

# Context-dependent vocal mimicry in a passerine bird

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How do birds select the sounds they mimic, and in what contexts do they use vocal mimicry? Some birds show a preference for mimicking other species' alarm notes, especially in situations when they appear to be alarmed. Yet no study has demonstrated that birds change the call types they mimic with changing contexts. We found that greater racket-tailed drongos (*Dicrurus paradiseus*) in the rainforest of Sri Lanka mimic the calls of predators and the alarm-associated calls of other species more often than would be expected from the frequency of these sounds in the acoustic environment. Drongos include this alarm-associated mimicry in their own alarm vocalizations, while incorporating other species' songs and contact calls in their own songs. Drongos show an additional level of context specificity by mimicking other species' ground predator-specific call types when mobbing. We suggest that drongos learn other species' calls and their contexts while interacting with these species in mixed flocks. The drongos' behaviour demonstrates that alarm-associated calls can have learned components, and that birds can learn the appropriate usage of calls that encode different types of information.

**Keywords:** alarm calls; context-dependent mimicry; *Dicrurus paradiseus*; mixed-species flocks; mobbing calls; vocal mimicry

## 1. INTRODUCTION

Vocal learning is considered by cognitive scientists to be a special form of social learning that is not as complex as other forms of imitation (Shettleworth 1998). This is because motor output can be directly compared to audio input; in contrast, visual imitation (imitating the externally visible actions of another organism) is considered to require greater cognitive processing because the performer often cannot see the output in order to compare it to the input (Bryne 2005). But vocal learning is not simply a process by which animals learn to produce a particular sound: in some cases animals also learn how to use that sound, and in what contexts it is appropriate (Janik & Slater 2000). Such contextual vocal learning requires the cognitive capacity to store information from multiple stimuli detected at different times and in different conditions, and then choose, from among the different sets of stored information, the set appropriate for the current condition (Pepperberg 1998).

Bird song has been a major model for vocal learning, and thus the study of contextual learning has focused for birds on how they learn to match the songs of other individuals (Burt *et al.* 2002) or learn the sequence of different songs in a song repertoire (Todt & Hułtsch 1996). But birds also have a large repertoire of calls that encode different types of information, such as the presence of food or predators (Marler 2004). Although many calls are believed to be unlearned, evidence is accumulating that some are copied from other individuals (Mundinger 1970; Nowicki 1989; Wright 1996). If a bird has the potential to learn an array of different calls, this leads to

the question of whether birds have the cognitive capacity to learn the context of these different calls as well.

One way to study the contextual learning of bird calls is to investigate birds that mimic other species. If a bird mimics the calls of a diversity of other species accurately, one can trace the source and context of the modelled calls and then determine whether mimicry is random or whether certain calls are used only in certain circumstances. One laboratory study has focused on African grey parrots (*Psittacus erithacus*), which have learned to use English words both referentially (as labels) and functionally (to produce a result; Pepperberg 1998). In-depth field studies of wild birds, however, have yet to show systematic non-random patterns in sound selection (Hindmarsh 1984; Chu 2001). Some authors have noted that birds appear to preferentially mimic the calls of predators or the alarm or mobbing calls of other birds (Robinson 1974; Greenlaw *et al.* 1998) especially during alarm contexts (Chisholm 1932; Vernon 1973; Morton 1976). But, as yet, no study has shown that birds change the calls they mimic depending on the context.

We here investigate whether birds have the cognitive capacity to learn the context of calls, by studying the greater racket-tailed drongo (*Dicrurus paradiseus*), a species renowned for the accuracy of its mimicry (Ali & Ripley 1987; Henry 1998). We have previously studied the alarm calls of drongos and other species that participate with them in mixed-species flocks in Sri Lanka (Goodale & Kotagama 2005). We found that drongos were imitating the alarm calls of other species, as well as their songs and contact calls. In the current study, we investigated two questions. We first examined whether drongos preferentially mimic alarm-associated calls.

