Fork-Tailed Drongos (*Dicrurus adsimilis*) use different types of mimicked alarm calls in response to different alarm threats

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1. **Abstract**

Vocal mimicry is a fascinating phenomenon in the animal kingdom, noted in scientific research as early as the 18th century. Approximately 20% of bird species use vocal mimicry, yet very little is understood regarding why species use vocal mimicry, whether it provides functional benefits and in which contexts vocal mimicry is produced. I propose that some of these species produce alarm mimicry in the appropriate alarm contexts, matching the context of call production by the model species whose calls are mimicked. Previous research suggests that alarm mimicry in the appropriate context could provide heterospecifics with information regarding predators that are in the area. Aerial alarm call mimicry could indicate that an aerial predator is present and may cause individuals to flee, while terrestrial mob call mimicry could indicate the presence of a terrestrial predator and could prompt heterospecifics to aid in the mobbing of the predator. I investigate this possibility in the Fork-Tailed Drongo (*Dicrurus adsimilis*), a species renowned for its use of mimicry of other species alarm calls. Natural alarm responses to predators show that drongos produce alarm mimicry in alarms and never in non-alarm contexts. Overall drongos were more likely to mimic alarms in response to terrestrial predators. I then explored whether drongos use mimicked aerial and terrestrial 'mobbing' alarm calls in appropriate aerial or terrestrial predator alarm contexts using recordings of responses by drongos both to natural predators, and to experimental presentations of aerial and terrestrial predator and control models . Drongos were more likely to mimic aerial than 'mob' terrestrial alarm calls in response to natural and experimentally presented aerial predators. Conversely, they were more likely to mimic 'mob' terrestrial than aerial alarm calls in response to natural and experimentally presented terrestrial predators. Comparison of aerial and mob alarm call mimicry with the drongos production of their own equivalent aerial and terrestrial 'drongo-specific' alarm calls, revealed that mimicked and drongo-specific alarm calls were produced in similar contexts. These results support research showing that some bird species produce context-dependent alarm mimicry and the implications for the possible function of alarm call mimicry are discussed.

Keywords: Vocal mimicry; Fork-tailed Drongo (*Dicrurus adsimilis);* Context-specific signaling; Alarm calling, predator defense

2. Introduction

Vocal mimicry is the ability of some species to reproduce the vocalizations made by other animals, even humans (Dalziell *et al*. 2014). This phenomenon is a common trait in passerine birds, approximately 20% of which use vocal mimicry to some extent (Igic & Magrath 2014), though only 5% of these passerine birds are classified as regular mimics (Goodale & Kotagama 2006b). Originally, mimicry was only associated with species that were visually remarkably similar to one other, but today it encompasses signals that are sent through other sensory pathways like chemical and acoustic signals (Dalziell *et al*. 2014). A signaling system involving mimicry has three main role players: 'the mimic', the animal who reproduces the vocalizations of a different species, 'the model', the species being mimicked, and 'the receiver' the animal receiving the signal (Vane-Wright 1980). The behaviour of the receiver changes after mistaking the mimic for the model, which is advantageous for the mimic, or at least it must be advantageous in order for such mimicry to be functional.

Many hypotheses have been put forward to aid our understanding of the possible functions of vocal mimicry in both interspecific and intraspecific communication. Importantly, for each of these functions, specific types of mimetic calls need to occur in a specific contexts.

2.1 Functions for vocal mimicry: intraspecific communication

The idea that mimicry plays a role in mate choice and sexual selection has been one of the most prominent hypotheses for the possible functions of vocal mimicry. Vocal mimicry could be selected if the use of mimicry is a sign of quality in males, both to potential mates as well as other males (Dalziell *et al*. 2014). Male Satin Bowerbirds (*Ptilonorhynchus violaceus*) are known to create elaborate bowers which are decorated with objects from the surrounding area. It is within these bowers that courtship and copulation occurs (Coleman *et al*. 2007). Borgia (1985) showed that the amount of decorations at the bower as well as the quality of the bower played a significant role in the mating success of males and further research shows that mimetic accuracy and number of species mimicked correlates with these bower attributes (Coleman *et al*. 2007). This suggests that males that produce the best mimicry also have higher quality, more attractive bowers and that mimicry therefore has a possible role in male mating success (Coleman *et al*. 2007).

Mimicry might also play a role in the rearing of chicks, because parents could mimic heterospecific's alarm calls so that chicks learn to associate these calls with attacks or threats by predators (Dalziell *et al*. 2014). The frequency of vocal mimicry associated with danger varies due to proximity to nest and nesting stage in a passerine bird (Goodale *et al*. 2014). However, it is possible this is only a secondary function of mimicry, because there is evidence that, in the absence of mimicry, chicks still learn to respond to heterospecifics alarm calls in the appropriate manner (Haff & Magrath, 2012, 2013).

2.2 Functions for vocal mimicry: interspecific communication

Vocal mimicry may function to increase foraging success by aiding in the formation and subsequent maintenance of mixed-species flocks (Dalziell *et al*. 2014). An experiment was conducted that involved playback experiments of Greater Racket-tailed Drongos (*Dicrurus paradiseus*) mimicking heterospecific calls and these call play backs attracted bird species which usually form foraging associations with the drongos (Goodale & Kotagama 2005). Drongos are also able to mimic the calls of several heterospecifics consecutively, as heterospecifics are more likely to form groups after hearing calls made by more than one species (Goodale & Kotagama 2005). Drongos may be imitating mixed-species flocks when producing these multiple species calls, which may increase their chances of forming mixed-species flocks (Goodale & Kotagama 2006a).

Vocal mimicry also plays a role in brood parasitism. Common cuckoo (*Cuculus canorus*) chicks are not raised by their own parents. The cuckoo lays its eggs in the nest of another species and the chicks are raised by the host (Avilés & Møller 2004). As a result, the host species often suffers decreased reproductive output, because soon after hatching, the cuckoo chicks often remove the other eggs from the nest (Avilés & Møller 2004). However, to ensure that they are fed, the cuckoo chicks must produce begging calls that elicit feeding from the host parents (Langmore *et al*. 2003). Recent studies have shown that the Horsfield's Bronze-cuckoo (*Chalcites basalis*) will mimic the nestling calls of its host to ensure that it is not rejected

(Langmore *et al*. 2003). The cuckoo chick does not mimic the begging call of the host perfectly the first few times. It learns the begging call through trial and error. The cuckoo will change the structure of its initial call until it gets the best response from its host parent (Langmore *et al*. 2008). In this instance, the cuckoo nestling benefits by tuning its begging calls to match those to which host parents respond through mimicry (Langmore *et al*. 2008).

When associating with other species, birds frequently mimic alarm calls and the calls made by predators, which can collectively be termed sounds of danger (Goodale & Kotagama 2006b). Alarm mimicry often contains information about the predator, as different predators are associated with different threats (Caro 2005). This information could be about what type of predator is present (Evans *et al*. 1993), how much risk there is (Blumstein 1999) and how the predator is behaving (Griesser 2008). Mimicked alarm calls could function to reduce an individual's risk of predation by recruiting other species to mob the predator, directly deterring the predator or attracting other predators. An experiment involving playbacks of Greenish Warbler (*Phylloscopus trochiloides*) mobbing calls with and without mimics of Buff-barred Warbler (*P. pulcher*) mobbing notes elicited a stronger mobbing response from Buff-barred Warblers when mimicry was present (Chu 2001, Wheatcroft & Price 2013). This suggests that alarm mimicry could function to recruit other species in predator defense.

