continued until an alarm call occurred, the group moved to a new habitat, or the focal individual flew off or became engaged in activities other than foraging (e.g., became a sentinel or started preening). At least 1 h was left between watches on the same individual to enhance the independence of sampling. During focal watches, we recorded the behavior of the babbler individual as (1) foraging (whenever it was probing or pecking), (2) vigilant (whenever it had its head raised), or (3) moving. We also recorded each change of sentinel status (be it a babbler or a drongo sentinel), as well as each successful foraging attempt and the size of prey captured by the focal individual. Prey items were classified as follows: tiny = barely visible; small = visible in the bill; medium = hanging out the side of the bill; large = size of the bill; items larger than this were scored as multiples of “large.” Fifty prey items representative of each size category were weighed and prey sizes were subsequently converted to biomass values as follows: tiny = 0.02 g; small = 0.11 g; medium = 0.45 g; large = 0.84 g (Radford and Ridley 2006). These values were used for the calculation of both biomass capture rate (food caught per minute of observation time) and foraging efficiency (biomass caught per minute of foraging time).

All data were recorded on a Palm TX PDA (Palm, Sunnyvale, CA), which automatically noted the time of each event. To assess the impact of the presence of a drongo sentinel on babbler foraging and vigilance behavior, we extracted data from those focal watches in which there was a 2-min period both immediately before and after the start of a drongo sentinel bout, and as long as the drongo had remained in position during the second 2-min period. Any extracted focal-watch pairs (4-min period) that included a babbler sentinel bout, an alarm call, or a change in habitat or foraging group size were discarded before analysis.

PLAYBACK EXPERIMENT

To test whether foraging babblers respond to drongo sentinel calling (the “twank” calls given while perched; Hockey et al. 2005), we presented eight groups with two trials: one involved 5-min playback of the sentinel calls of a drongo that associated with that particular babbler group; the other involved 5-min playback of background noise from the territory of the same babbler group (as a control). We constructed playback loops, using Wavelab, version 2 (Steinberg Media Technologies, Hamburg, Germany), by editing original recordings previously made using a Sennheiser MKH416T (Old Lyme, CT) microphone and a Marantz PMD670 (Eindhoven, The Netherlands) hard-drive sound recorder, and which had been digitized

(44.1 kHz, 16 bits). Recordings of background noise were made when there were no babblers or drongos in the vicinity; recordings with conspicuous loud noises (such as the alarm calls of other species or passing motor vehicles) were not used in the construction of playback loops. No playback loop was used more than once in the experiment, thus avoiding pseudoreplication.

The playback experiment was conducted in March–May 2007. Trials to the same group were on separate days, with the order of trial presentation counterbalanced across the eight groups, and occurred when foraging group size and habitat type were the same. Playbacks were of the same sound intensity as natural sentinel calls and background noise (determined using a Tandy sound-level meter), were broadcast from a Sony SRS-A35 (Tokyo, Japan) speaker positioned 2.5 m above the ground on a pole placed next to a tree in the middle of the foraging babbler group, and were conducted when there had been no alarm calls and no natural sentinel of either species for at least 5 min. One observer conducted scan samples at the end of each minute of the trial to record babbler group spread and the proportion of babblers foraging in the open; a second observer continuously recorded the vigilance and foraging behavior of one adult individual (the same one in both trials to the same group) throughout the trial. This is exactly the protocol used in Hollén et al. (2008) for an investigation of the importance of the watchman’s song given by conspecific sentinels.

DATA ANALYSIS

We analyzed observational data with mixed models because these allow the inclusion of random as well as fixed terms and can thus take account of repeated measures of the same group, individual, scan pair and focal watch, where appropriate. All models had a normal error structure (Linear Mixed Model; LMM), except those examining the proportion of individuals foraging in the open, which had a binomial error structure and a logit link function (Generalized Linear Mixed Model; GLMM). In all models, variance components were estimated using the Restricted Maximum Likelihood (REML) method, and random terms were retained unless the variance component was found to be zero (and hence their removal did not influence the findings reported). The significance of fixed terms was determined using the Wald statistic, which approximates the χ^2 distribution.

