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Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird

Amanda R. Ridley[1,*], Matthew F. Child[1] and Matthew B. V. Bell[2]

[1]*Percy Fitzpatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch, Cape Town 7701, Republic of South Africa*
[2]*Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*
Author for correspondence (amanda.ridley@uct.ac.za).

Audience effects are increasingly recognized as an important aspect of intraspecific communication. Yet despite the common occurrence of interspecific interactions and considerable evidence that individuals respond to the calls of heterospecifics, empirical evidence for interspecific audience effects on signalling behaviour is lacking. Here we present evidence of an interspecific audience effect on the alarm-calling behaviour of the kleptoparasitic fork-tailed drongo (*Dicrurus adsimilis*). When foraging solitarily, drongos regularly alarm at aerial predators, but rarely alarm at terrestrial predators. In contrast, when drongos are following terrestrially foraging pied babblers (*Turdoides bicolor*) for kleptoparasitic opportunities, they consistently give alarm calls to both aerial and terrestrial predators. This change occurs despite no difference in the amount of time that drongos spend foraging terrestrially. Babblers respond to drongo alarm calls by fleeing to cover, providing drongos with opportunities to steal babbler food items by occasionally giving false alarm calls. This provides an example of an interspecific audience effect on alarm-calling behaviour that may be explained by the benefits received from audience response.

Keywords: alarm calls; kleptoparasitism; audience effect; fork-tailed drongo; pied babbler

1. INTRODUCTION

Audience effects, where a signaller uses a signal differently depending on the composition of its audience, can provide valuable insight into the complex ways that external factors influence signalling behaviour (Marler & Evans 1996). Previous research on audience effects has focused primarily on intraspecific interactions (e.g. Doutrelant *et al.* 2001; Striedter *et al.* 2003; Radford & Ridley 2006). However, where interspecific associations are common, such as in mixed-species flocks, interspecific audience effects on signalling behaviour may occur (Munn 1986; Goodale & Kotagama 2005).

Alarm calls provide a good opportunity to observe interspecific audience effects because when two species have predators in common, they may benefit from responding to each other's alarm calls (Cheney & Seyfarth 1990; Rainey *et al.* 2004), allowing individuals to reduce their investment in vigilance behaviour or increase the probability of escaping predation (Griffin *et al.* 2005; Ridley & Raihani 2007). In such situations, the caller may use the response of others to their benefit, for example by displacing rivals from food sources (Munn 1986; Ridley & Raihani 2007). To achieve this benefit, the caller may be more likely to give alarm calls to predators that threaten their audience, even if the predator is not a direct threat to the caller, in order to establish themselves as reliable indicators of predator risk. The caller may then use dishonest signals (e.g. false alarm calls) to exploit receivers. Despite sound theoretical models supporting this type of interaction (e.g. Rowell *et al.* 2006), empirical evidence is lacking.

In this paper we investigate the alarm-calling behaviour of the kleptoparasitic fork-tailed drongo (*Dicrurus adsimilis*), a passerine bird that forages both solitarily and by kleptoparasitizing food from terrestrially foraging species such as pied babblers (*Turdoides bicolor*; Ridley & Raihani 2007). When following pied babblers, drongos perch above the group and give alarm calls when a predator is sighted, causing the group to alert and commonly move to cover (Ridley & Raihani 2007). However, drongos also occasionally give alarm calls when no predator is present (false calls), which elicit a similar response as true alarm calls, allowing drongos to swoop down and steal food items dropped by fleeing babblers (Ridley & Raihani 2007). Here we investigate whether drongos change their alarm-calling behaviour when following pied babblers compared with when foraging solitarily, and whether this change may be affected by the benefits received from audience response.

2. MATERIAL AND METHODS

(a) *Study species*
Pied babblers are medium-sized (75–95 g) cooperatively breeding passerines (average group size during study = 3.5 ± 0.4 adults, range 2–6). They are primarily terrestrial foragers (more than 95% of foraging time spent on the ground); since individuals use their bills to dig in the substrate for prey, they cannot forage and remain vigilant simultaneously (Ridley & Raihani 2007). Foraging babblers therefore rely on alarm calls from sentinels (individuals scanning the horizon from greater than 1 m above the foraging group) to alert them to the presence of predators (Ridley & Raihani 2007).