Another experiment done on the Northern Flicker (*Colaptes auratus*), shows that nestlings possibly deter predatory squirrels from entering the nest by producing a buzzing sound similar to the sounds of a bee hive. Similar work has been done on burrowing owls, which roost and form their nests in ground squirrel burrows, often also frequented by rattlesnakes. When threatened by a predator at their nest, burrowing owls produce vocalizations that resemble the rattles of a rattlesnake, which deters predators (Rowe *et al*. 1986).

False alarm mimicry is also often used by some species and can facilitate kleptoparasitism (Dalziell *et al*. 2014). When foraging alongside other species, Fork-tailed Drongos (*Dicrurus adsimilis*) produce both heterospecific as well as their own drongo-specific alarm calls in a false alarm context. When an individual hears the alarm it may flee for cover, abandoning any food that it was handling enabling the drongo to steal abandoned food (Flower 2011).

The use of mimicry during alarms is quite a common occurrence in several bird species (Oatley 1970) and as stated above, has many possible functions, particularly in interspecific communication. However, aerial and terrestrial alarm call mimicry often elicit separate responses, because of the different threats presented by aerial and terrestrial predators (Igic & Magrath 2014). Mimicked aerial alarm calls often prompt individuals who hear the mimicked aerial alarm to flee, while mimicked mobbing (terrestrial) alarm calls often prompts individuals who hear the mimicked mob alarm to mob the predator (Igic & Magrath 2014). It has been suggested that many species, including drongos, decrease their own risk of predation by producing mimicked mob alarm calls in true terrestrial alarms as other species are often recruited to mob and drive away the predator (Chu 2001). Similarly, production of mimicked aerial alarms might function to confuse an attacking predator as more birds flee to cover (Caro 2005). However, for such functions to be possible, mimicry of these different alarm call types must be produced in the appropriate behavioural contexts.

2.3 Context-specific mimicry

For vocal mimicry to be used functionally in a specific context matching that in which it was produced by the model, the mimic must not only learn to produce the calls of other species, but also need to learn to produce these calls in the appropriate context in order to prompt the appropriate functional response (Goodale & Magrath 2006b). For example, to decrease risk of predation in true aerial predator alarms, these calls must occur only when the mimic alarms at an aerial threat and should be uncommon in other contexts (Kelley & Healy 2012). Unfortunately, for most mimics, we know very little about the contexts in which mimicry occurs (Igic & Magrath 2014). Learning to reproduce multiple mimicked calls in the appropriate context is considered harder than learning simple calls. The ability to produce many mimicked alarm calls is made harder by the fact that species produce various alarm calls for different alarm contexts, specifically, aerial alarms for aerial predators and terrestrial mobbing calls for terrestrial predators.

Recently, studies on the Greater Racket-tailed Drongos, have suggested that alarm calls mimicked by birds are being produced in the correct context (Goodale & Kotagama 2006b). Racket-tailed Drongos produce aerial mimicked alarm calls when an aerial predator is present, but it remains unclear whether they produce mimicked terrestrial mobbing alarm calls in the presence of a terrestrial predator (Goodale & Kotagama 2006b). More recent research on the Brown Thornbill (*Acanthiza pusilla*) shows that their use of mimicry changes according to behavioural context (Igic & Magrath 2014). Brown Thornbills were most likely to produce mimicked alarm calls when they were captured and during nest approaches by humans which suggests that mimicry could function to deceive or deter predators (Igic & Magrath 2014). Brown Thornbills were less likely to produce mimicked alarm calls at terrestrial and aerial threats, but when they did so, they produced aerial alarms for aerial predator and terrestrial alarms for terrestrial predators (Igic & Magrath 2014). However, no study to date has conclusively shown that mimicked alarm vocalizations are produced in the appropriate context in response to both natural predators and in experimental manipulations.

Here I investigated vocal mimicry by the Fork-tailed Drongo, a common bird throughout southern and eastern Africa that is renowned for its vocal mimicry of both alarm calls, and the calls of predators. Drongos are known to form associations and forage with other species like Dwarf Mongooses (*Helogale parvula*), Pied Babblers (*Turdoides bicolor*) and Sociable Weavers (*Philetairus socius*) (Sharpe *et al*. 2010, Flower *et al*. 2013). In these associations, the drongos act as sentinels, alerting other species to the presence of a predator by making true alarm calls (Flower *et al.* 2013; Ridley and Raihani 2007). However, drongos also produce false alarms in the absence of predators, in order to scare other species and steal their food (Flower 2011). These false-alarms include mimicked alarm calls and the deceptive function of vocal mimicry produced in this false alarm context has been well explored (Flower 2011, Flower *et al*. 2014). However, drongos also produce mimicked alarm calls in response to true predators and observations suggest they mimic different alarm call types in different alarm contexts.

Here, I will investigate whether drongos mimic alarm calls in appropriate true predator contexts. Specifically, I will try to confirm whether drongos produce mob call mimicry in response to terrestrial predators and aerial alarm calls in response to aerial predators, using a combination of natural observations and experimental data collection techniques. First, I will investigate whether drongos specifically produce alarm call mimicry in alarms, but not non-alarm contexts. Furthermore, I will explore whether drongos produce alarm call mimicry in response to experimentally presented aerial and terrestrial predator models. I will then determine whether drongos use alarm call mimicry in the appropriate alarm contexts, by investigating whether drongos produce aerial alarm call mimicry to aerial predators and terrestrial 'mob' mimicry in response to terrestrial predators. Finally, to explore the possible specific functional benefits of producing mimicry, I will investigate whether aerial or terrestrial alarm call mimicry is produced more or less frequently in different contexts than the corresponding drongo-specific call type, where increased production of mimetic alarm calls relative to drongo-specific alarm calls would suggest a specific benefit to alarm call mimicry.

3. <u>Materials and Methods</u>

3.1 Study site and population

Data were collected on a population of wild Fork-tailed Drongos between March and July 2008 (natural observational data) and April and May 2014 (experimental data) on the Kuruman River Reserve (KRR). The KRR is located in the Southern African Kalahari, 30 kilometres west of Van Zylsrus (26^{o}58'S, 21^{o}49'E) in the Northern Cape. This reserve spans 3300 hectares of former farmland which was restocked with Kalahari game species in 2003. The habitat in the region is characterized by herbaceous sand flats and dunes which are sparsely covered in grass (Russel *et al*. 2002). The dry riverbed of the Kuruman River goes through the reserve and is dominated by 'Drie Doring' bushes (*Rhigozum trichotomum*) and Camel Thorn trees (*Acacia erioloba*). The Kalahari is a summer rainfall region (October – April), receiving approximately 230mm of rain during this time (Russel *et al*. 2002) with less than 20mm of rain on average in the winter months (May – September) . During winter, maximum temperatures range from 10^{o}C to 38^{o}C and minimum from -3-5^{o}C to 19^{o}C. During the summer, maximum temperatures range from 18^{o}C to

45°C and minimum from 0°C to 29°C (Russel *et al*. 2002). Temperature and rainfall data were collected between December 1996 and April 2000 (Russel *et al*. 2002)

The study population was made up of 21 drongo groups and each had a territory of approximately 1km^2, containing an adult pair and up to four juveniles. These drongos have been habituated to observations at <5m (Flower 2011). More than 90% of the drongos in the 21 groups had unique colour rings which allowed for individual identification. Drongos are active in the morning and late afternoon, remaining relatively inactive during the heat of the day. For this reason, data was collected in the mornings between 06:00 and 11:00 and in the afternoon between 16:00 and 18:00.