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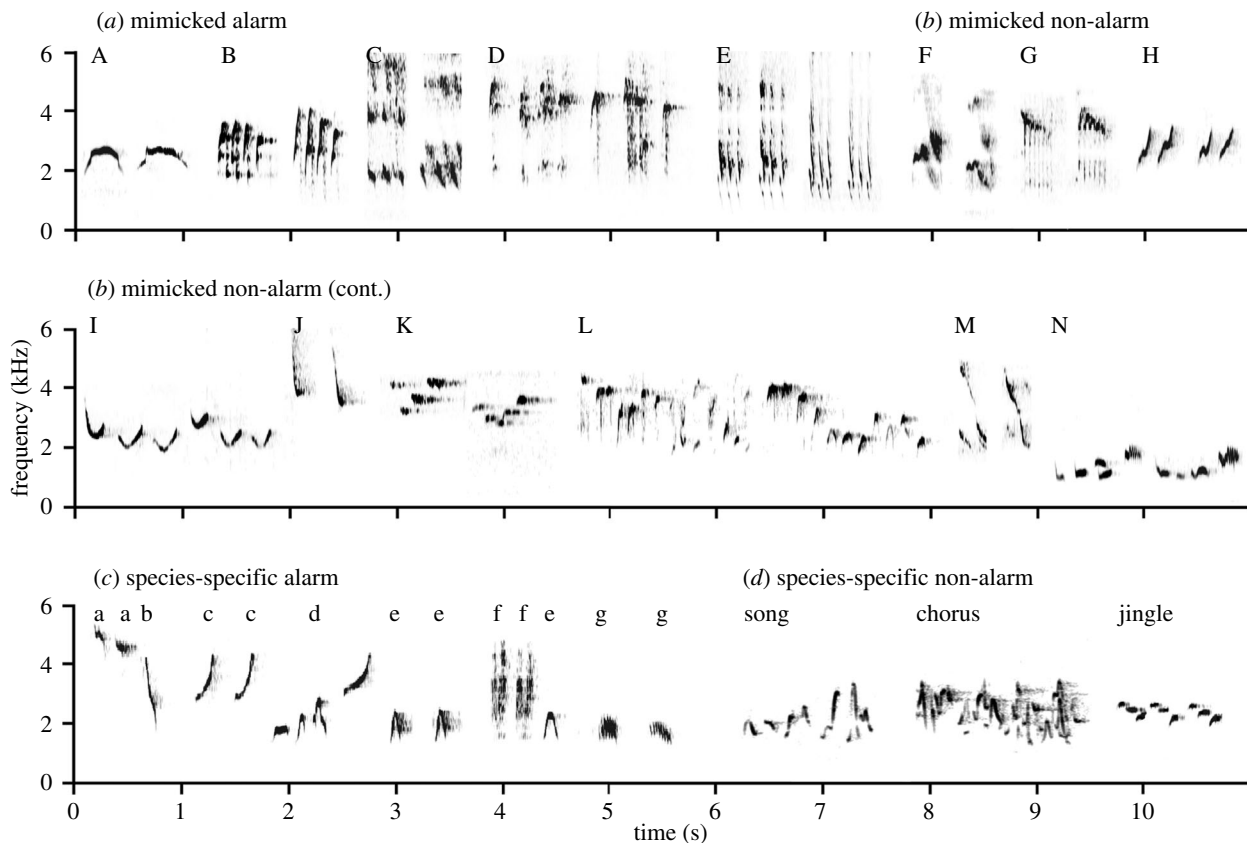


Figure 1. Spectrograms of the four categories of drongo notes: (a) mimicked alarm notes, (b) mimicked non-alarm notes, (c) species-specific alarm notes and (d) species-specific non-alarm notes. Uppercase letters represent the different types of mimicry recorded from at least three birds, as listed in table 1; a vocalization of the modelled species is followed by the imitation of a drongo. Lowercase letters designate the seven types of drongo alarm notes.

Then we investigated whether drongos selectively produce alarm mimicry when they are in alarm contexts.

