



# Vocal Mimicry of Alarm-Associated Sounds by a Drongo Elicits Flee and Mobbing Responses from Other Species that Participate in Mixed-Species Bird Flocks

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## Abstract

A growing number of studies have shown that vocal mimicry appears to be adaptive for some bird species, although the exact function of this behaviour varies among species. Previous work has looked at the function of the vocal mimicry of non-alarm sounds by the Greater Racket-tailed Drongo (*Dicurus paradiseus*). But drongos also imitate sounds associated with danger, such as predators' vocalisations or the mobbing-specific vocalisations of other prey species, raising the question of whether the function of mimicry can vary even within a species. In a playback experiment, we compared the effect on other species of different drongo vocalisations including: (1) predator mimicry, (2) mobbing mimicry, (3) drongo species-specific alarms, (4) drongo species-specific non-alarms and (5) a control (barbet) sound. Both mobbing mimicry and drongo species-specific alarms elicited flee responses from the most numerous species in the flocks, the Orange-billed Babbler (*Turdoides rufescens*). Mobbing mimicry also elicited mobbing responses from the Orange-billed Babbler and from another gregarious babbler, the Ashy-headed Laughingthrush (*Garrulax cinereifrons*); when responses from both species were considered together, they were elicited at a significantly higher level by mobbing mimicry than by the barbet control, and a level that tended to be higher ( $0.07 < p < 0.10$ ) than the response to drongo-specific alarms. Predator mimicry elicited flee and mobbing responses at an intermediary level. Our results support the hypotheses that mobbing mimicry is a specific category of mimicry that helps attract the aid of heterospecifics during mobbing and that alarm mimicry can in some cases be beneficial to the caller.

## Introduction

Bird song learning has become a model of vocal learning, illustrating the interaction between innate tendencies and environmental influences, as it has been shown that while birds can learn many different vocalisations, they tend to learn some vocalisations, specifically conspecific ones, better than others, such as heterospecific vocalisations (Marler & Peters 1987). Interestingly, however, the strength of this filter varies: while some species almost never sing heterospecific songs, others do quite frequently (Vernon 1973). The benefits of such vocal mimicry are controversial

(Baylis 1982). Two recent reviews found that there was 'little evidence for vocal mimicry having evolved to serve important functions in most birds' (Gámszegi et al. 2007), and 'there is no compelling evidence to support any of the functional hypotheses' (Kelley et al. 2008), although both these reviews emphasised that their conclusions were based on a small number of studies.

One potential problem in assigning a single function to vocal mimicry is that it has been shown to have different functions in different species. In some brood parasitic species, for example, male birds imitate the songs of their host species, which allows females to

identify and mate with the correct species (Payne et al. 2000). Mimicry might help birds attract mates in other species, if females prefer males that use imitations to increase the size of their repertoires (Howard 1974), and/or judge the quality of males based on the accuracy of their imitation (Coleman et al. 2007; Zann & Dunstan 2008). These functions of mimicry have conspecific audiences, but other putative functions of mimicry have heterospecific audiences. For example, some birds could repel heterospecific competitors from their territory (Rechten 1978), although this hypothesis has yet to be supported by field data. A recent study did, however, demonstrate that birds in mixed-species groups can use the mimicry of alarm calls to scare other species away from food (Flower 2011). Mimicry can also be used to decrease the risk of predation, either by increasing the mobbing activity of other species of birds (Chu 2001) or by confusing or startling the predator itself, especially if the mimicry suggests the presence of another predator that might prey on the predator the calling bird is interacting with (Igic & Magrath 2013).