3.2 Call context mimicry – natural data

Observations and recordings of drongo vocalizations in non-alarm and alarm contexts were collected by Thomas Flower during 294 focal observations (mean focal length (± SE) 55 ± 1 minutes) collected from March to July 2008 on 27 habituated and individually ringed drongos. He recorded vocalizations made by drongos in non-alarm contexts during interactions with territorial neighbour's, other group-members, and heterospecific mixed-species foraging partners (Baigrie *et al*. 2014). Similarly, he recorded vocalizations made by drongos in alarm contexts during encounters with predator species including aerial predators such as Gabar Goshawk (*Melierax gabar*), Martial Eagle (*Polemaetus bellicosus*) and Pale-chanting Goshawk (*Melierax canorus*), and terrestrial predators, including Slender Mongoose (*Galerella sanguinea*), Cape Fox (*Vulpes chama*) and African Wild Cat (*Felis silvestris lybica*). False alarm calls recorded during food theft attempts on other species (Flower 2011) are excluded from analyses. Additionally, Dr Flower recorded the alarms produced by numerous species in the Kalahari environment, noting whether these alarms were exclusively produced by species to aerial predators, terrestrial predators or both. Call types were categorized accordingly as aerial alarm calls or terrestrial mob calls, or otherwise considered unknown where there was no single context where species produced the call, or the calls were mimics of predator's calls. (Flower 2012). Although the context of production and function of predator call mimicry warrants further attention, I did not consider this behavior within this study because the frequency of predator alarm mimicry to experimental models was insufficient for analysis. Drongos produced a large number of drongo-specific call types in different alarm contexts including drongo-specific non-alarm calls (territorial vocalizations etc), and seven different drongo-specific alarm calls, two of which were terrestrial mob alarms, three of which were drongo specific aerial alarms, and two of which were produced in both aerial and terrestrial alarm contexts (Flower 2011). Drongos also produced an array of mimetic alarm calls and these alarm calls were compared with the alarm vocalizations of model species in spectrograms resulting in the identification of 25 mimetic alarm calls made by drongos, for which the context of production was known for the model species (aerial = 20) (terrestrial = 5) and a further 32 where there was no specific context of production (Flower 2012). The number of times each mimetic alarm call type and drongo-specific alarm call type was produced per drongo in natural alarms to terrestrial and aerial predators was identified in spectrograms of alarm call recordings.

3.3 Call context mimicry – experimental data

Two aerial presentations and two terrestrial presentations were undertaken at each of the 21 groups. To represent the aerial predator, a hawk glider was used and a frisbee was used as a control. To represent the terrestrial predator a plastic snake was used and a plastic bottle was used as a control. At least one of the drongos in the group was present for every one of these trials and this was considered the focal individual. The order of the trials was randomized between groups and there was a waiting period of two consecutive days before revisiting a group for the next trial. Once in a group’s territory, habituation calls were made, luring the drongos to that location. Each drongo was rewarded with a mealworm upon arrival. Individuals present were identified and recording equipment were set up. A Sennheiser ME67 microphone was connected to a Marantz PMD660 digital recorder to record vocalizations made during presentations. Only alarm calls made while the hawk or frisbee was in flight were included while any alarm calls made in response to the sound of the frisbee or hawk hitting the ground, or to these models when on the ground, were not included.

When carrying out the hawk and frisbee trials, I positioned myself behind a bush approximately 10 -20m away from the drongos and prepared to throw the hawk or frisbee, while a field assistant prepared to record drongo vocalizations. Once ready, I threw the hawk/frisbee out from behind the tree in a direction perpendicular to the drongos; alarms made by drongos during the presentations were recorded. When carrying out the snake and bottle trials, the snake/bottle was buried in the sand below the tree that the drongos were sitting in, but underneath a cover that obscured the drongos view. After the snake/bottle was buried, a few mealworms were thrown onto the ground around the snake/bottle which were then eaten by the drongos before they returned to a perch, ensuring that the birds remained perched at the location where the presentation occurred. The snake/bottle was attached to a fishing rod, which allowed me to stand approximately 5m away from the tree. Once drongos had returned to their perch at >2 metres, I then reeled in the line of the fishing rod exposing the head of the snake or lid of the bottle. Alarms made during the presentations were recorded and recordings lasted a maximum of five minutes. After all the trials were complete, the alarms that were produced were classified by type as mimicked or drongo-specific, aerial, mob or unknown context calls following the same methodology as defined above for natural recordings.

3.4 Statistical analysis

The statistical analysis was carried out in R (Version 3.0.3). Barnard's Exact tests were carried out using the function barnardw.test() in the Barnard package (Erguler 2012). We used the R package lme4 (Bates *et al.* 2012) for generalised linear mixed models (GLMMs), except where data were overdispersed because of zero-inflation, in which case quasi-binomial GLMMs adjusted for zero-inflation, were undertaken using the package glmmADMB (Skaug *et al*. 2012). Post-hoc Tukey tests were undertaken to check for significant differences between factor levels using the package multcomp (Hothorn et al. 2012). The residuals for each model were checked for normality (Shapiro-Wilk) for LMMs, or overdispersion for GLMMs and visually for homogeneity of variances.

3.4.1 Call context mimicry – natural data

To determine whether or not drongos produce alarm call mimicry in predator alarms, but not in non-alarm contexts (territorial vocalizations, duets, contact calls and aggressive interactions between drongos), I conducted a Barnard's Exact test comparing the proportion of drongo individuals that produced alarm mimicry during call bouts made in non-alarms (n = 24 drongos;

mean call bout per drongo (±SE) 11.75 ±1.11) and the presence of alarm mimicry during call bouts made in true alarms (n = 24 drongos; mean call bout per drongo (±SE) 6.08 ± 0.78).

To determine whether drongos more frequently produce alarm call mimicry in response to aerial or terrestrial predators, we undertook a generalized linear mixed model with the number of mimetic alarm calls produced per alarm as a proportion of all alarm calls set as the response term (107 alarms by 26 drongos). Alarm context (aerial, terrestrial) was included as an explanatory term and the identity of the alarm caller was set as a random term.

To determine whether drongos produce mimicry of ‘mob’ terrestrial and aerial alarm calls in the appropriate terrestrial or aerial alarm contexts, we investigated the likelihood of mob alarm call and aerial alarm call mimicry produced in each alarm where alarm mimicry occurred, to either aerial or terrestrial predators (80 alarms by 24 drongos). We undertook a quasi-binomial GLMM (adjusted for zero-inflation) with the number of alarm calls produced per alarm as a proportion of all alarm calls set as the response term and alarm context and alarm type (mob call, aerial call) set as the explanatory terms; random terms included the identity of the alarm caller with alarm call nested within this.

To compare drongo-specific and mimicked alarm call production in response to aerial and terrestrial predators, we used a quasi-binomial GLMM (adjusted for zero-inflation) on whether drongo-specific or mimicked, aerial or mob alarm calls were produced for each alarm as the response variable (1/0). Explanatory factors included the call type (drongo-specific aerial call, mimicked aerial call, drongo-specific mob call, mimicked mob call), call context (aerial predator, terrestrial predator) and the total number of calls as a weighting factor. Random terms included the identity of the alarm caller with alarm call nested within this

3.4.2 Call context mimicry – experimental data

To determine whether or not drongos responded to the hawk glider and plastic snake as if they were predators, we first investigated whether they were more likely to alarm at (i) the hawk than the frisbee, (ii) the snake than the bottle. To do this we conducted a Barnard’s Exact Test on the binomial data. This test was chosen, because of our relatively small sample size and because it is more powerful than a Fisher's Exact Test when working with 2x2 contingency tables.

To determine whether or not drongos produce alarm mimicry in response to predators, we investigated whether drongos were more likely to make at least one mimicked alarm call in response to (i) the hawk than the frisbee, (ii) the snake than the bottle. To do this we conducted a Barnard's Exact Test on the binomial data.