To assess the influence of drongo sentinel presence on babbler group spread and the proportion of babblers foraging in the open, we conducted models using the paired scans from 0 min and 2 min after the start of the same sentinel bout. These models were based on 54 paired scans from 11 groups, and we included scan pair nested in group identity as a random term. To assess the influence of drongo sentinel presence on the head-up rate, proportion of time spent vigilant, proportion of time spent foraging, number of prey items caught, mean prey size, foraging efficiency, and

biomass capture rate of babbler foragers, we conducted models using paired focal-watch data from the 2-min period before and after the start of the same sentinel bout. These models were based on 116 paired focal watches on 27 individuals in 11 groups, and we included group identity (not retained; see above) and focal-watch pair nested in individual identity as random terms. All analyses were two-tailed and conducted in Genstat (10th edition; Lawes Agricultural Trust, Rothamstead, Harpenden, UK).

Results

Pied babbler foragers exhibited a significant increase in biomass capture rate following the start of a drongo sentinel bout (LMM: Wald statistic = 5.68, $df = 1$, $P = 0.020$; Fig. 1A). This increase was the result of a greater number (Wald statistic = 9.22, $df = 1$, $P = 0.004$; Fig. 1B), rather than a larger mean size (Wald statistic = 0.03, $df = 1$, $P = 0.854$), of prey items caught.

Babblers did not spend a greater proportion of time foraging in the presence of a drongo sentinel (Wald statistic = 0.04, $df = 1$, $P = 0.833$; Fig. 1C), despite a smaller proportion of time spent vigilant (Wald statistic = 6.96, $df = 1$, $P = 0.011$; Fig. 1D); the time saved was used moving between patches (Wald statistic = 8.15, $df = 1$, $P = 0.006$). Instead, babblers caught more prey items in the presence of a drongo sentinel because of an increase in foraging efficiency (Wald statistic = 5.02, $df = 1$, $P = 0.029$; Fig. 1E), which potentially arose from a combination of three changes in behavior. First, individuals looked up less frequently when a drongo sentinel was present (Wald statistic = 8.47, $df = 1$, $P = 0.005$; Fig. 1F), which likely reduced disruption to foraging bouts and hence minimized the chance of mobile prey escaping into the sand. Second, foraging babblers spread out more widely in the presence of a drongo sentinel (Wald statistic = 21.01, $df = 1$, $P < 0.001$; Fig. 1G), which might have lessened their likelihood of encountering an already depleted foraging area. Third, individuals were more likely to forage in the open when a drongo sentinel was present (GLMM: Wald statistic = 8.41, $df = 1$, $P = 0.008$; Fig. 1H), thus providing access to a wider, and perhaps higher quality, choice of foraging areas.

The results of the playback experiment were similar to those obtained from the observational data. Babbler foragers spent a smaller proportion of time vigilant during the playback of drongo sentinel calling compared to the playback of background noise (paired t -test: $t = 11.85$, $n = 8$ individuals, $P < 0.001$; Fig. 2A), but this did not result in a greater proportion of time spent foraging ($t = 0.66$, $n = 8$ individuals, $P = 0.529$). However, they did forage more efficiently in response to drongo sentinel calling compared to background noise ($t = 3.12$, $n = 8$ individuals, $P = 0.017$; Fig. 2B), potentially because group members looked up less often ($t = 11.37$, $n = 8$ individuals, $P < 0.001$; Fig. 2C), spread out more widely ($t = 5.06$, $n = 8$ groups, $P = 0.001$;

