

Original Article

A songbird mimics different heterospecific alarm calls in response to different types of threat

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Birds frequently mimic other species' alarm calls, but the type of information conveyed to receivers, and therefore the function of mimetic alarm calls, is often unknown. Alarm calls can convey predator-specific information that influences how receivers respond: aerial alarms signal the presence of flying predators and provoke receivers to flee, whereas mobbing alarm calls signal the presence of less dangerous predators and provoke receivers to mob. The function of mimetic alarm calls may therefore depend on the type of heterospecific alarm calls mimicked. We examined the use of alarm call mimicry by brown thornbills (*Acanthiza pusilla*) across different contexts of danger: terrestrial threat, aerial threat, when captured by a predator and during nest attack. Thornbills were most likely to include mimetic alarm calls among their vocalizations when captured and during nest attack, less likely in response to terrestrial and aerial predator threats, and least likely in the absence of any threat. Furthermore, the type of danger affected the type of mimetic alarm calls used: thornbills mimicked mobbing alarm calls in response to terrestrial threat and aerial alarm calls in response to aerial threat but also during capture and nest attack where no aerial danger was present. We suggest that mimicking predator-appropriate heterospecific alarm calls in response to aerial and terrestrial threats may facilitate interspecific alarm communication with other prey species, whereas mimicking heterospecific aerial alarm calls in the absence of aerial predators might deceptively startle predators to release captured callers or offspring when attacked.

Key words: *Acanthiza pusilla*, alarm communication, brown thornbill, context-dependent mimicry, predator type, vocal mimicry.

INTRODUCTION

It is estimated that 15–20% of songbirds worldwide incorporate sounds produced by other species or the environment (models) into their vocal repertoires (Baylis 1982). These species can differ in how they acquire mimetic vocalizations, which types of sounds they mimic, and how frequently and in which circumstances they use mimetic vocalizations (Kelley et al. 2008). Although mimetic function can depend on what types of sounds are mimicked and in which circumstances (Langmore et al. 2008; Flower 2011), this information is unknown for the majority of vocal mimics.

Heterospecific alarm calls are regularly mimicked in contexts of danger (Morton 1976; Goodale and Kotagama 2006; Kelley and Healy 2012; Igic and Magrath 2013), suggesting a possible role in avoiding predation. For example, greater racket-tailed drongos (*Dicrurus paradiseus*) are more likely to mimic alarm calls than non-alarm calls when they use their own alarm calls (Goodale and Kotagama 2006), whereas male spotted bowerbirds (*Ptilonorhynchus*

maculatus) mimic alarm calls more frequently when threatened by humans (Kelley and Healy 2012). Although a common function of nonmimetic alarm calls is warning kin and other conspecifics about predators (Caro 2005), the functions of mimetic alarm calls in alarm communication are poorly understood, and in some cases could be a nonadaptive side effect of learning mechanisms (Kelley et al. 2008; Kelley and Healy 2012).

One potential function of mimetic alarm calls is communicating information about predators to heterospecifics (Chu 2001a; Goodale and Kotagama 2006; Wheatcroft and Price 2013). Where species in a community share similar predators, they often benefit from information encoded in each other's alarm calls. Indeed, a variety of animals regularly eavesdrop on and respond appropriately to heterospecific alarms (Caro 2005; Zuberbühler 2009). Callers can also benefit from heterospecifics responding appropriately to their alarms; for example, a caller can reduce risks associated with mobbing predators by provoking heterospecifics also to mob predators (Ficken 1989). However, acoustic diversity in alarm call structure can impede interspecific alarm communication, and recognition of heterospecific alarm calls can require individuals to

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learn the association between heterospecific alarm calls and danger (Fallow et al. 2011; Magrath and Bennett 2012). By incorporating heterospecific alarm calls into alarm vocalizations, a mimic may bypass the need for nearby heterospecifics to learn to recognize the mimic's species-specific alarms. In support of this function, greenish warbler (*Phylloscopus trochiloides*) alarm calls that include copies of buff-barred warbler (*Phylloscopus pulcher*) alarm elements are better at provoking mobbing behavior by buff-barred warblers than greenish warbler alarms alone (Wheatcroft and Price 2013).