## 2. MATERIAL AND METHODS

We observed and recorded drongos in the Sinharaja World Heritage Reserve (6°26' N 80°21' E, 450–600 m above sea level), a rainforest in Sri Lanka, between July and December, 2003. We banded seven drongos, and extensively radio-tracked four birds (radio-transmitters were designed by Wildlife Materials, Carbondale, IL and placed on birds in a manner similar to Rappole & Tipton 1991). After we found that drongos' home-ranges were less than 1.5 km in diameter, we recorded the seven banded drongos and unbanded drongos in four separate sites at least 1.5 km away from each other. To make a recording, one observer tape-recorded the focal bird's vocalizations, while another observer watched the bird with 8×42 binoculars, verbally noting when the focal bird vocalized. We recorded using a Sennheiser ME 62 omnidirectional microphone, a Telinga parabolic reflector and a Marantz PMD 430 cassette recorder. A recording started when both observers focused on the same bird and ended when the bird flew to a perch on which it could no longer be seen.

For acoustic analysis, we digitized each recording from start to finish, thus including the drongo's species-specific vocalizations as well as mimicry (sampling rate of 22 050 Hz on Avisoft v. 3.9, Berlin, Germany). We identified mimicry, by comparing the spectrograms of the drongo calls to spectrograms of other species' calls recorded throughout the reserve (spectrograms were 1020 point FFT, equivalent to a

frequency bandwidth of 56 Hz; figure 1). A total of 145 recordings included mimicked calls. All seven marked birds mimicked, although there were relatively few recordings from each (range 1–17 recordings with mimicry per bird; mean 6), and we exclude from further analysis two birds with less than three recordings with mimicry. The four sites at which unbanded birds were recorded were sampled more heavily (range 17–30 recordings with mimicry per site; mean 22).

We first investigated whether drongos preferentially mimic calls associated with alarm. Alarm mimicry was defined as the imitation of a predator, nest-predator or the alarm or mobbing call of another species; non-alarm mimicry was defined as the imitation of the song or contact call of a non-threatening species. We found 12 different types of alarm mimicry and 20 types of non-alarm mimicry (table 1). For each type of mimicry, we found the proportion of drongo recordings in which it was included, averaging across the nine independent sets of recording (five marked birds and four separate sites). The frequency of mimicry was then compared to a sample of 263 15 s duration recordings of the acoustic environment inside mixed flocks, in which drongos spend the majority of their time (two-third of observations of drongos in this study were inside flocks; vocal birds outside of flocks could also be heard in these recordings). Through linear regression, we investigated the relationship between the proportion of flock trials in which a call type was produced by the modelled species and the proportion of drongo recordings in which it was mimicked; proportion variables were square root transformed to improve normality. An ANCOVA

Table 1. The species imitated by drongos. Only those types of mimicry recorded from at least three different drongos are listed.

modelled species		recordings	birds <sup>a</sup>
<i>predators (total of two species)</i>			
A	crested serpent eagle <i>Spilornis cheela</i>	25	8
<i>nest predators (total of two species)</i>			
B	Sri Lanka blue magpie <i>Urocissa ornata</i>	58	9
<i>alarm calls (total of four species)</i>			
C	orange-billed babbler <i>Turdoides rufescens</i> 'cuk'	16	6
<i>mobbing calls (total of four species)</i>			
D	ashy-headed laughing-thrush <i>Garrulax cinereifrons</i> 'high-pitched emphasis'	11	5
E	orange-billed babbler 'stacatto chatter'	7	4
<i>song/contact calls (total of 20 call types of 15 species)</i>			
F	orange-billed babbler 'babble'	65	10
G	ashy-headed laughing-thrush 'ting'	32	9
H	yellow-browed bulbul <i>Iole indica</i>	31	9
I	common iora <i>Aegithina tiphia</i>	22	6
J	white-faced starling <i>Sturnus albobronnatus</i>	15	8
K	tickle's blue flycatcher <i>Cyornis tickelliae</i>	10	4
L	ashy-headed laughing-thrush 'song'	7	4
M	ashy-headed laughing-thrush 'laugh'	7	4
N	indian scimitar babbler <i>Pomatorhinus horsfieldii</i>	5	3

<sup>a</sup> The most conservative estimate of the number of drongos represented by the recordings.

determined whether this relationship was different for alarm mimicry as compared to non-alarm mimicry.