To determine whether or not drongos mimic the appropriate alarm calls for the appropriate context, we investigated whether, on occasions when drongos produced alarm call mimicry, they (i) produced more aerial mimicry for aerial predators than terrestrial predators, and (ii) more terrestrial mimicry for terrestrial predators than aerial predators. To do this we conducted a Barnard's Exact Test on the binomial data of whether aerial mimicry was recorded for (i) hawk versus snake, or whether terrestrial mimicry was recorded for (ii) hawk versus snake.

To determine whether drongo-specific alarm calls are produced at similar frequencies to mimicked alarm calls to aerial and terrestrial predators we conducted a series of Barnard's Exact Tests on the amount of drongo-specific and mimicked aerial or mob alarm calls in both the aerial and terrestrial contexts. Binomial data was generated based only on the occasions in which drongos alarmed (Terrestrial: 13; Aerial: 6).

4 Results

4.1 Production of alarm mimicry in non-alarm contexts

Drongos only produce alarm mimicry in alarm contexts (Barnard's Exact Test: Z = 4.17, P < 0.001, n = 24, Figure 1).

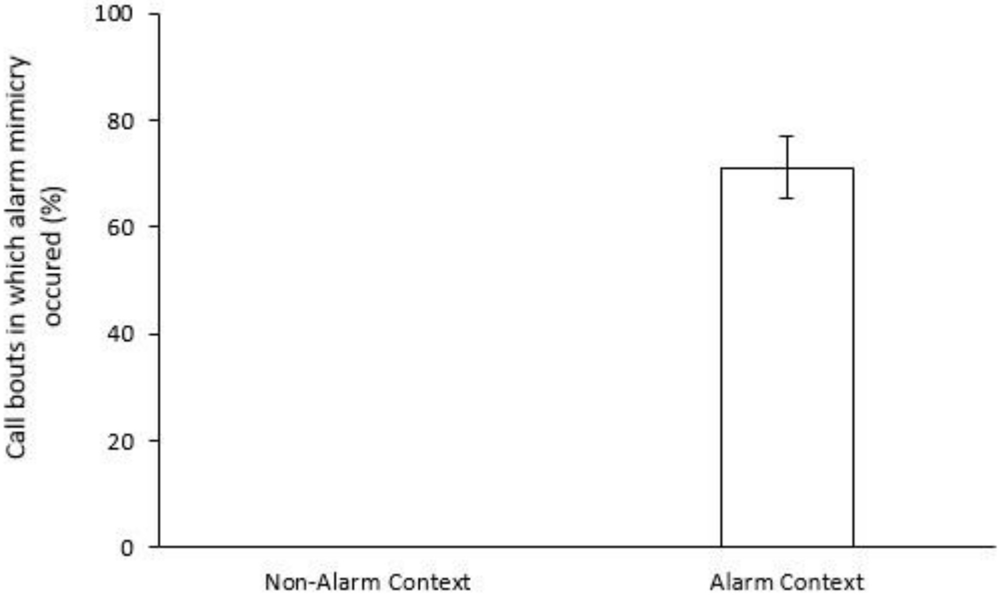

Figure 1: Percentage of call bouts in which mimicry occurred

4.2 Treatment of model stimuli as predators

Drongos produced a large range of alarms, both drongo-specific and mimicked, at the four different trials (Table 1). Drongos were more likely to alarm at the snake (29% of trials in which alarm produced) than the bottle (0% of trials in which alarm produced) (Barnard's Exact Test: Z = -2.31, P = 0.02, n = 21), but there was no significant difference in the number of alarms produced to the hawk (62% of trials in which alarm produced) compared to the frisbee (29% of trials in which alarm produced) (Barnard's Exact Test: Z = -1.34, P = 0.20, n = 21).

Table 1: The mean percentage of alarm calls that were of each call type, given in response to the different experimental models

Call type	Hawk %	Frisbee %	Snake %	Stick %
Mimicked aerial	50.5	33.3	4.7	N/A
Mimicked mob	0.0	0.0	48.0	N/A
Mimicked unknown	8.5	25.0	15.1	N/A
Drongo-specific aerial	33.3	25.0	0.0	N/A
Drongo-specific mob	7.7	0.0	17.0	N/A
Drongo-specific unknown	0.0	16.7	15.1	N/A
Total presentations in which alarm calls were made	13/21	6/21	6/21	0/21

4.3 Production of alarm mimicry in alarm contexts

There was no significant difference in the amount of alarm mimicry (including both aerial and terrestrial alarm mimicry) produced to the hawk and frisbee trials (Barnard's Exact Test: Z = -1.021, P = 0.356, n = 21; Figure 2). However, the experimental data suggests that drongos produce more alarm mimicry at the snake than at the bottle (Barnard's Exact Test: Z = -2.13, P = 0.04, n = 21; Figure 2). Analysis of natural data indicates that alarm mimicry is more frequent in terrestrial alarms than aerial alarms (GLMM: Z= 3.76 p = 0.002; Figure 3, Table 2).

Table 2. GLMM (Zero-inflated negative binomial) of the factors affecting the likelihood that a drongo produced a mimicked alarm call to a terrestrial or aerial predator (106 predator alarms recordings on 27 drongos).

Model term	**Level**	**Effect ± S.E.**	***Z***	***P***
Intercept		0.23 ± 0.20	1.16	0.248
Context	Aerial predator Terrestrial predator	0.00 ± 0.00 0.74 ± 0.20	3.76	<0.001

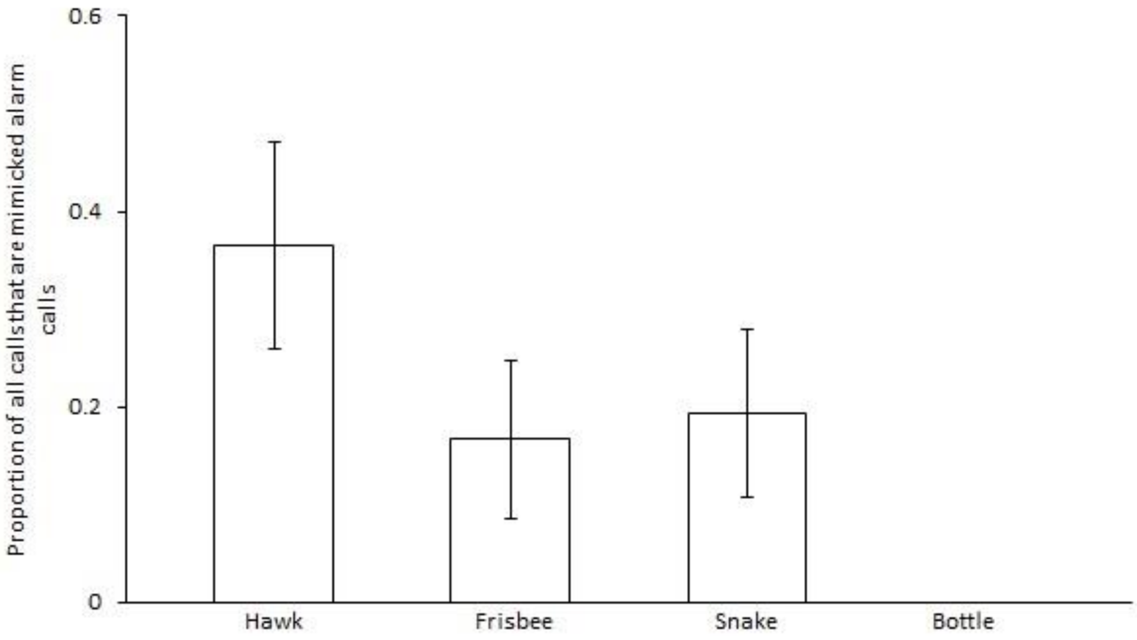

Figure 2: Proportion of all calls made that are mimicked alarm calls (mean ± standard error) produced during the hawk (n=21), frisbee (n=21), snake (n=21) and bottle (n=21) trials.