Another potential function of mimetic alarm calls is directly deterring predators from attacking the mimic (Dobkin 1979; Rowe et al. 1986). Mimicking heterospecific alarm calls may deter predators from attacking callers by causing predators to misidentify them as dangerous organisms (Rowe et al. 1986) or simulate the presence of other predators (Kelley and Healy 2012; Igic and Magrath 2013), either of which may startle predators or provoke other individuals to flee, increasing the mimic's chance of escaping predation. Although there is currently no evidence that mimetic alarm calls can function this way, there is evidence that mimicry of predator sounds can deter potential attackers. Mimicry of rattle snake (*Crotalus viridis*) rattling produced by burrowing owls (*Athene cunicularia*) when disturbed in the nest deters a mammalian competitor from entering occupied burrows and thereby possibly prevents owls from being evicted (Rowe et al. 1986). As predator sounds can convey similar information to heterospecific alarm calls (Schneider and Griesser 2012), mimicry of alarm calls and predator sounds could potentially have similar functions. Indeed, predator sounds and heterospecific alarm calls are regularly mimicked in similar contexts (Ratnayake et al. 2010; Kelley and Healy 2012).

As an alternative to functional hypotheses, alarm mimicry might be a nonadaptive consequence of learning. Mimicry of heterospecific alarm calls in contexts not associated with alarm (inappropriate contexts) can suggest that heterospecific alarms are learnt and used by mistake (Hindmarsh 1986; Kelley et al. 2008). Indeed, some species mimic heterospecific alarm calls in nonalarm contexts, such as during song (Greenlaw et al. 1998), whereas others appear to be nonselective in the types of sounds they mimic in alarm contexts (Chu 2001b). Heterospecific alarm calls may be particularly susceptible to being learnt by mistake because their acoustic structure is often simple (Marler 1955; Hindmarsh 1986) and because they are usually heard in stressful contexts, which might facilitate learning and perhaps even production in circumstances of stress (Kelley and Healy 2011, 2012). Although nonadaptive processes might lead to some context specificity of mimetic alarm call use, examining the contexts in which heterospecific alarm calls are mimicked can help identify both intended receivers and potential functions.

We suggest that context-specific mimicry of different types of alarm calls can help identify the function of mimicry. Different predators can pose different types of threat (Caro 2005), and alarm calls often convey predator-specific information, such as predator type (Seyfarth and Cheney 1980; Evans et al. 1993), level of risk (Blumstein 1999), or predator behavior (Griesser 2008), which in turn influences how receivers respond. In general, aerial alarm calls are produced in response to flying avian predators and provoke receivers to flee and take cover (Leavesley and Magrath 2005), whereas mobbing alarm calls are produced in response to terrestrial, or perched avian, predators and provoke receivers to inspect or mob the source of danger (Curio et al. 1978). How receivers respond to mimetic alarm calls can also depend on the type of information their corresponding model alarm call conveys. For example, mimetic aerial alarm calls can provoke receivers to flee

(Flower 2011), whereas mimetic mobbing alarm calls can provoke receivers to mob (Goodale et al. 2014; Wheatcroft and Price 2013). Therefore, the preferential use of mimetic aerial or mobbing calls in specific contexts, rather than merely alarm calls in stressful contexts, suggests that mimicry could be adaptive. Furthermore, the function of mimetic alarm calls may also depend on whether they are used to communicate reliable information about predators (Wheatcroft and Price 2013), or inaccurate and potentially deceptive information (Flower 2011). Deceptive use may be implied when mimetic alarms are used in different contexts to species-specific equivalents (Flower 2011). No study has yet specifically tested whether different types of alarm calls are mimicked in response to different types of danger or whether mimetic alarm calls are used with their species-specific equivalents.

Here, we examined the use of alarm call mimicry by brown thornbills (*Acanthiza pusilla*) in different contexts of danger. Thornbills are competent vocal mimics with the capacity to mimic a range of acoustically diverse heterospecific alarm calls that convey different types of predator-specific information (Figure 1; Igic and Magrath 2013). Furthermore, thornbills commonly mimic heterospecific aerial alarm calls when captured in mist nets (Igic and Magrath 2013), suggesting they might be selective regarding the types of heterospecific alarm calls they mimic. In this study, we test whether thornbills mimic alarm calls specifically in dangerous contexts, and if so whether they mimic different types of alarm calls in different contexts. Thornbills also produce different species-specific alarm calls in response to aerial and terrestrial threats (Igic and Magrath 2013), presenting an opportunity to test if mimetic and nonmimetic alarm calls convey similar types of predator information. We recorded individually marked thornbills while foraging and undisturbed, and in the presence of 4 different types of experimentally simulated danger: terrestrial threat, aerial threat, capture by a predator, and nest disturbance. First, we tested if thornbills were more likely to mimic sounds associated with danger, including alarm calls and predator calls, in contexts of danger. Second, we tested if thornbills mimicked aerial and mobbing alarm calls in response to different types of danger. Third, we tested if mimetic aerial and mobbing calls were used in similar contexts to equivalent nonmimetic alarm calls.