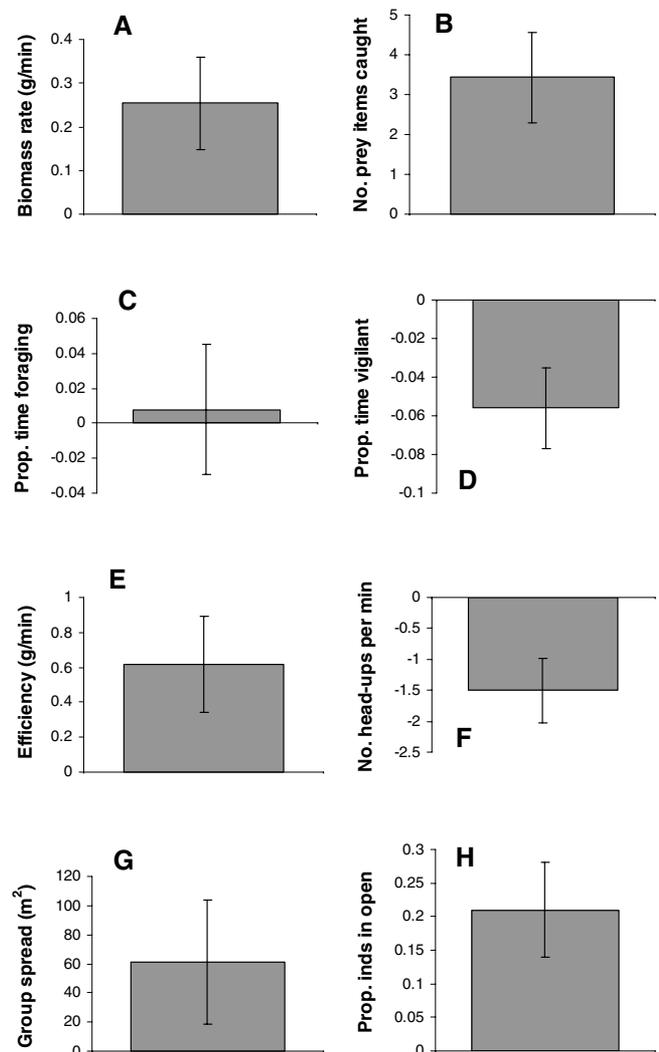


Figure 1. Change in behavior and foraging success of pied babbler foragers following the start of a fork-tailed drongo sentinel bout. (A) Biomass capture rate (amount of food caught per minute of observation time). (B) Number of prey items caught. (C) Proportion of time spent foraging. (D) Proportion of time spent vigilant. (E) Foraging efficiency (amount of food captured per minute of foraging time). (F) Look-up rate. (G) Group spread. (H) Proportion of group foraging in the open. Shown in (A–F) are mean \pm 1 SEM differences between the 2-min periods immediately before and after the start of a drongo sentinel bout for individual babbler foragers ($n = 116$ paired focal periods, 27 individuals); shown in (G) and (H) are mean \pm 1 SEM differences between 0 and 2 min after the start of a drongo sentinel bout by whole babbler groups ($n = 54$ paired scans, 11 groups).

Fig. 2D), and ventured into the open more ($t = 4.12$, $n = 8$ groups, $P = 0.004$; Fig. 2E). Consequently, babbler foragers had a higher biomass capture rate during the playback of drongo sentinel calling compared to the playback of background noise ($t = 2.72$, $n = 8$ individuals, $P = 0.030$; Fig. 2F). These changes in behavior were, however, generally less pronounced than those in response