We then analysed whether mimicry was used in a context-dependent manner, by using the number of the drongo species-specific alarm notes within a recording as a measure of the alarm context. We categorized each note (defined as a continuous trace on a spectrogram) on the 145 recordings as one of four types: (i) mimicked alarm note; (ii) mimicked non-alarm note; (iii) drongo species-specific alarm note—one of seven note types associated with alarm (figure 1), which together comprised 79% of 1705 notes in a dataset of 39 alarm calls made to aerial predators or predator models (Goodale & Kotagama 2005; alarms are often long in duration and may also function as mobbing vocalizations); and (iv) drongo species-specific non-alarm note. Drongo non-alarm vocalizations include simple, variable notes jumbled together, sung individually or in a chorus of several birds (for a description of one anomalous call type, the jingle, see §4). We then tested for the correlation between the proportion of the drongos' species-specific notes that were of alarm type and the proportion of mimicked notes that were of alarm type. Correlation coefficients were calculated using Spearman's rank-order test for the nine sets of independent recordings separately, and the overall significance level adjusted by the Dunn-Šidák method (Sokal & Rohlf 1995).

We also specifically investigated drongo mimicry of other species' mobbing calls. Earlier studies indicated that two flocking babbler species, the orange-billed babbler (*Turdoides rufescens*) and the ashy-headed laughing-thrush (*Garrulax cinereifrons*), produce specialized call types when they encounter ground predators (Goodale & Kotagama 2001, unpublished data). We tested whether drongo renditions of these two call types were included in the same vocalization bout more than would be expected by chance, using a *G*-test for independence with Williams correction (Sokal & Rohlf 1995) and including in the analysis an additional 10 observations of mobbing mimicry collected during several years previous to this study.

### 3. RESULTS

Drongos mimicked alarm-associated calls more than would be expected by their frequency of occurrence in the acoustic environment. Although drongos preferentially mimicked both alarm and non-alarm call types that were common in the acoustic environment (non-alarm mimicry:  $F_{1,18} = 32.20$ ,  $p < 0.0005$ ,  $r^2 = 0.64$ ; alarm mimicry:  $F_{1,10} = 1.66$ ,  $p > 0.20$ ,  $r^2 = 0.14$ ), the drongos mimicked alarm call types out-of-proportion to their mimicry of non-alarm call types (figure 2). Especially noticeable was the high rate of mimicry of the calls of a nest predator, the Sri Lanka blue magpie (*Urocissa ornata*) and a predator, the crested serpent eagle (*Spilornis cheela*), which were heard just once and twice, respectively, in 263 recordings of flocks and background sounds.

As drongos used more of their own species-specific alarm notes, they increasingly incorporated more of the alarm-associated notes of other species (figure 3). All nine independent sets of recordings showed positive correlations between the proportion of species-specific alarm notes and the proportion of mimicked notes associated with alarm, and in two of these sets, both samples from sites with large sample sizes, the correlation was statistically significant ( $r_s = 0.684$ ,  $n = 25$ ,  $p_{\text{adj}} < 0.002$  and  $r_s = 0.856$ ,  $n = 14$ ,  $p_{\text{adj}} < 0.001$ ). Four of the five marked birds, all with relatively small sample sizes, had regression coefficients greater than 0.60.

Drongos showed a further level of context specificity by mimicking other species' mobbing call types when performing mobbing behaviour. Drongos mimicked the two mobbing call types in a highly non-random way: on six of the seven occasions when the babbler mobbing call was recorded (representing at least four different drongos), the laughing-thrush mobbing call was also recorded (the latter call was heard on only five occasions by itself;  $G_{\text{cor}} = 22.13$ ,  $p < 0.0001$ ). Mobbing mimicry (as defined by the presence of one of these two call types) was accompanied by distinctive behaviour: in 11 of the 22 observations the