METHODS

Study site and species

We studied a color-banded population of brown thornbills in the Australian National Botanic Gardens, Canberra, Australia (35°16'S, 149°6'E) where most birds are habituated to human presence. Thornbills are a 6–8-g, long-lived (up to 17 years) passerine, common, and endemic to southeastern Australia (Higgins and Peter 2002). They breed in pairs, and both sexes defend year long territories against conspecific intruders. The typical breeding season is between July and December, during which pairs produce between 1 and 3 clutches, but generally only a single brood is raised successfully to maturity per year as a result of high rates of nest predation (Green and Cockburn 1999; Green 2001).

Recording and experimental protocol

We recorded vocalizations produced by brown thornbill mated pairs ($n = 33$ pairs) in the absence and presence of threat, near and away from their nest (see contexts a–f, outlined below). These contexts are defined by both the presence of visual cues (e.g., presence

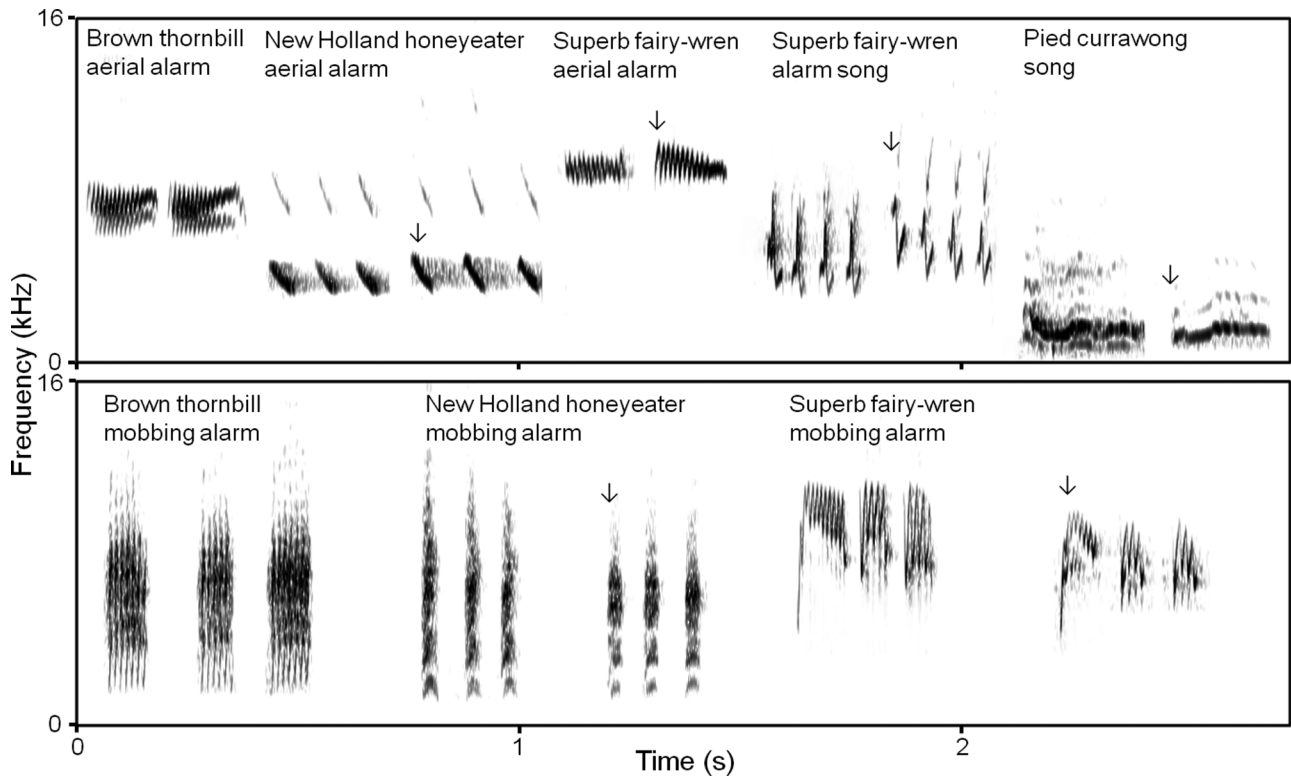


Figure 1

Spectrograms of brown thornbill nonmimetic alarm calls, New Holland honeyeater (*Phylidonyris novaehollandiae*) and superb fairy-wren (*Malurus cyaneus*) alarm calls, pied currawong (*Strepera graculina*) song, and corresponding brown thornbill mimicry (arrows). The top panel illustrates mimicry associated with nonmimetic aerial alarm calls and the bottom panel illustrates mimicry associated with nonmimetic mobbing alarm calls.