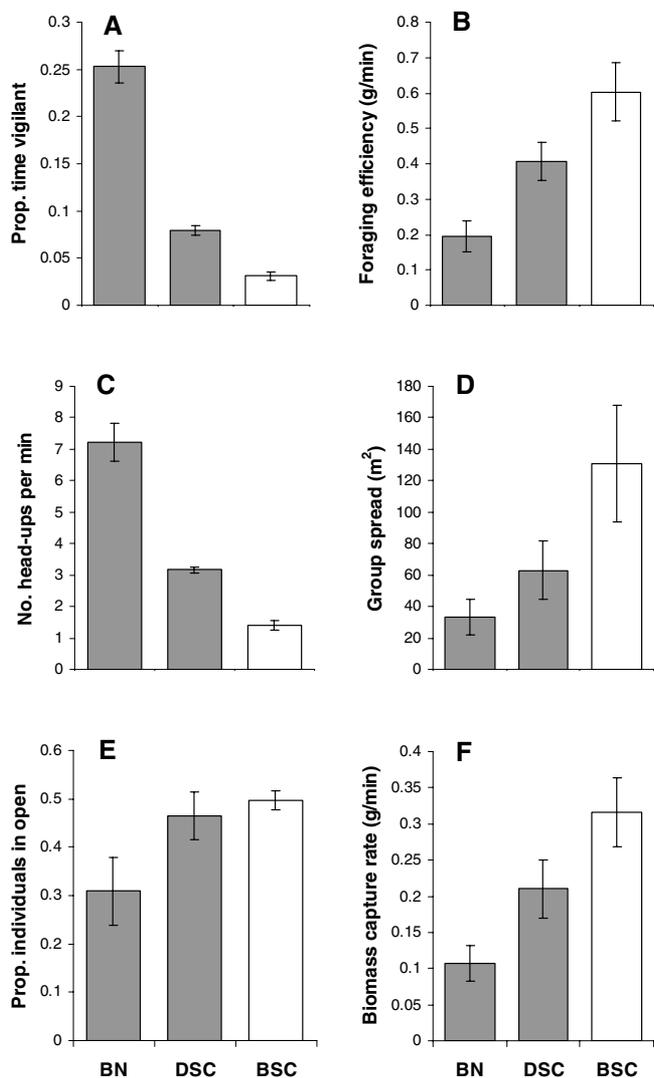


Figure 2. Behavior and foraging success of the same pied babbler foragers in response to different 5-min playback trials. (A) Proportion of time spent vigilant. (B) Foraging efficiency (amount of food captured per minute of foraging time). (C) Look-up rate. (D) Group spread. (E) Proportion of group foraging in the open. (F) Biomass capture rate (amount of food caught per minute of observation time). Shown in gray are the responses to playbacks of background noise (BN) and fork-tailed drongo “sentinel” calling (DSC) (this study). Shown in white are the responses of the same pied babbler foragers to playback of babbler sentinel calling (BSC) (data from Hollén et al. 2008). Means ± 1 SEM are presented for eight individuals in (A–C) and (F), and for eight groups in (D) and (E).

to the playback of a conspecific sentinel (Fig. 2; data from Hollén et al. 2008).

Discussion

We demonstrate that the presence of a fork-tailed drongo giving “sentinel” calls allows pied babbler foragers to capture more food.

This is a rare instance of a parasite actively advertising its presence and thus providing a benefit to its victim, potentially improving its own effectiveness as a parasite. However, we also reveal that the changes to babbler foraging behavior and food capture are less pronounced in response to the calls of drongo “sentinels” than to those of conspecific individuals acting as true sentinels.

Our observational and experimental data indicated that the increased food capture rate of babbler foragers was the consequence of increased foraging efficiency; although babbler individuals reduced their vigilance when foraging in the presence of a heterospecific sentinel (see also Sharpe et al. 2010), they did not spend more time foraging. Our playback experiment also showed that pied babblers can detect drongo sentinels from their vocalizations alone, in the same way that they can use vocal cues to obtain information about the presence and position of conspecific sentinels and foragers (Radford and Ridley 2007; Hollén et al. 2008; Radford et al. 2009), and the current level of risk (Bell et al. 2009). For ground foragers generally unable to use peripheral vision (cf. Bednekoff and Lima 2005), there are clear benefits to using vocalizations in this way: because foraging need not be suspended to check visually, disruption to foraging bouts is minimized. This is likely to be particularly important for species feeding on mobile prey and in marginal habitats where food acquisition has critical effects on fitness (see Clutton-Brock et al. 1998).