Previous research on the Greater Racket-tailed Drongo (*Dicrurus paradiseus lophorhinus*) has shown that this species uses mimicry in a variety of contexts and in a context-specific manner (Goodale & Kotagama 2006a), raising the question of whether vocal mimicry can serve different functions even within a species. The imitation of non-alarm vocalisations of other species, which drongos incorporate into their own species-typical non-alarm vocalisations, is attractive to other species and may help drongos reform mixed-species flocks (Goodale & Kotagama 2006b), from which drongos benefit (Satischandra et al. 2007). Drongos also incorporate sounds associated with danger (hereafter referred to as 'danger mimicry') into their own species-typical alarm vocalisations. Danger mimicry includes the imitation of the vocalisations (usually advertisement or contact calls) of predators and nest predators ('predator mimicry'), and the imitation of other (non-predator) species' mobbing vocalisations ('mobbing mimicry') and alarm calls in response to aerial predators ('aerial alarm mimicry', Goodale & Kotagama 2005). Given that animals have been shown to respond to different kinds of alarm calls in different ways (i.e. the idea of 'referential alarm calls', Seyfarth et al. 1980) and that they may respond to predator vocalisations differently than the alarm calls of prey species (Barrera et al. 2011), it is possible that these various forms of danger mimicry could have separate functions.

Here, we test the hypothesis that danger mimicry functions to affect the behaviour of other species that

participate with drongos in mixed-species flocks. In a playback experiment, we compared five different treatments that included different drongo vocalisations: (1) predator mimicry, (2) mobbing mimicry, (3) species-specific alarms, (4) species-specific non-alarms and a (5) control sound. We looked at both immediate flee responses to playback and more delayed mobbing responses, when birds grouped together and approached the speaker. For the immediate responses, we chose as subjects Orange-billed Babblers (*Turdoides rufescens*), the most numerous species in mixed-species flocks (Kotagama & Goodale 2004), which respond to heterospecific alarms immediately by jumping or flying into vegetation (Goodale & Kotagama 2008). We noted any delayed mobbing response from any flock participant.

We specifically hypothesised that (1) drongo mimicry of predators may be used by drongos to startle other species away from food resources (similar to the result of Flower 2011). This hypothesis predicts that babblers would immediately flee into vegetation upon the playback of predator mimicry. Further, we hypothesised that (2) drongo mimicry of other species' mobbing vocalisations may be used to dilute the risk of mobbing to drongos by increasing the mobbing of other species (Chu 2001). This hypothesis predicts that other species would make a mobbing response specifically to the playback of mobbing mimicry. Both hypotheses predict that response to mimicry should be higher than response to the drongo species-specific alarm notes, because otherwise drongos might be better served using their own species-specific vocalisations instead of mimicry.

## Methods

### Study Site

This study was conducted in the Sinharaja World Heritage Reserve (6°26'N 80°21'E, 450–600 m), the most extensive remaining lowland rainforest in Sri Lanka. Mixed-species bird flocks in Sinharaja average 11 species and nearly 41 individuals (in an average of 45 minutes of observation, Kotagama & Goodale 2004). These flocks are led by the highly gregarious Orange-billed Babbler, but Greater Racket-tailed Drongos are also found in a high percentage of them (89%) and occasionally lead the flocks.