of a predator) and auditory cues (e.g., alarm calls of other individuals). We recorded birds using a hand-held Sennheiser ME66 directional microphone, with the exception of birds foraging near their nest, which we recorded using a Sennheiser ME62 omnidirectional microphone placed on the ground 3 m in front of the nest. Microphones were connected to a Marantz PMD671 digital recorder, either using a 1 m cable for the directional microphone or a 15 m cable for the omnidirectional microphone. Recordings were saved in a wave file format at 44.1 kHz and 16 bits. All recordings were collected between March 2010 and August 2011.

Context (a): no danger away from nest

We made 5 min focal observations and recordings of thornbill pairs during undisturbed activity away from their nest. Recordings started after identification of focal individuals and were collected by a single observer following pairs from distances that minimized disturbance and produced clear recordings (generally between 5 and 30 m). We excluded recordings where focal birds displayed aggressive behavior to conspecific intruders because attributing vocalizations to specific thornbills was difficult. In total, we collected 24 recordings ($N = 13$ pairs) outside the breeding season and 13 recordings ($N = 11$ pairs) between the start of nest building and start of egg incubation.

Context (b): no danger near nest

We recorded pairs with nestlings while undisturbed near their nest. We recorded parental vocalizations for 60 min, starting 20 min after setting up the recording equipment, and immediately after a feeding visit to reduce the likelihood that our presence, or the presence

of predators, was affecting parental behavior. During recordings, an observer made focal observations using binoculars from a hide placed 15 m from the nest. We protected nests using green wire mesh to reduce any impact our presence near nests might have had on nest predation. Cages were built at least 2 weeks prior to recordings and removed after nestlings fledged. Mesh size excluded medium-sized predators while allowing free access to parents with minimal impact on behavior (Haff and Magrath 2011). In total, we recorded at 14 nests ($N = 14$ pairs) when nestlings were between 6 and 9 days old and extracted the first 10 min to use for our analyses.

Context (c): terrestrial threat

We recorded vocalizations of thornbill pairs when mobbing a stationary avian predator on the ground. We used a taxidermic mount of a Southern boobook owl (*Ninox novaeseelandiae*), a predator of small birds (McNabb 2002), and recordings of white-browed scrubwren mobbing vocalizations (*Sericornis frontalis*), a species common at our study site, to simulate a natural mobbing interaction (for details see Igic and Magrath 2013). Both taxidermic predator mounts and broadcasting recordings of heterospecific mobbing vocalizations are common techniques for provoking mobbing behavior and production of mobbing alarm calls by birds (Curio et al. 1978; Templeton and Greene 2007), and indeed they provoke similar behavior by thornbills as do real perched predators (Igic B, personal observation). We constructed 20 s playbacks of scrubwren mobbing vocalizations (187.7 alarms/min \pm 35.8 standard deviation) from recordings of scrubwrens mobbing humans or perched avian predators at our study site. We broadcast scrubwren mobbing to thornbill pairs on their territory through a Response Dome

Tweeter speaker connected to a custom-built amplifier and played from an Edirol R-09HR solid-state digital player. Once pairs were located on their territory, we placed the owl model and playback equipment nearby and started broadcasting scrubwren alarm calls. We placed the speaker facing up on the ground 50 cm from the owl. Scrubwren alarm calls were broadcast at 55 dBA from 4 m (average amplitude measured over 20 s) calibrated using a Brüel & Kjær integrating-averaging sound level meter (model type 2240). If 20 s of scrubwren mobbing vocalizations were not sufficient in provoking thornbill pairs to come within 10 m of the model, we replayed the same 20 s sequence of scrubwren alarm calls. Pairs that did not come within 10 m of the owl after the second loop of scrubwren alarm calls were excluded from our analysis. We recorded thornbills for as long as they were within 10 m of the owl and extracted 2 min from these recordings starting from the first thornbill vocalization recorded after scrubwren mobbing playbacks stopped. We analyzed 2 min per recording because it sampled a sufficient number of vocalizations (Supplementary Table 1). Furthermore, long sampling periods are likely to run in to problems of habituation. A single observer recorded birds from a distance of 15 m from the owl model. Although we presented all pairs with the same owl model, we tried to limit pseudoreplication by presenting each pair with a unique mobbing playback. Behavior of birds quickly returned to normal following owl model and playback presentations, and therefore, our methods were unlikely to have any long-term detrimental impacts. In total, we collected 10 recordings outside the breeding season ($N = 10$ pairs) and 10 recordings of pairs between the start of nest building and start of incubation ($N = 10$ pairs).