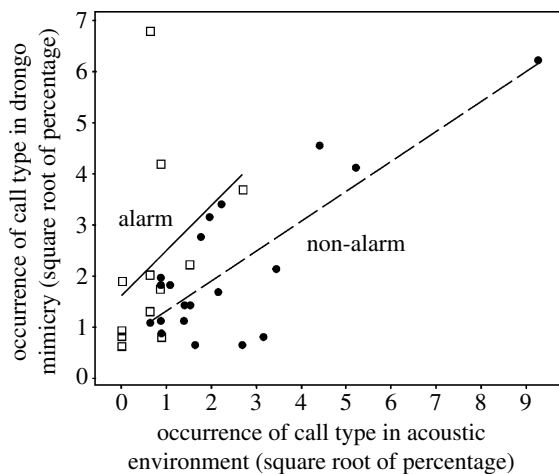


Figure 2. Drongos preferentially mimic alarm calls (open squares and solid regression line) to non-alarm calls (solid circles and dotted line) that occur in their acoustic environment (ANCOVA  $F_{1,29} = 4.63$ ,  $p < 0.04$ ).

calling drongo was within 2 m of the ground (unusual, since the drongo's average perch height is more than 5.5 m; Kotagama & Goodale 2004), and three times the drongo was obviously directing its calls towards the observer within 3 m of him.

#### 4. DISCUSSION

Drongos select sounds to mimic non-randomly and use these sounds with high context specificity. Drongos' selection of sounds to mimic is non-random in that alarm-associated notes are mimicked out-of-proportion to their frequency in the acoustic environment. Drongos' performance of mimicry is context-dependent in that they change the notes they select depending on the alarm context. In effect, drongos call like other species would do in a particular situation: they use the song and contact calls of other species in non-alarm contexts, alarm calls of other species in alarm contexts and the mobbing calls of other species when they mob a ground predator. Exceptions to this rule are the vocalizations of predators and nest predators, which drongos mimic in alarm contexts.

We believe that similar behaviour is likely to be found in a diversity of passerine birds. We know that other species of drongos practice the behaviour, as we have seen white-bellied drongos (*D. caerulescens*) mimic cat 'meow' calls and the alarm calls of squirrels while performing mobbing behaviour. Such behaviour is described matter-of-factly in the older ornithological literature: Vernon (1973) states that *D. adsimilis* 'imitates when it is alarmed and often includes the alarm notes of other birds', although he does not elaborate on how he judged the birds' level of alarm. The observations of Robinson (1974); Morton (1976); Greenlaw *et al.* (1998) and Chu (2001) suggest that the behaviour is found in oscine passerines throughout the world. The relationship between mimicry and the alarm context has not been clear in earlier studies, however, because observers have noted that some alarm-associated calls were incorporated into song (e.g. Remsen 1976; Greenlaw *et al.* 1998), and that some non-alarm mimicry occurred in distress situations (e.g. Chu 2001). It is probable that in these species, as in drongos, the correlation between the alarm context and the mimicry

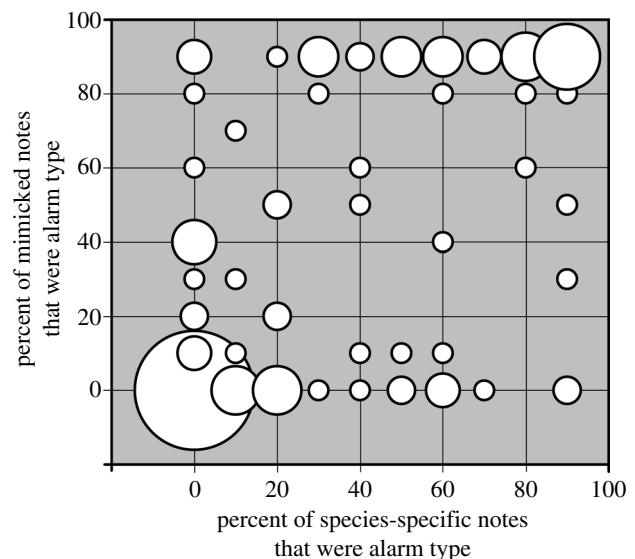


Figure 3. The more drongos use their own alarm notes, the more likely they are to use mimicked alarm notes of other species, too. Of the 129 recordings that included both drongo species-specific notes and mimicked notes, 36 contained no alarm content (largest circle in lower left; the size of the bubbles reflects the number of data points). In contrast, in recordings in which at least 30% of species-specific notes were of alarm type, nearly all mimicry was of alarm type. This pattern was shown by all nine independent sets of recordings (Binomial test, expectation 0.5,  $p < 0.002$ ). Data rounded to the nearest 10%.

of alarm-associated calls is far from perfect. The 'noise' in the data may be intrinsic to the behaviour, or may result from inadequate human knowledge about rapidly changing contexts.