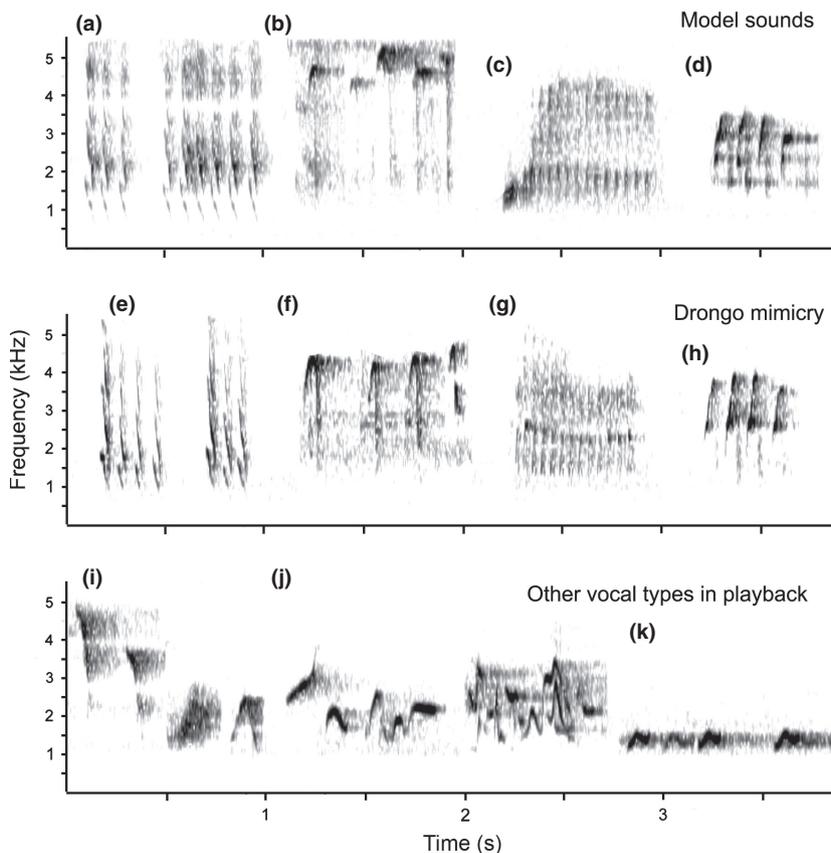
### Construction of Playback Exemplars

The majority of the audiorecordings used for making the playback exemplars were made during a

simultaneous study that concentrated on mimicry by drongos at the nest (during the nesting season, January – April, 2008 and 2009, Goodale et al. 2014), and the vocal development of juvenile drongos (between April and August of 2008). Drongos make nests year-after-year in the same trees (for similar behaviour in another drongo species, see Li et al. 2009), and we considered the nesting tree as the unit of replication. During the nesting season, recordings were made from a natural hide 10–15 m from the nest or fledgling birds, as well as in mixed-species flocks >50 m from the nest, to compare the frequency of mimicry in these different contexts (a total of 682 recordings, 86 of which were in flocks, Goodale et al. 2014). As many as three two-minute recordings were taken at a nest or in a flock per day (for more detail, see Goodale et al. 2014). As to the juvenile birds, four sets of young drongos from the breeding study were marked in the nest and then they and their unmarked parents were followed for several months (939 recordings). The vocalisations of the juveniles were rudimentary (i.e. begging calls) until late in the sampling period and were not analysed or included in the playback exemplars; however, recordings of their parents were

included. These consisted of 2-min recordings taken randomly throughout the day and some opportunistic recordings of adult drongos vocalising when young were present, both in mixed-species flocks and outside of them. All recordings were made at a sampling rate of 22.5 kHz on a Marantz PMD 670 hard-disk recorder attached to a Telinga parabola and Sennheiser ME 62 microphone.

In listening to these recordings, each recording was scored for the presence of drongo species-specific alarm notes or species-specific non-alarm notes, following Goodale & Kotagama (2006a). We also scored each recording as to whether it included the three types of danger mimicry we have previously described: predator mimicry, mobbing mimicry and aerial alarm mimicry (Goodale & Kotagama 2005), by comparing spectrograms of the mimicry (made with Hann window, 512 FFT) to spectrograms of the putative models, using Raven, version 1.4 (Cornell Laboratory of Ornithology, Ithaca, NY, Fig. 1). The identity of aerial alarm and mobbing vocalisations was made while working on an earlier project describing alarm calling in mixed-species flocks (Goodale & Kotagama 2005); mobbing vocalisations were those made in



**Fig. 1:** The sounds imitated by Greater Racket-tailed Drongos (*Dicrurus paradiseus lophorinus*), drongo mimicry and other vocalisations used in playback. Model sounds included several specific vocalisations made during mobbing by several species – (a) Orange-billed Babbler (*Turdoides rufescens*) ‘staccato chatter’ (b) Ashy-headed Laughing-thrush (*Garrulax cinereifrons*) ‘high-pitch emphasis’ (c) Sri Lanka Scimitar Babbler (*Pomatorhinus melanurus*) ‘bring call’ – and (d) the advertising call of Mountain Hawk Eagle (*Nisaetus nipalensis kelaarti*), also imitated by the nest predator Sri Lanka Magpie (*Urocissa ornata*), as here. Imitations of these vocalisations by drongos are shown from (e) to (h). Other vocalisation types used in playback included (i) drongo species-specific alarms (j) drongo species-specific non-alarms and (k) the song of the Yellow-fronted Barbet (*Megalaima flavifrons*).