Context (d): aerial threat

We recorded vocalizations produced by thornbill pairs toward aerial predators by throwing a gliding sparrowhawk model in the presence of thornbill pairs (for details see Igic and Magrath 2013). Gliding model predators are effective in prompting aerial alarm vocalizations from many species of birds and provoke similar aerial alarm calls as real predators (Magrath et al. 2007; Fallow et al. 2011). We presented the gliding model to social pairs on their territory, outside the breeding season, and while they were foraging. A single observer threw the gliding model and simultaneously recorded pairs from within 10 m. The models typically flew for 1–3 s, so we presented the model 5 times per pair ($N = 10$ pairs) to collect sufficient samples of vocalizations. Although we presented all pairs with the same gliding model, studies of other local passerine species show that different gliding models and real predators prompt similar aerial alarm calls (Magrath et al. 2007; Fallow et al. 2011). Furthermore, the model flew differently on different throws so that there was variability in predator “behavior” within this context. Behavior of birds quickly returned to normal after gliding predator model presentations. We limited disturbance to pairs by generally presenting the model once per day. For our analysis, we only included vocalizations produced by thornbill pairs while the glider was in flight.

Context (e): capture by a predator

To sample vocalizations produced by thornbills when captured by predators, we recorded individual thornbills while being extracted from mist nets during routine banding procedures (for details see Igic and Magrath 2013). Behavior of birds during mistnet capture reflects the behavior of individuals when attacked or captured by predators in the wild (Norris and Stamm 1965; Stefanski and Falls 1972a, 1972b; Conover 1994; Chu 2001a; Møller and Nielsen 2010) and therefore is a useful technique to examine the response of individuals in contexts of extreme danger. Birds were recorded

for the duration of removal (mean duration \pm standard error: 3 ± 0.97 min) from mist nets using a directional microphone held 20 cm away from the bird by an observer and while another person extracted birds. All captured birds were released 5–30 min after being captured, returned to normal activity shortly after release, and were subsequently seen alive on a later date. In total, we included 14 thornbills ($N = 12$ pairs) recorded outside the breeding season and 10 thornbills ($N = 9$ pairs) recorded following the start of breeding. We used full-length recordings in our analysis.

Context (f): nest disturbance

We took advantage of routine nestling banding procedures to record vocalizations of thornbill parents during nest disturbance. When disturbed, nestlings produce distress calls that appear to provoke parents to mimic heterospecific vocalizations (Chandler 1909; Hindwood 1933). Natural nest predation events are difficult to anticipate and are rare when nests are protected. Therefore, we used the extraction of nestlings for banding procedures as a behavioral proxy for nest predation. One observer stood within 5 m of the nest and recorded parental vocalizations using the directional microphone, whereas another removed nestlings from the nest. We always took care to extract and return nestlings to the nest in the absence of predators nearby. Nestlings were banded and returned to the nest within 15 min. Parents never abandoned nests as a result of nestling banding procedures. In total, we recorded at 22 nests ($N = 19$ pairs), and for our analyses we extracted the first 2 min from recordings starting from the first parental vocalization following the onset of nestlings’ distress calls.

Ethics permissions

All experiments were conducted under permits from the Environment ACT, the Australian Bird and Bat Banding Scheme, the Australian National Botanic Gardens, and the Australian National University Ethics Committee (B.EEG.06.10).