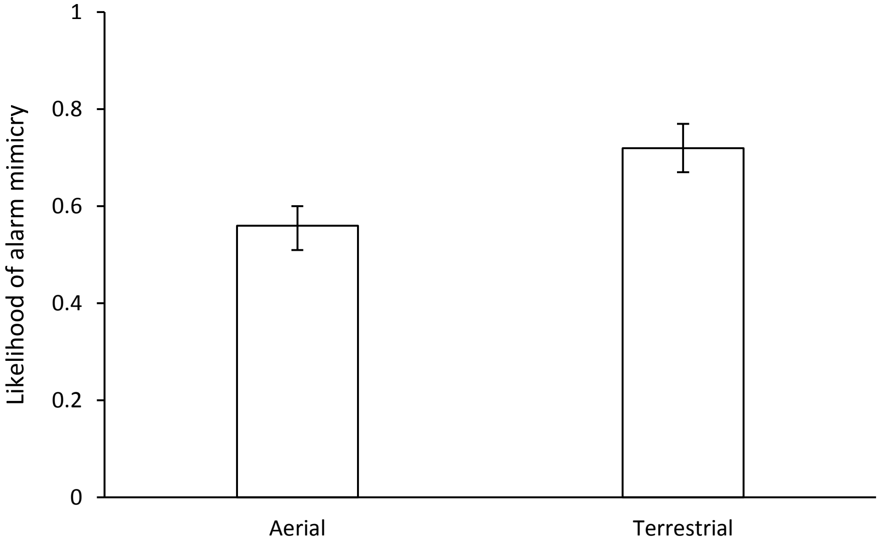

Figure 3: Likelihood of alarm call mimicry (mean ± standard error) in aerial and terrestrial predator threat contexts (n=107 alarms by 27 drongos)

4.4 Production of the appropriate mimicked alarm calls in the appropriate contexts

In response to natural aerial threats, drongos were significantly more likely to mimic aerial alarm calls than terrestrial alarm calls, while in response to terrestrial predators they were more likely to mimic terrestrial than aerial alarm calls (GLMM: $Z= 4.71$ $p < 0.001$; Figure 4; Table 3 and 4). Similarly, mobbing alarm mimicry was more likely in response to terrestrial predators than aerial predators, but aerial alarm mimicry was not more likely to either aerial or terrestrial predators. In response to an experimentally presented aerial predator model, drongos produced more mimicked aerial alarms than mimicked terrestrial alarms (Barnard's Exact Test: $Z = -2.14$, $p = 0.037$, $n = 21$; Figure 5). In response to a terrestrial predator model, drongos produced more mimicked mob (terrestrial) alarm calls than mimicked aerial alarm calls (Barnard's Exact Test: $Z = 2.13$, $p = 0.037$, $n = 21$; Figure 5)

Table 3. GLMM (Zero-inflated negative binomial) of the factors affecting the likelihood that a drongo produced a mimicked aerial or mobbing alarm call to a terrestrial or aerial predator (106 predator alarm recordings on 27 drongos).

Model term	Level	Effect ± S.E.	*Z*	*P*
Intercept		0.23 ± 0.20	6.78	<0.001
Call type * context		See Fig. 4	4.71	<0.001
Call type	Aerial alarm call Mob alarm call	0.00 ± 0.00 -4.07 ± 0.46	-3.99	<0.001
Context	Aerial predator Terrestrial predator	0.00 ± 0.00 0.51 ± 0.46	1.11	0.27

Table 4: Tukey contrast showing differences between mimicked aerial and terrestrial alarm calls made during aerial and terrestrial alarm contexts

Comparison	**Estimate (SE)**	**Z-value**	**p**
Aerial Predator x Terrestrial Alarm- Aerial Predator x Aerial Alarm	-4.07 (1.02)	-3.99	<0.001
Terrestrial Predator x Aerial Alarm - Aerial Predator x Aerial Alarm	0.51 (0.46)	1.11	0.439
Terrestrial Predator x Terrestrial Alarm - Aerial Predator x Terrestrial Alarm	5.87 (1.09)	5.41	<0.001
Terrestrial Predator x Terrestrial Alarm - Terrestrial Predator x Aerial Alarm	1.30 (0.57)	2.28	0.047

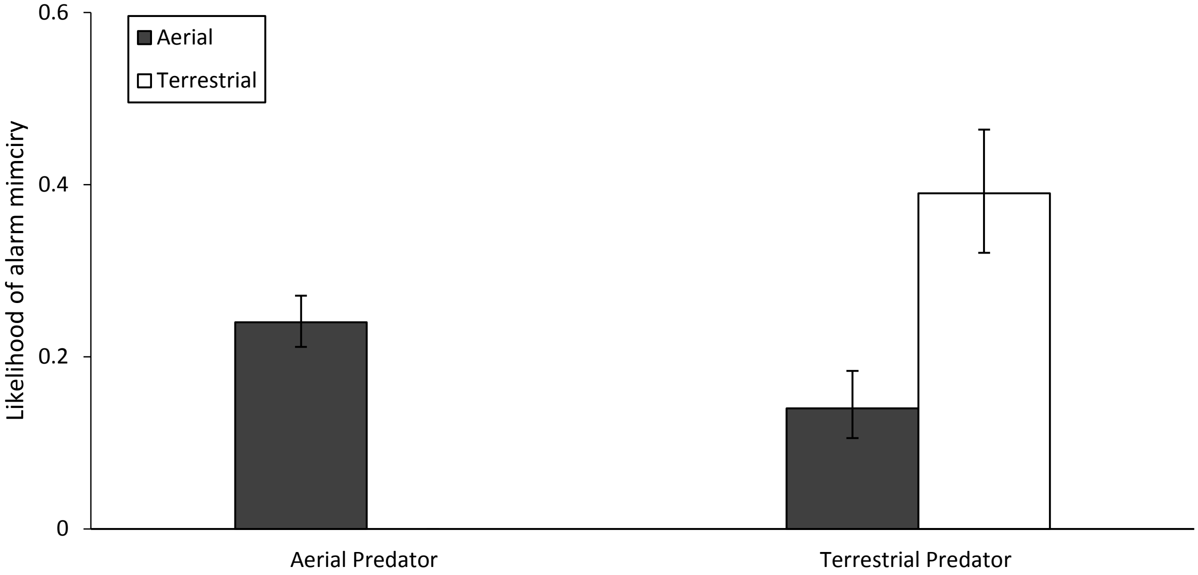

Figure 4: Likelihood of aerial (aerial – grey bars) or mobbing (terrestrial - white bars) alarm mimicry (mean ± standard error) to aerial or terrestrial predators (n=80) alarms in which alarm mimicry occurred, by 24 drongos). Predicted means ± SE's for mobbing mimicry in response to aerial predators are not visible but were 0.001 +0.003 and -0.0005.