Babblers were generally less responsive to drongo calls than to conspecific calls (see Fig. 2). This species-specific effect might arise, in part, from babblers maintaining some vigilance against potential kleptoparasitism when drongos are perched above them. Babblers might also respond less strongly to the calls of drongos if they perceive drongos to be less-reliable alarm callers, because sentinel reliability is known to influence the behavioral decisions of babbler foragers (Radford et al. 2009). Differences in perceived reliability may arise for several reasons. First, drongo sentinels might be less likely than babbler sentinels to detect all predators if drongos spend much of their time watching foragers for potential kleptoparasitism opportunities, rather than scanning for danger. Second, drongos may be less likely than babblers to give alarm calls to terrestrial predators because they themselves are rarely threatened by them (Hockey et al. 2005); drongos do, however, increase their alarm calling to such predators when associating with babbler groups compared to when alone (Ridley et al. 2007). Third, babbler foragers may have limited familiarity with specific individual drongos, because drongos were only observed at babbler groups on average 12% of observation time (Ridley and Raihani 2007). Hence, babblers have fewer opportunities to assess the reliability of particular drongos than they do to determine the reliability of their own group mates; assessment of individual reliability has been previously demonstrated in other species (Blumstein et al. 2004). Babbler foragers may therefore be less prepared to rely on social information from drongo sentinels

compared to that from conspecific sentinels, preferring instead to gather a greater proportion of information through private vigilance (see Jackson and Ruxton 2006).

Eavesdropping on heterospecific alarm calls is common (Magrath et al. 2007, 2009; Templeton and Greene 2007; Goodale et al. 2010), but any benefits arising to the responding species in terms of reduced predation risk are incidental in terms of selection on the caller. Here, we present strong evidence for an interspecific signal that is likely to be adaptive, generated because of the effect it has on the receiver. Continuous vocalization by drongos while waiting to steal food is unexpected because parasites are generally selected to conceal their presence (Davies and Brooke 1988; Spear and Ainley 1993; Lorenzi 2002). Drongos could certainly be less conspicuous by perching silently, so their “sentinel” calling is probably adaptive. It may have evolved as a means of communication between conspecifics, with pied babblers subsequently exploiting the signal. This seems unlikely, however, because drongos are usually solitary foragers, tending to hawk insects from relatively safe perches (Hockey et al. 2005), so the benefits of an intraspecific sentinel system appear limited (cf. Manser 1999; Hollén et al. 2008). Moreover, drongos produce sentinel calls even in the absence of conspecifics (T. Flower, unpubl. data), implying that these vocalizations are not necessarily directed at other drongos. We suggest, therefore, that drongo “sentinel” calling may be a manipulative signal, adapted to exploit the behavior of their victims: foraging babblers venture into the open more and find more prey items in the presence of a calling drongo, which may increase the opportunities for kleptoparasitism.

Increased foraging efficiency in the presence of a drongo sentinel provides babblers with a consistent and continuous benefit. They also obtain more sporadic anti-predator benefits because drongo sentinels give true alarm calls to genuine predators and mob those that present an aerial threat (Ridley et al. 2007). Such mitigating benefits may lower the net cost of parasitism to the extent that there is insufficient selection for defense mechanisms; here, babblers may simply tolerate the periodic presence of kleptoparasitic drongos. Theoretically, the selection pressure on parasites to exploit their victims more effectively could even lead to alterations in behavior that is sufficiently beneficial to the victim to form the basis for a mutualism (Ewald 1987; Roy and Kirchner 2000). In the studied relationship, drongos probably began associating with babblers to steal food. Hypothetically, babblers may then have started to eavesdrop on drongo alarms and alter their foraging behavior in the presence of drongos. This might incidentally have provided additional benefits to more conspicuous drongos, in turn selecting drongos to make themselves more, rather than less, conspicuous and leading to further benefits to babblers.