Acoustic Analysis

We used spectrograms to categorize each thornbill vocalization as a 1) nonmimetic nonalarm vocalization, 2) nonmimetic aerial alarm call, 3) nonmimetic mobbing alarm call, 4) mimetic aerial alarm call, 5) mimetic mobbing alarm call, 6) mimetic predator vocalization, 7) mimetic alarm of unknown category (alarm calls whose context of production and function is unclear), 8) mimetic nonalarm vocalization, and 9) unknown vocalization (Supplementary Table 1). We generated spectrograms using Raven Pro 1.3 (Charif et al. 2008) and used them to identify calls based on their acoustic structure. We excluded all recordings where signal-to-noise ratio impeded accurate identification or where we could not identify if vocalizations were produced by the focal pair. Spectrograms were generated using a Hann window function, a temporal grid resolution of 5.8 ms with 50% overlap and a frequency grid resolution of 172 Hz. We identified mimicry and vocalization types by inspecting spectrograms and listening to recordings of thornbill and sympatric heterospecific vocalizations (protocol described in Igic and Magrath 2013). Visual inspection of spectrograms produces similar results to quantitative spectrogram analysis when identifying thornbill mimetic vocalizations (Igic and Magrath 2013). We categorized thornbill vocalizations as mimetic if they were similar to vocalizations of sympatric heterospecifics and nonmimetic vocalizations if they did not show resemblance to any heterospecific vocalizations. We used recordings of vocalizations produced by heterospecifics toward real or simulated predators and published literature to identify if a mimetic

heterospecific vocalization was an alarm call, and if so, if it was an aerial, mobbing, or another type of alarm call (see [Igic and Magrath 2013](#) for details). Thornbill nonmimetic alarm calls were identified as the most common type of vocalization produced by thornbills toward real and simulated predators. We scored vocalizations as “unknown” if they could not be easily categorized. Mimetic alarms of unknown category, mimetic predator vocalizations, and unknown vocalizations were all uncommon ([Table 1](#)).

Statistical analyses

Mimicry of sounds of danger across contexts

We used a generalized linear mixed model (GLMM) to test if thornbills were more likely to mimic sounds associated with danger in contexts of danger. Comparing usage of mimicry would help in identifying the contexts in which mimicry is most likely to be functional ([Kelley and Healy 2012](#)). We included mimicry of both heterospecific alarm calls and predator vocalizations because predator vocalizations can convey similar information to heterospecific alarm calls ([Ratnayake et al. 2010](#); [Schneider and Griesser 2012](#)). For each recording, we calculated the relative proportion of mimetic sounds of danger from the total number of vocalizations produced by pairs. We compared the proportion of mimetic sounds of danger from total calls produced, rather than comparing the total number of calls produced or rate of production ([Kelley and Healy 2012](#)), because it controls for differences in vocalization patterns and sampling duration among contexts. This is, in part, because calling was

not always uniform within recordings, and therefore, measuring calling rate can be difficult and may produce inaccurate results. In addition, the choice of a sampling period could influence apparent calling rate, such as whether to time exposure to a hawk model from the launch of the model or from the first call. Furthermore, the rate of mimetic calling is not obviously a more meaningful measure than the proportion of mimicry among total calls. For example, if the rate of mimicry increased in a particular context, but less so than the overall rate of calling, then the proportion of mimicry declines. By using proportions, the overall rate of calling of any type provides the context to judge the relative prominence of mimicry within the sample period. We fit a GLMM with the proportion of mimetic sounds of danger from total vocalizations as a response; context, timing in the breeding season (yes/no) and their interaction as fixed effects; pair ID as a random effect; and the total number of vocalizations as weights. The mixed model would not converge with the interaction term included; therefore, we refit this as a generalized linear model (GLM) to test if the interaction was significant. The interaction was nonsignificant ([Table 2](#)), so we fit our data with a mixed model excluding the interaction term.

Mimicry of different types of alarm calls in different alarm contexts

We used a GLMM to test if thornbills mimicked aerial and mobbing alarm calls in different contexts in which they used any mimicry. Identifying whether aerial or mobbing alarm calls are selectively mimicked may help clarify if mimicry functions in attracting others

Table 1
Calls produced by brown thornbills, as a proportion from total calls, across 6 different contexts