response to the presence of terrestrial predators such as mongooses, dogs and snakes (E. Goodale, personal observations).

While we identified recordings of all three types of danger mimicry in the sample, aerial alarm call mimicry was rare (Goodale et al. 2014) and the recordings were of poor quality, so we did not include an aerial alarm mimicry treatment in the experiment. We selected as the control sound the loud and continuous vocalisations of the Yellow-fronted Barbet (*Megalaima flavifrons*; Fig. 1); recordings of this species were made over 10 yr throughout the Sinharaja Reserve.

In making the playback exemplars, our goal was to use natural recordings that only contained vocalisations of one of the four drongo treatments (species-specific alarms, predator mimicry, mobbing mimicry and species-specific non-alarms). Specifically, we selected segments of recordings that had a continuous 20 s of vocalisations of the particular treatment, no vocalisations of other treatments and no more than 10 s of continuous silence. For each of the five treatments, we used seven exemplars recorded at different nesting trees and therefore representing different individuals. There were many potential recordings of drongo species-specific alarm and non-alarm vocalisations (473 and 213 recordings, respectively), and these recordings were selected randomly within nesting trees, using the above criteria. In contrast, mimicry was relatively rare (134 recordings for predator mimicry and 21 recordings for mobbing mimicry). We supplemented the pool of recordings for mimicry with high-quality recordings made in the Sinharaja Reserve within the previous 10 yr, using one older recording for predator mimicry and four older recordings for mobbing mimicry; these older recordings were only selected if they were made near (approximately 250 m) one of the nesting trees, to again ensure the representation of different individuals (the nests themselves were, with one exception, more than 500 m from each other).

Playback exemplars were made using Raven, version 1.4. Each exemplar consisted of 15 s of background noise followed by 30 s of drongo vocalisations, followed by another 15 s of background noise and a subsequent 30 s of drongo vocalisations, for a total of 90 s. Playback exemplars could be made from no more than three different recordings, all from the same nesting tree. The playback exemplars of mobbing mimicry all contained imitations of the mobbing vocalisations of the Orange-billed Babbler and the Ashy-headed Laughing-thrush (*Garrulax cinereifrons*), a ground and understory dwelling species quite

sensitive to ground predators, and three exemplars included the mobbing vocalisations of the Sri Lanka Scimitar Babbler (*Pomatorhinus melanurus*; Fig 1). In making the playback exemplars of predator mimicry, we decided to only include mimicry of the Mountain Hawk Eagle (*Nisaetus nipalensis kelaarti*), a raptor that is also imitated in the same forest by the Sri Lanka Magpie (*Urocissa ornata*) itself a nest predator (Ratnayake et al. 2010). This is the most common form of predator mimicry recorded in the forest (Goodale & Kotagama 2005; Goodale et al. 2014); we were unsure if other types of predator mimicry (e.g. mimicry of the nest predator Sri Lanka Toque Macaque *Macaca sinica*) would have similar effects to the Mountain Hawk Eagle vocalisation and thus decided to limit the variation within this treatment.