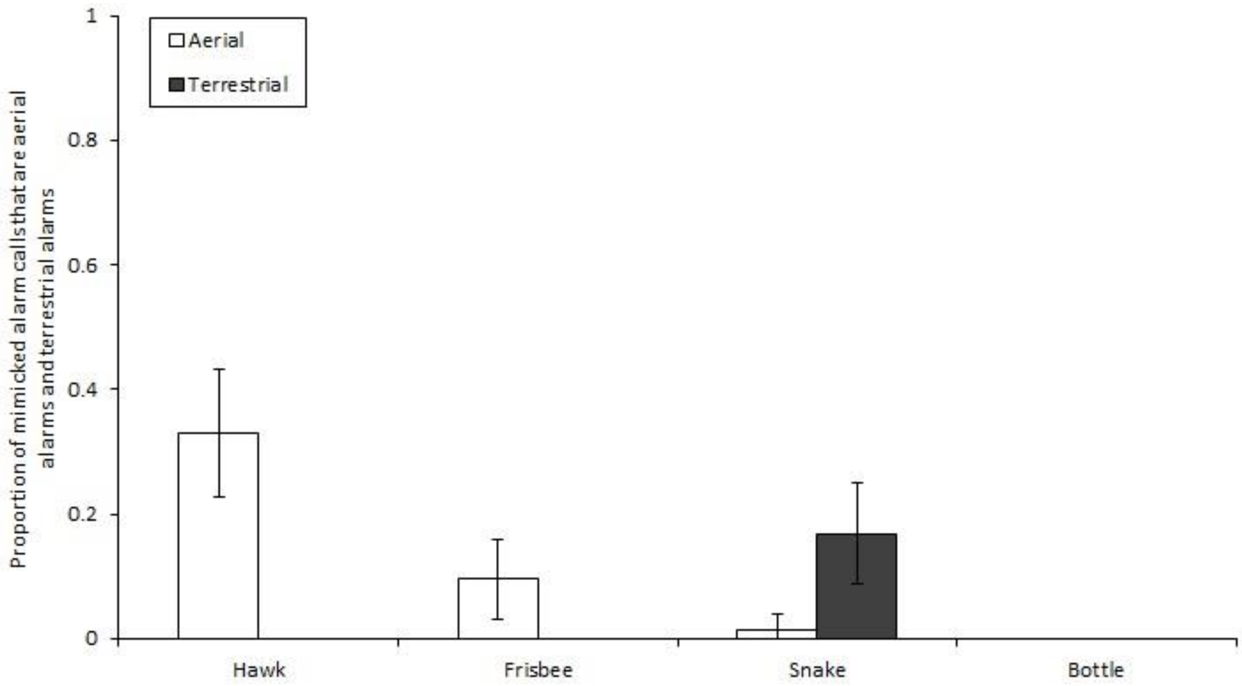

Figure 5: Proportion of all mimicked alarm calls (mean ± standard error) that are aerial alarm calls (white bars) and terrestrial alarm calls (shaded bars) in response to the hawk (n=21), frisbee (n=21), snake (n=21) and bottle (n=21) trials.

4.5 Comparison of mimicked and drongo-specific alarm call production in different alarm contexts

To a certain degree, drongos make use of both mimicked and drongo-specific aerial and terrestrial alarm calls in both the aerial as well as terrestrial alarm context (Figure 6). However, in the presence of an aerial predator, drongos more frequently made their own aerial or mobbing alarm calls, than mimicked alarms of these types (GLMM: $Z = -5.69$ $p < 0.001$; Figure 6; Table 5 and 6). There is also a non-significant trend suggesting that drongos are more likely to produce mimicked aerial alarm calls than drongo-specific aerial alarms in response to terrestrial predators (GLMM: $Z = -5.69$ $p < 0.001$; Figure 6; Table 5 and 6).

Experimental data shows that during the hawk trial there was no significant difference in the use of drongo-specific and mimicked aerial alarm calls (Barnard's Exact Test: $Z = 0.68$, $p = 0.59$, n=13; Figure 7). There was also no significant difference in the use of drongo-specific and mimicked mob alarm calls in the aerial context (Barnard's Exact Test: Z = -0.98, p = 0.58, n = 13; Figure 7). During the snake trial there was no significant difference in the use of drongo-specific and mimicked aerial alarm calls (Barnard's Exact Test: Z = 0, p = 1, n = 6; Figure 7). There was also no significant difference in the use of drongo-specific and mimicked mob alarm calls (Barnard's Exact Test: Z = 0.55, p = 0.65, n = 6; Figure 7)

Table 5: GLMM (Zero-inflated negative binomial) of the factors affecting the likelihood that a drongo produced their own drongo-specific or mimicked aerial or mobbing alarm calls in response to aerial or terrestrial predators (106 predator alarms recordings on 27 drongos).

Model term	**Level**	**Effect ± S.E.**	***Z***	***P***
Intercept		1.52 ± 0.16	9.26	<0.001
Call type * context		See Fig. 6	4.47	<0.001
Call type	Drongo air alarm	0.00 ± 0.00	-5.69	<0.001
	Mimic air alarm	-0.47 ± 0.21		
	Drongo mob alarm	-1.80 ± 0.32		
	Mimic mob alarm	-4.34 ± 1.01		
Context	Aerial predator	0.00 ± 0.00	-2.27	0.024
	Terrestrial predator	-2.29 ± 1.01		

Table 6: Tukey contrasts for comparison of the likelihood that drongo-specific or mimicked aerial and mob alarm calls are produced in response to aerial or terrestrial predators

Tukey contrast	Alarm context	Estimate ± S.E.	Z	Pr(>|z|)
Drongo-specific mob Vs. Mimicked mob	Aerial	1.56 ± 0.54	2.887	0.0142
Drongo-specific aerial Vs. Mimicked aerial	Aerial	-3.64 ± 0.71	-5.111	<0.001
Drongo-specific mob Vs. Mimicked mob	Terrestrial	-0.34 ± 0.59	-0.575	0.9448
Drongo-specific aerial Vs. Mimicked aerial	Terrestrial	1.79 ± 1.17	1.525	0.3719

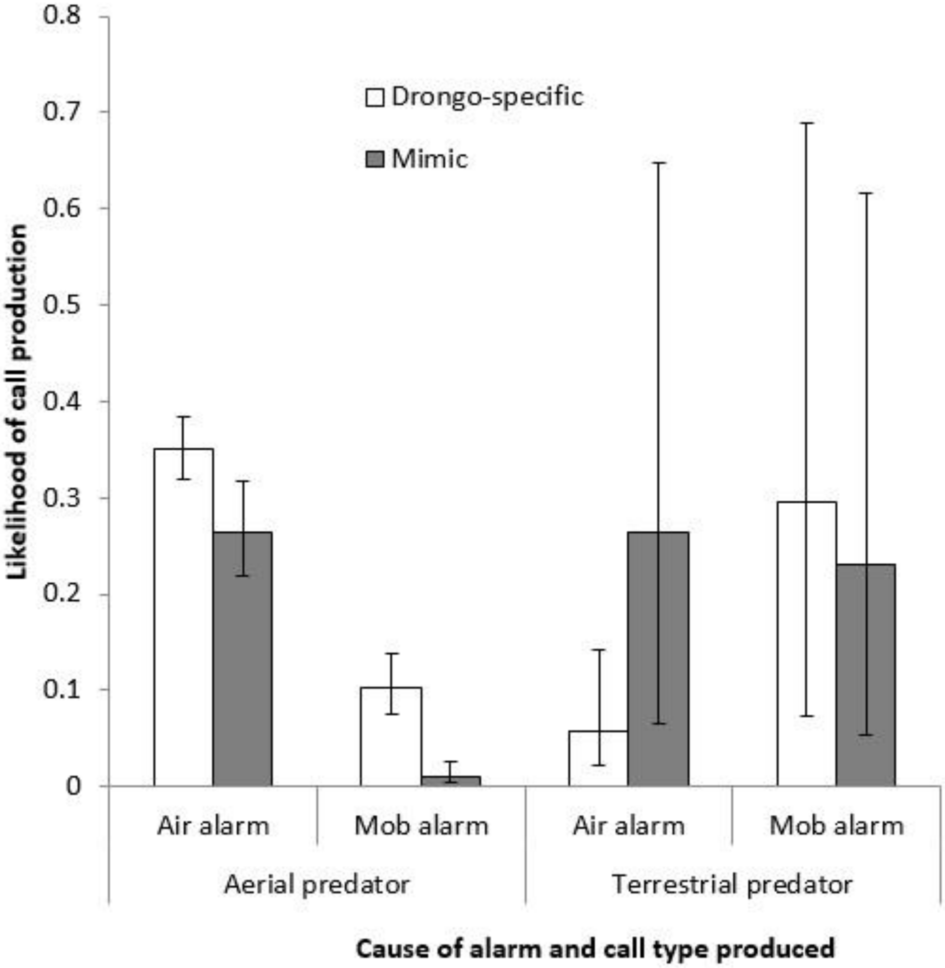

Figure 6: Likelihood that drongos produced drongo-specific and mimicked, aerial (air) or terrestrial (mob) alarm calls at aerial and terrestrial predators (106 predator alarms recordings on 27 drongos)