Drongos (45–65 g) are solitary foragers that periodically invest in interspecific kleptoparasitic behaviour (Ridley & Raihani 2007). During solitary foraging, they primarily capture prey on the wing (aerial hawking), and their most common food items include orthopteran and lepidopteran species (M. Child 2006, unpublished data). The food items kleptoparasitized by drongos are usually subterranean prey dug up by their host species, including beetle and moth larvae, solifugids and scorpions.

(b) *Data collection*
A 10-min focal watch was conducted on each ringed, habituated drongo (*n* = 17 drongos) twice a week using handheld data loggers. During each focal watch, we noted foraging mode (solitary or kleptoparasitic, see electronic supplementary material for foraging mode definitions), perch height (m) and foraging success. All drongos used both foraging modes, and we conducted a minimum of six focals for each foraging mode per individual (mean 9.9 ± 1.5, range 6–15 focals per foraging mode per individual). A drongo was considered vigilant (rather than foraging) when it was scanning the horizon from an elevated position, and considered foraging when it was aerially hawking prey, pecking at a substrate, or picking prey off

the ground. For each prey item captured, we recorded item size (for size classification, see Raihani & Ridley (in press)) and location of capture (terrestrial or aerial). Prey items were converted to biomass values by weighing 50 prey items representative of each size class.

When a predator was seen, we recorded predator type (aerial or terrestrial) and drongo response ('alarm' or 'no alarm'). Pied babbler response to each drongo alarm call was recorded as 'response' or 'no response'. Pied babblers were considered to have responded, if at least 50% of group members alarmed and took flight, or immediately fled to cover. In all cases where babblers responded to a drongo alarm call, the immediate response was to move to cover rather than towards the predator. Since predator distance may affect alarm-calling behaviour (Leavesley & Magrath 2005), alarm call data were confined to predators less than 100 m from the focal drongo at the time of alarm. Yellow and slender mongoose (*Cynictis penicillata* and *Galerella sanguinea*) were considered the primary terrestrial predators at the study site, accounting for more than 80% of all terrestrial predator sightings (see electronic supplementary material for a detailed predator list).

(c) *Analysis*

All analyses are based on 349 focal watches. We used non-parametric matched-pairs comparisons to investigate differences in drongo behaviour between foraging modes. First, we compared the proportion of observation time spent foraging terrestrially between foraging modes for each individual drongo. Second, we calculated the number of predator sightings that were associated with an alarm call as a proportion of total predator sightings for each category (aerial or terrestrial) for each drongo and compared these between foraging modes. Third, we calculated the total biomass caught as a proportion of total foraging time and compared this value between foraging modes for each drongo.

3. RESULTS

Drongos spent a high proportion of time foraging (table 1), but for both foraging modes very little time was spent foraging terrestrially (average $8.9 \pm 0.8\%$ of foraging time, range 0–17.3%), with no difference in terrestrial foraging behaviour between foraging modes (Wilcoxon matched-pairs test: $Z_{16} = 0.19$, $p = 0.82$; table 1). Despite this, there were considerable differences in alarm-calling behaviour (table 1). When foraging solitarily, drongos rarely alarm called at terrestrial predators (2 calls/33 sightings), but regularly did so when following pied babbler groups (41 calls/47 sightings, $Z_{15} = 3.07$, $p = 0.02$). In contrast, drongos consistently gave alarm calls to a high proportion of all aerial predator sightings, and this behaviour was unaffected by foraging mode (solitary, 43 calls/47 sightings; kleptoparasitic, 64 calls/67 sightings; $Z_{15} = 0.21$, $p = 0.83$). It is unlikely that this effect occurred owing to a difference in proximity to terrestrial predators because there was no difference in drongo perch height between foraging modes ($Z_{16} = 1.24$, $p = 0.213$).