### Conducting Playback Trials

To conduct a playback trial, we first encountered a flock on ~ a 15-km network of paths and old logging trails inside the Sinharaja World Heritage Reserve. For each flock, we conducted a total of 5 playback trials, in random order; the playback exemplars presented to one flock were all made at the same nesting tree. To ensure independence, we then did not conduct playback with another flock that was encountered within the same 250 m of path. Although flocks can move further than this, different individuals move in and out of the flock as it moves and individuals rarely move more than 250 m; thus, the 250-m criterion makes it unlikely that individuals were tested repeatedly in the same treatment. A single playback speaker made by Mineroff Electronics (Elmont, NY) was carried at shoulder level. When the two observers had been following a flock for at least 15 minutes, they then began a trial by selecting a focal Orange-billed Babbler approximately 10 m away (babblers average 16 individuals per flock, so one can usually be found close by). One observer watched the focal bird with binoculars while the second observer sound recorded the whole trial on the same recording equipment mentioned above. Then, the observer with the binoculars turned on the playback speaker. The playback exemplar was played at a peak volume of 90 dB re 20  $\mu$ Pa measured at 1 m by a Realistic Sound Level Meter (now Radio Shack Brands, Fort Worth, TX), with the majority of the sound being approximately 86 dB re 20  $\mu$ Pa at 1 m. Such a playback volume was judged by ear to be similar to the natural production of this mimicry by drongos.

We watched for both 'immediate' flee (<5 s from the beginning of playback) and 'delayed' mobbing

responses (from 5 s to the end of the trial). We noted flee movements of flying or jumping away from the speaker into thicker vegetation; because this movement was sudden and the observer was using binoculars and thus had a limited field of view, we only noted the responses of the focal Orange-billed Babbler. The observer then watched for a mobbing response, including non-focal individuals, in which birds bunched together and then began to move towards the speaker, until the end of the trial, which occurred 30 s after the end of the playback. After a trial was finished, the observers would follow the flock, waiting 15 minutes until they tried a trial of another treatment. In some cases, we were unable to complete all five treatments for one flock; if this happened, we then finished the remaining treatments in a separate 'replacement' flock, used only for these replacement trials. Each of the seven playback exemplars for a treatment was played three times, for a total of 21 trials per treatment, using 27 flocks. Trials were conducted between 22 February and 29 April 2009.

### Statistical Analysis

For the immediate responses, we scored a response as a 1 if the focal Orange-billed Babbler moved quickly into the vegetation and a 0 if there was a lack of such a response (Goodale & Kotagama 2008). For the delayed responses, we scored a response 1 if a bird (including a non-focal individual of any species) moved close to other individuals and slowly approached the speaker; a lack of this response was scored 0.

We used generalised linear mixed models with a binomial error distribution to analyse this data. Models included the random factors of (1) playback exemplar (the nest at which the playback was made) and (2) flock to which the playback was conducted, as well as the fixed factors of (3) treatment and (4) order. A potential problem with this model is that not all flocks had all five treatments played to them. To investigate the potential effect of this problem, we conducted an additional, hypothetical analysis in which there were only 21 flocks (each replacement flock was treated as if it was the flock it replaced).

Models were run in R, version 3.0.1 (R Core Team 2013), using library lme4 (Bates et al. 2011); they were followed by multiple comparisons using the library multcomp (Bretz et al. 2010), adjusting the experiment-wide p-values by the Tukey Honestly Significant Difference method. Comparison of full versus reduced models showed that the factor of order did not significantly contribute to the overall model (for