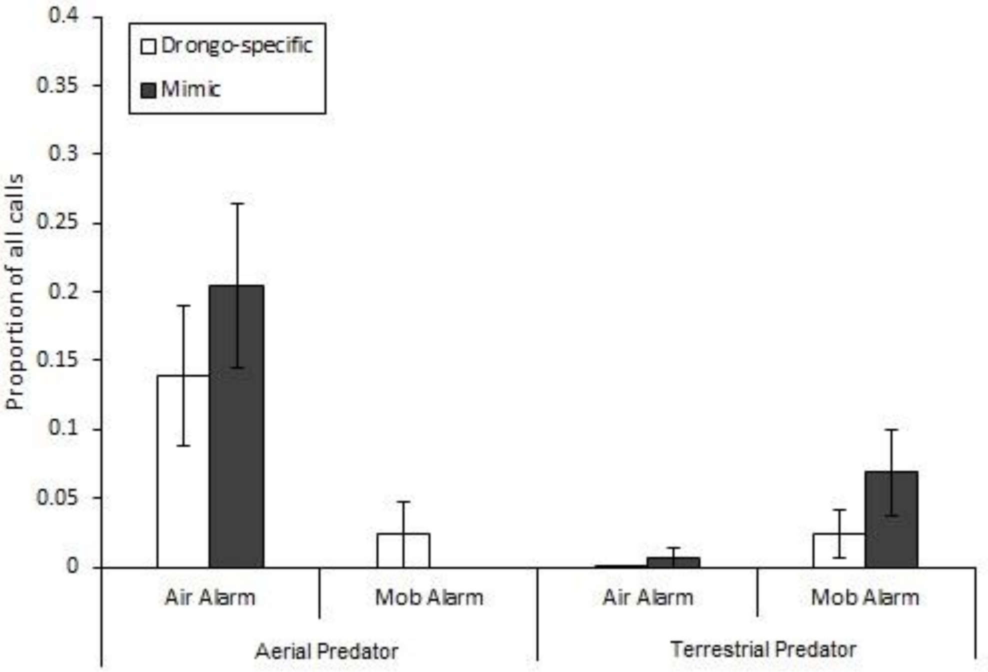

Figure 7: Proportion of all calls that are drongo-specific and mimicked aerial (air) or terrestrial (mob) alarm calls at aerial and terrestrial predators

5. Discussion

Results show that Fork-tailed Drongos produce context-specific alarm call mimicry. Drongos only produced alarm mimicry in alarm contexts and were more likely to do so to terrestrial predators. Furthermore, experimental and natural data suggest they produce mimicked and drongo-specific aerial alarms at aerial predatory threats, and terrestrial mob mimicry and terrestrial drongo-specific alarm calls at terrestrial predatory threats. Drongo-specific alarms were marginally more likely to be produced to aerial threats in natural predator alarms than were mimicked aerial alarms. Overall results suggest that drongos mimic aerial and mobbing alarm call types in true alarm contexts that match the predatory threat type, either aerial or terrestrial, in which model species produce these alarm calls. Mimicked alarms were also produced alongside corresponding drongo-specific alarm call types, suggesting that they supplement these, rather than providing a distinct function in this species.

Previous research has similarly found that species which mimic alarm calls, often do so in the appropriate context for the alarm call type. A study by Goodale & Kotagama (2006) shows that Greater Racket-tailed Drongos mimic the vocalizations of predators, heterospecific alarm calls and more specifically heterospecific mobbing calls while mobbing a terrestrial predator. However, this study did not fully examine the use of aerial alarm call mimicry by the Greater Racket-tailed Drongo. More recent research by Igic & Magrath (2014) showed that the Brown Thornbill changed the types of alarm calls used according to the type of threat faced, thus creating mimicked mob calls at the terrestrial predator model and mimicked aerial alarm calls at the aerial predator model. Brown Thornbills alarmed most frequently when they were captured and when their nest was being attacked and less frequently to aerial and terrestrial predatory threats (Igic & Magrath 2014). However, neither of these studies provided data on the responses of species to natural predator threats. Here we show that context-specific mimicry is produced to both experimentally presented, and natural aerial and terrestrial threats, and thereby provide the necessary evidence of this behaviors' occurrence in the wild.

Such context-specific mimicry is important for the functional use of vocal mimicry, because mimetic calls must be produced within a specific context to illicit the appropriate behaviour in receivers that benefits the signaler. With respect to alarm calls, aerial alarms typically cause receivers to flee to cover, while terrestrial mobbing alarms typically recruit receivers to harass and deter predators. Such context-specific alarm mimicry of aerial and terrestrial alarm calls could function to illicit such responses in heterospecifics. What remains unclear is precisely why this would benefit the vocal mimic, in this case, the Fork-tailed Drongo. Terrestrial mob mimicry may function to recruit other species to help mob a predator, thereby decreasing the drongos risk of predation. Mimicked aerial alarm calls probably functions to cause conspecifics and heterospecifics to flee. This mass movement could confuse the predator, giving the drongo a better chance to escape and in so doing decrease the hunting success of the predator (Caro 2005).

The prevalence of drongo alarm mimicry in response to terrestrial predators, and bias towards terrestrial alarm mimicry, suggests that these calls could indeed function in the attraction of other species to mob and deter the predator, or even attract predators which might eavesdrop on avian alarm calls to locate prey. Many more alarms were produced at the snake model than at the hawk model. For one snake trial, a total of 646 alarm calls were made in the space of five minutes. In four of the six trials in which drongos alarmed at the snake model, other bird species came over to the location where the drongos were alarming. Species that responded to the mimicked terrestrial alarm calls included White-browed Sparrow weavers (*Plocepasser mahali*), Scimitarbills, Yellow-billed Hornbills (*Tockus leucomelas*), Crimson-breasted Shrikes (*Laniarius atrococcineus*) and drongos from neighboring territories. However, insufficient drongos alarmed at the terrestrial threat to determine whether these calls were more likely to attract other species compared with aerial alarm calls. In contrast, in only one of the hawk trials were heterospecifics recruited and the calls made were not mimicked alarm calls, but drongo-specific alarm calls. This result is supported by the natural data which shows that drongos preferentially use drongo-specific aerial alarm calls in the aerial alarm context. During the hawk trial, very few alarms were created. The most alarm calls produced in one trial was five alarm calls. Furthermore, in approximately 86% of the trials most, if not all, drongos present fled to cover once the hawk model was seen and an alarm made, rather than approaching the caller. This provides some support for the idea that there are different signals for different threat contexts that correspondingly require different responses (Seyfarth *et al*. 1980). Aerial alarm call mimicry also possibly has a function in terrestrial predator alarms, because the natural data suggests that drongos are more likely to produce mimicked aerial alarm calls than drongo-specific aerial alarms in response to terrestrial predators. However, more data is needed to show this conclusively. Although this study did not focus on possible functions for vocal mimicry, the fact that some heterospecifics came to the location where a drongo was alarming provides some evidence that alarm mimicry functions to recruit heterospecifics to mob a terrestrial predator. This supports research done by Chu (2001) that showed that when phainopeplas (*Phainopepla nitens*) were captured or in distress due to the presence of a predator, the use of mimicry in conjunction with their scream calls, elicited a stronger response from heterospecifics. More heterospecifics approached and mobbed a predator decoy when the phainopeplas scream call was played in combination with mimicry than when the scream calls were played alone (Chu 2001).