Pied babblers commonly responded to drongo alarm calls (87% response to 105 true alarm calls by 16 drongos at nine babbler groups), and this response was important to the success of kleptoparasitism attempts (92.7% of 55 cases of successful kleptoparasitism by 15 drongos were preceded by a false alarm call). The prey items that drongos captured via kleptoparasitism were substantially larger than those captured during solitary foraging ($Z_{15} = 3.06$, $p = 0.002$). However, owing to the lower frequency and success of kleptoparasitism events, there was no difference in the average biomass captured per unit time between foraging modes ($Z_{15} = 1.79$, $p = 0.64$; table 1).

Table 1. Summary of drongo behaviour according to foraging mode. (Means ($\pm$s.e.) represent averages for all drongos combined.)

behaviour	foraging mode	
	solitary	kleptoparasitic
proportion of observation time spent foraging		
aerial and terrestrial foraging combined	0.83 (0.03)	0.49 (0.07)
terrestrial foraging only	0.05 (0.01)	0.04 (0.02)
average perch height (m)	4.28 (0.56)	3.70 (0.32)
proportion of observation time spent vigilant	0.06 (0.02)	0.38 (0.07)
alarm calls given/total predator sightings		
aerial predators	0.92 (0.14)	0.95 (0.15)
terrestrial predators	0.06 (0.19)	0.87 (0.15)
average mass of items caught (g)	0.28 (0.04)	0.72 (0.39)
biomass captured (g) per hour	1.61 (1.40)	3.49 (5.20)

4. DISCUSSION

Despite no difference in the time spent foraging terrestrially (and thus exposed to terrestrial predators), drongos gave alarm calls to terrestrial predators more often when following pied babbler groups. This difference may be explained by the benefits received from audience response. Drongos foraging solitarily regularly alarmed at aerial predators providing support for the idea that individuals may use alarm calls as signals to warn approaching predators that they have been detected (Zahavi 1977; Bergstrom & Lachmann 2001). Since solitary drongos primarily forage by hawking aerial prey, terrestrial predators are unlikely to pose a threat to them, and thus there is little benefit in giving an alarm call to this predator type. In contrast, drongos following pied babbler groups benefit from giving alarm calls to terrestrial predators because these predators are a direct threat to their host species (Ridley & Raihani 2007). While drongos in kleptoparasitic mode spent a greater proportion of time vigilant, potentially increasing the likelihood of detecting terrestrial predators, this is unlikely to affect the results presented here because (i) self-foraging drongos alarmed at a high proportion of observed aerial predators, suggesting that they were able to effectively detect predators and (ii) the proportional increase in terrestrial predator alarms during kleptoparasitic foraging was not paired with an increase in aerial predator alarms.

Providing their audience with reliable information about the presence of terrestrial predators may benefit drongos in two ways: (i) it may make babblers more tolerant of drongos and (ii) it may make babblers more responsive to future drongo alarm calls. While it is possible that an individual may be more likely to alarm if those around it are already alarming (Seyfarth & Cheney 2003), it is unlikely that this explains the observed variation in drongo alarm-calling behaviour because when drongos are present, pied babblers rely on drongo alarm calls and invest less time in vigilance

themselves (Ridley & Raihani 2007), and thus rarely detect predators before drongos.

Since the low frequency of kleptoparasitic attacks (compared with solitary foraging attempts) results in no difference in rate of biomass capture between foraging modes, the selective advantage of a variable alarm-calling strategy appears unclear. However, obtaining food via kleptoparasitism may benefit drongos in several ways. First, drongos gain access to subterranean foods with higher energy content than aerial prey (e.g. beetle larvae; Illgner & Nel 2000), that are not normally accessible to them. Second, during inclement weather when aerial prey is at low densities, drongos can switch to kleptoparasitism of terrestrial prey as an alternative foraging technique (M. Child 2006, unpublished data).