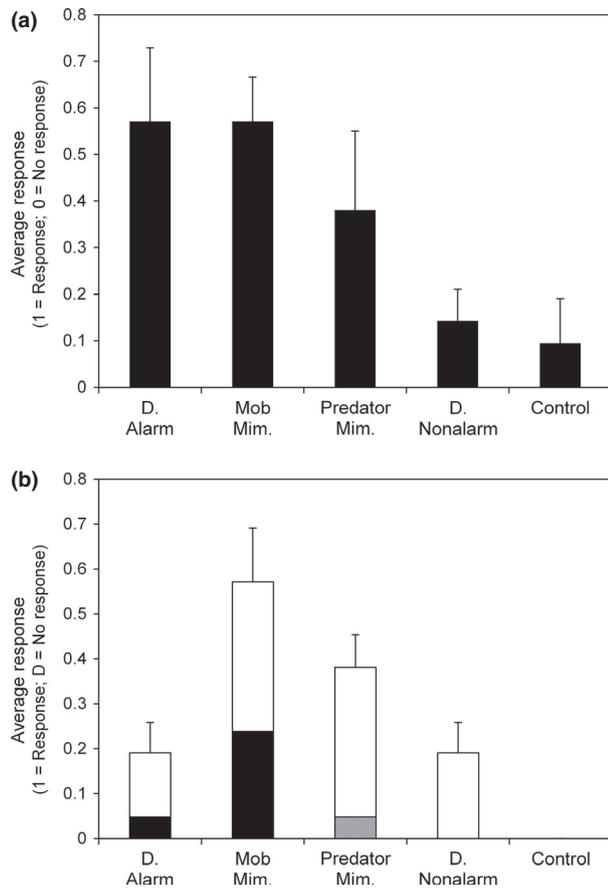
immediate response, the comparison between the model with order, and its interaction with treatment, and a model without order, was  $\chi^2_{20} = 20.19$ ,  $p = 0.45$ ; for delayed response,  $\chi^2_{20} = 20.34$ ,  $p = 0.44$ ), and this factor was not included in the final analysis.

One problem encountered in the analysis was that there was no delayed response to any trial of the barbet control, and the probability of such a response occurring is not calculable by the maximum-likelihood algorithms that underlie generalised linear mixed models (Firth 1993). We therefore used the following conservative approach: we replaced a '0' (no response) for a single trial of this treatment with a '1' (response). We applied this method 21 times, for each different trial of the barbet control treatment. We present the range of results of these 21 trials and their mean.

### Results

Playback treatment was a significant factor in predicting the flee response by Orange-billed Babblers (log-likelihood  $\chi^2_4 = 23.32$ ,  $p < 0.001$ ; Fig. 2a). The flee response was significantly higher to drongo species-specific alarm vocalisations (12/21 trials) and mobbing mimicry (12/21 trials) than to drongo species-specific non-alarm vocalisations (3/21 trials) and the barbet control (2/21 trials, Z values  $>2.96$ , Tukey corrected  $p < 0.025$ ). The flee response to predator mimicry was intermediate (8/21 trials). Note that the unbalanced design (conducting the trials on 27 flocks instead of 21, because we were unable to complete all five treatments with every flock) slightly reduced the significance level of tests, but otherwise did not affect the conclusions of the model: a model run on hypothetical, balanced data ( $n = 21$  flocks) produced similar results, with a slightly higher significance (log-likelihood  $\chi^2_4 = 23.51$ ,  $p < 0.001$ ).

We observed mobbing responses from Orange-billed Babblers and Ashy-headed Laughingthrushes (Fig. 2b). Babblers were the primary mobbers, responding in 26 trials, whereas laughingthrushes responded in 7 trials, 6 of them in conjunction with babblers (in the field, it was not possible to judge which species was the first to start mobbing). When the mobbing response of these two species was considered together, playback treatment was a significant factor in predicting the mobbing response (21 tests had log-likelihood  $\chi^2_4$  values that ranged from 18.22,  $p = 0.0011$  to 18.98,  $p = 0.0008$ ; mean = 18.44,  $p = 0.0010$ ). Mobbing response was highest to mobbing mimicry (12/21 trials), significantly higher than



**Fig. 2:** Responses to playback of drongo vocalisations by other species. Responses averaged among the three trials using the same playback exemplar, and SE calculated using the seven playback exemplars per treatment. (a) Immediate flee movements of focal Orange-billed Babblers within 5 s of the start of the exemplar, with a movement away into the vegetation scored as a 1, and the absence of this behaviour scored as a 0. (b) Delayed mobbing responses in which babblers or Ashy-headed Laughingthrushes clustered together and moved towards the speaker (scored as a 1), beginning 5 s after the start of the playback exemplar and continuing until 30 s after the exemplar was finished. The black area of the bars represents simultaneous responses by Orange-billed Babblers and Ashy-headed Laughingthrushes, the grey area represents responses only by laughingthrushes, and the white area represents responses only by babblers. The error bars are constructed considering response by either or both species. There were no mobbing responses to the barbet control treatment. D. Alarm = Drongo species-specific alarms; D. Non-Alarm = Drongo species-species non-alarms; Mob Mim. = Mobbing mimicry; Predator Mim. = Predator mimicry.