The likelihood of a parasitism evolving into a mutualism will be influenced by factors such as the exclusivity of the relationship

between parasite and victim, and the extent to which parasite-mediated benefits are influenced by variation in victim ecology (Ewald 1987; Roy and Kirchner 2000). Fork-tailed drongos kleptoparasitize a variety of different species (Hockey et al. 2005) and can thus potentially switch victims when the pay-offs decrease; they are not reliant on pied babblers. Moreover, the value of drongo sentinels to a babbler group declines with increasing group size (Ridley and Raihani 2007). It is clear, therefore, that additional data on the relevant pay-offs are needed to establish the exact current state of the babbler–drongo relationship, and whether both parties are gaining an overall net benefit from the association. In the meantime, our study provides strong evidence that particular parasite behaviors can at least mitigate the cost to victims.

ACKNOWLEDGMENTS

We thank the Kotze family, the Kalahari Research Trust, and T. Clutton-Brock for access to land, the Northern Cape Conservation Authority for permission to conduct research in South Africa, and the Percy FitzPatrick Institute, University of Cape Town for helping to fund the Pied Babbler Project. N. Raihani and M. Nelson-Flower helped establish and maintain the habituated population, and T. Flower, A. Goldsmith, and two anonymous referees provided helpful comments on the manuscript. ANR was funded by a BBSRC David Phillips Fellowship; MBVB by a Junior Research Fellowship from Magdalene College, Cambridge; LIH by a Marie Curie Fellowship; and ARR by the CoE at the Percy FitzPatrick Institute, University of Cape Town.

LITERATURE CITED

- Bednekoff, P. A., and S. L. Lima. 2005. Testing for peripheral vigilance: do birds value what they see when not overtly vigilant? *Anim. Behav.* 69:1165–1171.
- Bell, M. B. V., A. N. Radford, R. Rose, H. M. Wade, and A. R. Ridley. 2009. The value of constant surveillance in a risky environment. *Proc. R. Soc. Lond. B* 276:2997–3005.
- Bell, M. B. V., A. N. Radford, R. A. Smith, A. M. Thompson, and A. R. Ridley. 2010. Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. *Proc. R. Soc. Lond. B* 277:3223–3228.
- Blumstein, D. T., L. Verneyre, and J. C. Daniel. 2004. Reliability and the adaptive utility of discrimination among alarm callers. *Proc. R. Soc. Lond. B* 271:1851–1857.
- Brockmann, H. J., and C. J. Barnard. 1979. Kleptoparasitism in birds. *Anim. Behav.* 27:487–514.
- Clutton-Brock, T. H., D. Gaynor, R. Kinsky, A. D. C. MacColl, G. McIlrath, P. Chadwick, P. N. M. Brotherton, J. M. O’Riain, M. Manser, and J. D. Skinner. 1998. Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. Lond. B* 265:185–190.
- Davies, N. B., and M. D. Brooke. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim. Behav.* 36:262–284.
- Davies, N. B., A. F. G. Bourke, and M. D. Brooke. 1989. Cuckoos and parasitic ants: interspecific brood parasitism as an evolutionary arms-race. *Trends Ecol. Evol.* 4:274–278.
- Davies, N. B., M. D. L. Brooke, and A. Kacelnik. 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc. R. Soc. Lond. B* 263:925–931.
- Ewald, P. W. 1987. Transmission modes and evolution of the parasitism-mutualism continuum. *Ann. Acad. Sci.* 503:295–306.