Aerial alarm mimicry probably does not have the same function as terrestrial mob mimicry (Igic & Magrath 2014). Instead, such aerial alarm mimicry may benefit drongos by causing heterospecifics to flee for cover, thereby confusing an attacking predator. Drongos spend over a quarter of their foraging time associating in mixed-species foraging flocks comprising over 25 different species within the Kalahari alone (Flower *et al* 2013). Consequently, mimicry could expand the range of species with which drongos can communicate, potentially representing a significant anti-predation benefit if flee responses reduce predation success.

Although a possible function of the use of heterospecific alarm calls may be to provide heterospecifics with information about predators, receivers of the alarm calls need to determine the relevance and reliability of the alarm calls being produced (Magrath *et al*. 2009). As stated previously, drongos and several other species (Møller 1988) can produce false alarm calls when foraging with heterospecifics (Flower 2011). For the most part, it would be more costly for an individual not to respond to an alarm call, regardless of whether or not it may be a false alarm call. However, if specific alarm calls are used too frequently, heterospecifics may stop responding to that alarm call all together (Magrath *et al*. 2009). This raises the intriguing possibility that drongos could therefore incorporate mimicry into their alarm calls to reinforce the relative honest frequency of these alarm call types. Recent research suggests that drongos do adjust their communication tactics in response to their audience, by producing specific sentinel signals for their heterospecific foraging mutualists (Baigrie *et al.* 2014). Similarly, when associating with other species, drongos specifically alarm at terrestrial predators that threaten associating species, but not the drongo itself, suggesting that they do alarm specifically for heterospecifics (Ridley *et al*. 2007). Vocal mimicry may consequently represent an adaptation to enhance the payoffs available to drongos from their deceptive false alarm behaviour.

Many authors believe that vocal mimicry is genetically encoded (Marler 2004), while others suggest that vocal mimicry is learnt (Kelley *et al.* 2008; Dalziell *et al.* 2014.) and that this learning process is not as difficult as other types of imitation (Goodale & Kotagama 2006b). However, most people do not take into consideration the difficulty of learning context-dependent mimicry. This type of learning would require the ability to remember information gathered from multiple stimuli. Animals would have to remember how to use that specific sound and in what context using that sound would be appropriate (Janik & Slater 2000). This means that the animal must be able to remember information collected from different stimuli at different times and under different conditions and then from this information, choose which call would be appropriate to use in the situation that the animal finds itself (Goodale & Kotagama 2006b).

If vocal mimicry is learnt, Fork-tailed Drongos could learn it within mixed-species flocks (Goodale & Kotagama 2006b). In these mixed-species flocks, drongos are constantly exposed to the alarm calls of other species. If a predator is in the area, many species could alarm simultaneously, exposing drongos to a multitude of heterospecific alarm calls as well as teaching drongos the context in which these calls were made. Drongos can also learn these mimicked alarm calls from other drongos. Juvenile Fork-tailed Drongos may also learn to use false alarm calls deceptively. Juvenile drongos often follow adults while they are foraging with other species. In these associations, adults commonly use false alarm calls to steal food, exposing the juveniles to this behaviour, but also produce mimicked ‘true’ alarms to approaching predators (Flower 2011).

A small sample size probably had a big effect on the results from the experimental data. In future, treatments should be conducted on more drongo groups. A possible problem with the hawk treatment was the relatively short time that the hawk model was airborne which potentially reduced the number of alarms made and therefore the likelihood of recording alarm mimicry. A similar problem was faced by Igic and Magrath (2014). Brown thornbills (*Acanthiza pusilla*) are able to mimic a wide range of heterospecific alarm calls and in so doing, convey information about predators to heterospecifics as well as conspecifics (Igic & Magrath 2014). A sparrowhawk glider was similarly used as an aerial predator and it was thrown in the presence of a pair of brown thornbills (Igic & Magrath 2014). However, in the wild, hawk attacks often occur quite quickly, so if one were to look at how drongos respond to an aerial predator during an attack, short flight times would provide the most accurate result. Longer flights may then provide non-relevant results. In reality, to get the most accurate idea of how drongos respond to an aerial predator, a real raptor would have to be present. In this regard, analyses of natural responses to predators provide a significant advance on previous studies. Nevertheless, small sample sizes for terrestrial predators prevented more detailed analysis of the frequencies of alarm calls to predator types and data were restricted to whether mimetic alarm calling was observed or not. Such small sample sizes for alarms at terrestrial predators are perhaps unsurprising since drongos rarely alarm at terrestrial predators they observe when foraging alone since these do not present a threat to them (Ridley *et al*. 2007).

Although drongos only alarmed at the frisbee six out of the twenty-one trials, this was higher than expected for a control model. There is some evidence that some species are not able to discriminate between which stimuli are threatening and which are non-threatening (Magrath *et al*. 2009). Orange-billed Babblers (*Turdoides rufescens*) occur within mixed-species flocks in Sri Lanka and do not discriminate between fast moving aerial predators that genuinely are a threat and fast moving harmless objects. This could similarly have been the case with the frisbee trial, though some discrimination clearly occurred since drongos alarmed at the hawk model stimulus more than twice as often as they did to the Frisbee model.

Further research has to be done to understand why some birds include vocal mimicry in their repertoire, while most use only conspecific alarm calls. We also need to determine how many species acquire and produce context-specific alarm mimicry. An interesting concept for future study would be to determine whether or not drongos still produce context-dependent mimicry when contexts are slightly switched around. For example, do drongos produce aerial alarm mimicry when an aerial predator is on the ground? The next question would be, do drongos produce terrestrial mob mimicry when a terrestrial predator, like a snake, is high in a tree? Brown thornbills produce terrestrial mob mimicry when aerial predators, like Pied Currawongs *(Strepera graculina),* are perched. They therefore do not produce mimicked aerial alarm calls at aerial predators if they are perched (Igic & Magrath 2014). This is however only one case where a species selectively produces terrestrial mob mimicry in response to a perched aerial predator and more research needs to be done to determine whether or not this is the case for other bird species that use mimicry. The benefits of using mimicry in the presence of a predator still needs to be fully tested. This can be done by looking at how exactly heterospecifics react to these mimicked alarm calls.

In summary, using both natural as well as experimental data, I have shown that Fork-Tailed Drongos indeed use context-specific mimicry and provide the first evidence of this behaviour under natural conditions. We can see that aerial and terrestrial mimicry probably have different functions when produced within these contexts. Aerial alarm mimicry likely functions to prompt heterospecifics to flee, while terrestrial mob mimicry functions to attract heterospecifics to aid in the mobbing of terrestrial predators. If such context-dependent alarm mimicry is learnt, the drongos probably learn this in mixed-species flocks. However, to learn such context-dependent mimicry is much harder than learning simple song. My research and that of others like Igic and Magrath (2014) go a long way to improve our understanding of mimicry as a whole, but what the functions of such context-dependent alarm mimicry are, remains to be determined.

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