the barbet control (0/21 trials, tested as 1/21 trials; Z-scores ranged from 2.93,  $p = 0.026$  to 2.95,  $p = 0.024$ ; mean = 2.95,  $p = 0.025$ ). Mobbing response to mobbing mimicry also tended to be higher than the response to drongo-specific alarms (4/21 trials; Z-scores ranged from 2.45,  $p = 0.098$  to 2.57,  $p = 0.072$ ; mean = 2.49,  $p = 0.089$ ) or to drongo-

specific non-alarms (4/21 trials; Z-scores ranged from 2.45,  $p = 0.098$  to 2.54,  $p = 0.078$ ; mean = 2.48,  $p = 0.090$ ). Again, response to the predator mimicry was intermediate (7/21 trials).

## Discussion

The flee response to drongo mobbing mimicry that we demonstrate here indicates that the babblers recognised that these sounds are associated with the predation context. Yet the flee response to drongo species-specific alarms was as high, suggesting that mimicry has no advantage over species-specific vocalisations in eliciting such responses. In contrast, however, drongo mobbing mimicry did tend to elicit more mobbing responses from babblers and laughingthrushes than did drongo-specific alarm calls ( $0.07 > p > 0.10$ ). We believe that the difference between these species' responses to mobbing mimicry and drongo species-specific alarms is biologically significant because of the high effect size (response in 12 trials vs. 4 trials), and the low power of our experimental design (five treatments, two of which were controls, leading to 10 multiple comparisons). These results, together with those of Chu (2001), who showed vocal mimicry to increase mobbing intensity, although not attraction to the mobbing site, suggest that mobbing mimicry can function in birds to manipulate the behaviour of a heterospecific audience and dilute the risk of predation to the caller. The responses to our predator mimicry treatment were intermediate and ambiguous; further research needs to focus on potential functions of such mimicry.

Before proceeding, we would like to address some questions about the study design that could affect our conclusion that mobbing mimicry increases the mobbing of heterospecifics. First, is it possible that the birds were not responding to the playback, but were instead responding to the behaviour of other species in flocks, particularly drongos, that themselves could have been responding to the playback? On average, flocks included 12 species (Kotagama & Goodale 2004), and we noted the presence of drongos in 93 of the 105 trials. However, we think it is likely that the flee responses of babblers were elicited by playback because of the short amount of time that passed between the start of the playback and the movement. The mobbing response of babblers and laughingthrushes, which slowly clustered together and then approached the speaker while watching the observers, also strongly suggests a direct response to playback and was never elicited by the barbet control sound. The response of drongos themselves to playback is not

predictable: their response to their own species-specific alarm vocalisations is not significantly different than their response to other sounds (Goodale & Kotagama 2008). Further, it is unlikely that playback elicited responses from species other than drongos, Orange-billed Babblers and Ashy-headed Laughingthrushes, primarily because of the numerical dominance of Orange-billed Babblers in these flocks. These babblers average 16 individuals per flock, composing 39% of all birds in a flock (Kotagama & Goodale 2004). In the area where the observers walked—the understory—Orange-billed Babblers are even a greater percentage of the flock, and they are clumped together; we would estimate that in the area closest to the speakers three-fourths or more of the birds were this species of babbler. Species other than the Ashy-headed Laughingthrush tend to be in the subcanopy and the canopy, and they tend to be represented by one or a few individuals. Therefore, most responses to playback would be expected to be by Orange-billed Babblers. The Ashy-headed Laughingthrush is a gregarious bird of the ground and understory and thus seems especially prone to mobbing.