Vocalization	No danger away from nest	No danger near nest	Terrestrial threat	Aerial threat	Capture	Nest disturbance
Nonmimetic nonalarm	0.70 ± 0.06	0.83 ± 0.04	0.08 ± 0.03	0.0 ± 0.0	0.002 ± <0.001	0.02 ± 0.004
Nonmimetic mobbing alarm	0.08 ± 0.03	0.02 ± 0.01	0.65 ± 0.06	0.05 ± 0.02	0.01 ± 0.006	0.30 ± 0.06
Nonmimetic aerial alarm	0.01 ± 0.005	0.004 ± 0.002	0.006 ± 0.003	0.76 ± 0.05	0.42 ± 0.05	0.07 ± 0.01
Mimetic nonalarm	0.06 ± 0.03	0.07 ± 0.03	0.005 ± 0.003	0.007 ± 0.007	0.004 ± 0.002	0.03 ± 0.005
Mimetic mobbing alarm	0.08 ± 0.04	0.05 ± 0.02	0.23 ± 0.04	0.02 ± 0.01	0.03 ± 0.009	0.10 ± 0.02
Mimetic aerial alarm	0.03 ± 0.02	0.003 ± 0.003	0.009 ± 0.004	0.16 ± 0.05	0.49 ± 0.04	0.43 ± 0.09
Mimetic alarm of unknown category	0.0 ± 0.0	0.001 ± 0.001	0.002 ± 0.001	0.0 ± 0.0	0.007 ± 0.004	0.03 ± 0.006
Mimetic predator vocalization	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.009 ± 0.004	0.004 ± <0.001
Unknown	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.007	0.0 ± 0.0	0.03 ± 0.01	0.005 ± 0.002
Average number of calls per recording	177.00 ± 31.55	220.64 ± 33.99	333.70 ± 38.19	3.90 ± 0.34	191.92 ± 35.83	569.64 ± 121.45
Calls per min ^a	35.40 ± 5.48	22.06 ± 3.40	166.85 ± 19.09	133.77 ± 12.28	98.45 ± 14.36	276.70 ± 22.90
Mimetic sounds of danger per min ^a	6.91 ± 3.40	1.03 ± 0.40	46.03 ± 11.62	24.93 ± 7.15	59.31 ± 2.54	158.43 ± 3.42
Total recordings collected	30	14	20	50	24	22

Shown are the mean proportions ± standard errors. Cases where the proportion is 10% or greater are highlighted in bold.

^aRate per minute was calculated for the duration of a recording. See [Supplementary Table 1](#) for a complete breakdown of the types of calls produced by thornbills across contexts.

Table 2
GLMM and GLM analyses of the factors affecting the proportion of calls produced by thornbills that are mimetic alarm sounds in 6 contexts

Term	GLMM				GLM		
	Estimate (SE)	Wald F	df	P	Wald F	df	P
Pair ID	Random effect				2.78	36, 123	<0.001
Context (6 levels)	See Table 3	21.64	5,117	<0.001	21.55	5,118	<0.001
Season (no - yes)	- 0.07 (0.24)	0.10	1,117	0.76	0.09	1,117	0.76
Context × Season	—	—	—	—	1.93	2,115	0.15

SE, standard error. Models were fit using a quasibinomial distribution, a logit link function, and either penalized quaslikelihood (GLMM) or maximum quaslikelihood (GLM).

to a caller's location (Chu 2001a; Wheatcroft and Price 2013) or provoking others to flee (Flower 2011). Furthermore, we focused our analysis on comparing the relative production of mimetic aerial and mimetic mobbing alarm calls because these were the most common calls mimicked by thornbills across contexts (94% of all mimetic sounds of danger; [Supplementary Table 1](#)) and the contexts in which heterospecifics produce these alarm calls and the information they convey to receivers are known (Igic and Magrath 2013). We only included contexts of terrestrial threat, aerial threat, adult capture, and nest disturbance in this analysis because only alarm calls produced in these contexts could be related to a known threat. For each recording, we calculated the proportion of mimetic aerial alarm calls from the sum of mimetic aerial and mimetic mobbing alarm calls. We were only interested in testing this for recordings where at least 1 mimetic alarm call was recorded, which reduced our sample size to 19 out of 20 terrestrial threat recordings, 11 out of 50 aerial threat recordings, 23 out of 24 mist-net capture recordings, and 21 out of 22 nest disturbance recordings. We fit a GLMM with the proportion of mimetic aerial alarm calls as the response, context as a fixed effect, pair ID as a random effect, and the sum of mimetic aerial and mimetic mobbing alarm calls as weights.