The most parsimonious hypothesis for how drongos acquire their mimicked repertoire is that they learn it directly from the species they interact with in mixed flocks. Drongo fledglings are fed by their parents in mixed-species flocks, thus exposing the young birds to other species' vocalizations. Drongos may learn predator vocalizations from the response of the flock as a whole: e.g. when serpent eagles fly over a flock they sometimes vocalize, and several species may make alarm calls simultaneously. There is also some evidence that drongos can learn mimicry from other drongos. Birds in several sites sang the distinctive jingle call (see figure 1) that was always combined with mimicked notes and stands out from the rest of the drongo species-typical repertoire in its predictable, repetitive acoustic structure, yet, it is not clearly derived from any other species' call, and hence is likely to be transferred from drongo to drongo. Even if young drongos initially acquire their mimicked sounds by copying adult drongos, however, the behaviour of the other species in flocks would continuously reinforce the proper usage of these sounds.

Drongo mimicry demonstrates that alarm-associated calls can have learned components. Calls have been traditionally assumed to be genetically encoded (Lanyon 1960; Marler 2004), and those calls that are known to be learned are usually flight or contact calls (e.g. Mundinger 1970; Nowicki 1989). Previous studies have shown that the usage of mobbing calls can be altered by experience: Curio *et al.* (1978) demonstrated that a mobbing response could be transferred to a novel object through a form of

imprinting. Presumably, the birds in Curio's experiment did not learn to produce the sounds associated with mobbing, but only learned the context the sounds should be associated with. In contrast, our data and those of Chu (2001) clearly indicate that some species of birds can learn how to produce mobbing and distress calls as well as how to use them. Our study further shows that birds can learn the production and context of alarm calls are associated with imminent threats (Klump & Shalter 1984). For example, we once saw a drongo utter the alarm call of an orange-billed babbler immediately upon being startled by the sudden flight of another bird. Intuitively, one might assume that calls used in such rare and urgent situations would be 'hard-wired'. Yet drongo mimicry, as well as experiments that show chickens (*Gallus gallus*) can suppress producing alarm calls in certain conditions (Evans *et al.* 1993), indicates that even alarm calls can be labile as a result of experience.

Drongo mimicry also shows that birds can learn to use heterospecific calls in appropriate contexts under natural conditions. It has been widely shown that animals can learn to recognize the context of the vocalizations of other species and react in appropriate ways (e.g. Hauser 1988; Zuberbuhler 2002). But using heterospecific signals in a contextually appropriate way has been previously shown only in artificial conditions by parrots (Pepperberg 1998) and marine mammals (Ralls *et al.* 1985). To understand why some bird species learn to produce heterospecific vocalizations whereas most species produce only conspecific sounds (e.g. Marler & Peters 1977), and why a subset of mimicking species are able to use heterospecific signals contextually, will require further work on the function of mimicry in the field.

More generally, drongo mimicry demonstrates that birds are able to learn the appropriate contexts to an array of call types. Contextual learning has previously been demonstrated for songs, as birds are able to adapt their song repertoires in ways to match other individuals and even can learn the correct usage of song types that are used in different times of the day and for different audiences (Kroodsma 1988; Spector *et al.* 1989). But calls are different from songs in that they provide much more direct information about environmental conditions (Marler 2004). Although we cannot conclude drongo mimicry is used as a label for an environmental stimulus (and is thus 'referential', *in sensu* Evans *et al.* 1993) because mimicry could also reflect the animal's sense of risk (Blumstein 1999), mimicked calls do provide reliable information to receivers. The ability to imitate calls contextually would allow drongos to use a novel signal associated with a particular environmental condition to communicate information about the environment to conspecifics and possibly heterospecifics. But such learning also has potential costs, because the correct usage of a call is an essential part of the signal, and improper learning of the context would thus jeopardize effective communication.

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