Second, how representative are the playback exemplars of the natural performance of mimicry? We emphasise that our playback exemplars were made directly from recordings, without us editing out any sounds (except occasional background noise of insects or running water or other species of birds). Due to our criterion for there to be a continuous 20 s of vocalisations of the same type, these recordings represent segments of our recordings in which there was a high amount of calling and vocal output was particularly exclusive to one type. Recordings of danger mimicry usually also included drongo species-specific alarm vocalisations (64 of 134 recordings that included predator mimicry, 10 of 21 recordings that included mobbing mimicry), but stretches of recordings could be found where such vocalisations were absent. Mobbing mimicry was very rarely associated with predator mimicry (only 1 of 21 recordings of mobbing mimicry also included predator mimicry). Hence, we believe our playback exemplars are representative of the most intense natural performances of mimicry.

How do our results fit with other studies focusing on the function of avian vocal mimicry? Recently, three recent studies—Goodale & Kotagama (2006a), Kelley & Healy (2011), and Igc & Magrath (2013)—have demonstrated that their study species (the Greater Racket-tailed Drongo, the Spotted Bowerbird *Ptilonorhynchus maculatus* and the Brown Thornbill *Acanthiza pusilla*) all imitate predators and the alarm and mobbing vocalisations of other species. It is interesting and a bit

perplexing that this blend of sounds associated with danger is imitated, because one might logically predict that the effects of these different classes of sounds (vocalisations of predators; alarm and mobbing calls) would be different. For example, if the targeted audience for this mimicry is other non-predator species, one might assume that the alarm calls of other species would repulse heterospecifics (Hailman 2009; Flower 2011), whereas the mobbing calls of other species would attract them. Vocalisations of predators might be repulsive (e.g. Barrera et al. 2011) or could potentially be attractive if a predator only naturally vocalises on the perch when it could be mobbed.

Mobbing mimicry would appear to be adaptive for species by recruiting other species to dilute the risk in an activity that is known to be dangerous (Curio & Regelmann 1986; Krams & Krama 2002). The performance of mobbing mimicry by drongos is also suggestive of a functional benefit: several times we have observed this behaviour when drongos came out of the flock close to the observers and watched them, rotating through the mobbing-specific calls of several other species (three observations described in Goodale & Kotagama 2005 and two observations since then). Besides the work of Chu (2001), Wheatcroft & Price (2013) have also recently documented avian vocal mimicry during mobbing.

The function of predator mimicry remains unclear. Igc & Magrath (2013) have recently suggested that predator mimicry could target the predator itself, and confuse or repel it, especially if the mimicry is of an additional, second predator that preys on the predator (e.g., see Perrone 1980). For Greater Racket-tailed Drongos, predator mimicry often occurs when predators are not noticeably present, and thus, we hypothesised for this project that drongos might be using predator mimicry as a type of 'false alarm' to startle other species away from food (Flower 2011). We also demonstrate separately (Goodale et al. 2014) that predator mimicry is especially frequent at nests when young is present, which raises the possibility that it may play a role in facilitating learning by the young about sounds associated with danger, as first hypothesised by Oatley (1969), although this idea requires experimental testing. As we mention in the methods, we only tested one type of predator mimicry (mimicry of the Mountain Hawk Eagle) here; further work is needed to determine whether different types of predator mimicry (i.e. different modelled predators) could have different effects.

The overall message then from our work on vocal mimicry in Greater Racket-tailed Drongos is that mimicry can be used in different circumstances for

different purposes. Drongo mimicry of the non-alarm vocalisations of other species can attract those species to reform mixed-species flocks (Goodale & Kotagama 2006b); drongo mimicry of mobbing vocalisations may attract heterospecifics to it during mobbing situations (this study). Predator mimicry may have a separate and potentially intraspecific function (Goodale et al. 2014). With all these different potential uses for mimicry in one species, it may not be a surprise that it is difficult to find one single overall function of avian mimicry (Garamszegi et al. 2007; Kelley et al. 2008).

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