- Goodale, E., G. Beauchamp, R. D. Magrath, J. Nieh, and G. D. Ruxton. 2010. Interspecific information transfer influences animal community structure. *Trends Ecol. Evol.* 25:354–361.
- Hauber, M. E., P. J. Yeh, and J. O. L. Roberts. 2004. Patterns and coevolutionary consequences of repeated brood parasitism. *Proc. R. Soc. Lond. B* 271:S317–S320.
- Hockey, P. A. R., W. R. J. Dean, and P. G. Ryan. 2005. Robert's birds of southern Africa, 7th edition. The Trustees of the John Voelcker Bird Fund, Cape Town.
- Hollén, L. I., M. B. V. Bell, and A. N. Radford. 2008. Cooperative sentinel calling? Foragers gain increased biomass intake. *Curr. Biol.* 18:576–579.
- Hosoi, S. A., and S. I. Rothstein. 2000. Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Anim. Behav.* 59:823–840.
- Jackson, A. L., and G. D. Ruxton. 2006. Toward an individual level understanding of vigilance: the role of social information. *Behav. Ecol.* 17:532–538.
- Lorenzi, M. C. 2002. Concealing identity and mimicking hosts: a dual chemical strategy for a single social parasite? *Parasitology* 125:507–512.
- Magrath, R. D., B. J. Pitcher, and J. L. Gardner. 2007. A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behav. Ecol.* 18:944–951.
- . 2009. Recognition of other species' alarm calls: speaking the same language or learning another? *Proc. R. Soc. Lond. B* 276:769–774.
- Manser, M. B. 1999. Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. *Proc. R. Soc. Lond. B* 266:1013–1019.
- Maxson, S. J., and N. P. Bernstein. 1982. Kleptoparasitism by south polar skuas on blue-eyed shags in Antarctica. *Wilson Bull.* 94:269–281.
- Morand-Ferron, J., D. Sol, and L. Lefebvre. 2007. Food stealing in birds: brain or brawn? *Anim. Behav.* 74:1725–1734.
- Munn, C. A. 1986. Birds that cry wolf. *Nature* 319:143–144.
- Radford, A. N., and A. R. Ridley. 2006. Recruitment calling: a novel form of extended parental care in an altricial species. *Curr. Biol.* 16:1700–1704.
- . 2007. Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance. *Biol. Lett.* 3:249–252.
- . 2008. Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Anim. Behav.* 75:519–527.
- Radford, A. N., L. I. Hollén, and M. B. V. Bell. 2009. The higher the better: sentinel height influences foraging success in a social bird. *Proc. R. Soc. Lond. B* 276:2437–2442.
- Raihani, N. J., and A. R. Ridley. 2007. Adult vocalisations during provisioning: offspring response and postfledging benefits in wild pied babblers. *Anim. Behav.* 74:1303–1309.
- Ridley, A. R., and M. F. Child. 2009. Specific targeting of host individuals by a kleptoparasitic bird. *Behav. Ecol. Sociobiol.* 63:1119–1126.
- Ridley, A. R., and N. J. Raihani. 2007. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behav. Ecol.* 18:324–330.
- Ridley, A. R., M. F. Child, and M. B. V. Bell. 2007. Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird. *Biol. Lett.* 3:589–591.
- Roy, B. A., and J. W. Kirchner. 2000. Evolutionary dynamics of pathogen resistance and tolerance. *Evolution* 54:51–63.
- Satischandra, S. H. K., P. Kodituwakku, S. W. Kotagama, and E. Goodale. 2010. Assessing “false” alarm calls by a drongo (*Dicrurus paradiseus*) in mixed-species flocks. *Behav. Ecol.* 21:396–403.
- Sharpe, L. L., A. S. Joustra, and M. I. Cherry. 2010. The presence of an avian co-forager reduces vigilance in a cooperative mammal. *Biol. Lett.* 4:475–477.
- Sheldon, B. C., and S. Verhulst. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends Ecol. Evol.* 11:317–321.
- Spear, L., and D. G. Ainley. 1993. Kleptoparasitism by kermadec petrels, jaegers, and skuas in the eastern tropical Pacific: evidence of mimicry by two species of *Pterodroma*. *Auk* 110:222–233.
- Templeton, C. N., and E. Greene. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proc. Natl. Acad. Sci. USA* 104:5479–5482.
- Tershy, B. R., and D. Breese. 1990. The influence of sexual dimorphism on kleptoparasitism of blue-footed boobies by brown boobies. *Can. J. Zool.* 68:197–199.
- Wickler, W. 1985. Coordination of vigilance in bird groups: the “watchman's song” hypothesis. *Z. Tierpsychol.* 69:250–253.

Associate Editor: C. Goodnight