This study provides one of the first examples of an interspecific audience effect on alarm-calling behaviour and, given the common occurrence of interspecific interactions (e.g. Goodale & Kotagama 2005), this behaviour is likely to be more widespread than currently realized. The behavioural interaction presented here provides empirical support for the model recently developed by Rowell *et al.* (2006), which predicts that where a signal is beneficial to the audience (e.g. for predator detection), the signaller can use a non-trivial frequency of dishonesty (e.g. false alarm calls) without causing listeners to lose belief.

Bergstrom, C. T. & Lachmann, M. 2001 Alarm calls as costly signals of antipredator vigilance: the watchful babbler game. *Anim. Behav.* **61**, 535–543. (doi:10.1006/anbe.2000.1636)

Cheney, D. L. & Seyfarth, R. M. 1990 *How monkeys see the world: inside the mind of another species.* Chicago, IL: University of Chicago Press.

Doutrelant, C., McGregor, P. K. & Oliveira, R. F. 2001 The effects of an audience on intrasexual communication in male Siamese fighting fish, *Betta splendens. Behav. Ecol.* **12**, 283–286. (doi:10.1093/beheco/12.3.283)

Goodale, E. & Kotagama, S. W. 2005 Alarm-calling in mixed-species bird flocks. *Auk* **22**, 108–120. (doi:10.1642/0004-8038(2005)122[0108:ACISLM]2.0.CO;2)

Griffin, A. S., Savani, R. S., Hausmanis, K. & Lefebvre, L. 2005 Mixed species aggregations in birds: zenaida doves *Zenaida aurita*, respond to the alarm calls of carib grackles, *Quiscalus lugubris. Anim. Behav.* **70**, 507–515. (doi:10.1016/j.anbehav.2004.11.023)

Illgner, P. & Nel, E. 2000 The geography of edible insects in sub-Saharan Africa: a study of the mopane caterpillar. *Geogr. J.* **166**, 336–351. (doi:10.1111/j.1475-4959.2000.tb00035.x)

Leavesley, A. J. & Magrath, R. D. 2005 Communicating about danger: urgency alarm calling in a bird. *Anim. Behav.* **70**, 365–373. (doi:10.1016/j.anbehav.2004.10.017)

Marler, P. & Evans, C. 1996 Bird calls: just emotional displays or something more? *Ibis* **138**, 26–33.

Munn, C. A. 1986 Birds that cry wolf. *Nature* **319**, 143–145. (doi:10.1038/319143a0)

Radford, A. N. & Ridley, A. R. 2006 Recruitment calling: a novel form of extended parental care in an altricial species. *Curr. Biol.* **16**, 1700–1704. (doi:10.1016/j.cub.2006.06.053)

Raihani, N. J. & Ridley, A. R. In press. Adult vocalisations during provisioning: offspring responses and post-fledging benefits in wild pied babblers. *Anim. Behav.*

Rainey, H. J., Zuberbühler, K. & Slater, P. J. B. 2004 Hornbills can distinguish between primate alarm calls. *Proc. R. Soc. B* **271**, 755–759. (doi:10.1098/rspb.2003.2619)

Ridley, A. R. & Raihani, N. J. 2007 Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behav. Ecol.* **18**, 324–330. (doi:10.1093/beheco/arl092)

Rowell, J. T., Ellner, S. T. & Reeve, H. K. 2006 Why animals lie: how dishonesty and belief can coexist in a signalling system. *Am. Nat.* **168**, E180–E204. (doi:10.1086/508809)

Seyfarth, R. M. & Cheney, D. L. 2003 Signalers and receivers in animal communication. *Annu. Rev. Psychol.* **54**, 145–173. (doi:10.1146/annurev.psych.54.101601.145121)

Striedter, G. M., Freibott, L., Hile, A. G. & Burley, N. T. 2003 For whom the male calls: an effect of audience on contact call rate and repertoire in budgerigars, *Melopsittacus undulatus. Anim. Behav.* **65**, 875–882. (doi:10.1006/anbe.2003.2135)

Zahavi, A. 1977 The cost of honesty (further remarks on the handicap principle). *J. Theor. Biol.* **67**, 603–605. (doi:10.1016/0022-5193(77)90061-3)