Comparison of use of mimetic and nonmimetic alarm calls within and across alarm contexts

First, we tested if thornbills were more selective in mimicking aerial versus mobbing alarm calls when they were more selective in using nonmimetic aerial versus mobbing alarm calls. That is, if there was an overall relationship between the proportion of mimetic alarm calls that are aerial alarm calls and the proportion of nonmimetic alarm calls that are aerial alarm calls. A positive relationship would suggest that similar mechanisms underlie the production of nonmimetic and mimetic alarm that convey similar types of information. We could only make this comparison using recordings where both mimetic and nonmimetic alarm calls were recorded, and this further reduced our aerial threat sample to 7 recordings. To test this relationship within contexts, we fit a GLMM with the proportion of mimetic aerial alarm calls (from total mimetic aerial and mobbing alarm calls) as the response, context and proportion of nonmimetic aerial alarm calls (from total nonmimetic aerial and mobbing alarm calls) as fixed effects, pair ID as a random effect, and the sum of mimetic aerial and mimetic mobbing alarm calls as weights ([Supplementary Table 2](#)). We then excluded context as an explanatory variable in the model to test this relationship across contexts ([Supplementary Table 3](#)).

Finally, we tested whether thornbills used mimetic alarm calls equivalently to nonmimetic alarm calls that convey similar types of information and whether this depends on the context. More specifically, we tested if the proportion of mimetic alarm calls that are aerial alarm calls was equal to the proportion of nonmimetic alarm calls that are also aerial alarm calls within contexts; therefore, whether mimetic alarm calls convey similar information to nonmimetic alarm calls when both types of alarms are used. To test this, we fit a GLMM with the proportion of alarm calls that were aerial alarm calls as a response, pair ID, context, a dummy variable identifying if the response was the proportion of mimetic or nonmimetic aerial alarm calls, and the interaction between context and the mimicry identifier as fixed effects, recording ID as a random effect, and total alarm calls as weights ([Supplementary Tables 4 and 5](#)).

Statistical protocol

Statistical analyses were conducted using R v2.14.0 (R Foundation for Statistical Computing, Vienna, Austria). We constructed GLMs using the `glm()` function of the base R library using logit link functions and quasibinomial error distributions to account for over dispersion. We constructed GLMMs using the `glmmPQL()` function of the MASS package (Venables and Ripley 2002) using quasibinomial error distributions, logit link functions, and penalized quasilielihood. We examined residual plots and q - q normal plots to identify if our models satisfied assumptions of normality and homogeneity of variance. Wald F tests for significance of model effects were implemented using the `anova.lme()` function of the nlme library (Pinheiro et al. 2012) for GLMMs and `anova()` function of the base R library for GLMs. Tukey Wald Z tests ($\alpha = 0.05$) were implemented using the `glht()` function of the multcomp package (Hothorn et al. 2008).

RESULTS

Mimicry of sounds of danger across contexts

Thornbills were most likely to include mimetic sounds of danger among their vocalizations when captured and during nest attack, less likely in response to terrestrial and aerial predator threats, and least likely in the absence of any threat ([Figure 2](#); [Tables 1 and 2](#)). The proportion of vocalizations that were mimetic sounds of danger did not simply increase in context of danger because other vocalizations were used less frequently than in the absence of danger ([Table 1](#)). Thornbills included a greater proportion of mimetic sounds of danger, including heterospecific alarm calls and predator calls, during capture and nest disturbance than in other contexts ([Figure 2](#); [Table 3](#)). In both cases, nearly 60% of all calls were mimetic sounds of danger. The proportion of mimetic sounds of danger was similar during terrestrial (25%) and aerial (18%) threat, and in the absence of danger away from the nest (12%; [Figure 2](#); [Table 3](#)). The aerial threat context generally had a higher variance than the other contexts, and this may have reduced our ability to detect significant differences when compared with other contexts, such as capture and nest disturbance ([Table 3](#)). The proportion of mimetic sounds of danger was greater in the presence of terrestrial threat and in the absence of danger away from the nest than in the absence of danger near the nest (5%; [Figure 2](#); [Table 3](#)). The proportion of mimetic sounds of danger did not differ between the breeding and nonbreeding season ([Table 2](#)).

Mimicry of different types of alarm calls in different alarm contexts

Thornbills usually mimicked mobbing and aerial alarm calls in different contexts when they used mimicry ([Figure 3](#); [Table 1](#)). The proportion of mimetic aerial calls relative to mimetic mobbing alarm calls differed among contexts ([Figure 3](#); [Table 4](#); Wald $F_{3,40} = 56.57$, $P < 0.001$). Thornbills generally mimicked mobbing alarm calls in response to terrestrial threat ($95 \pm 2\%$ of all mimicked sounds of danger), whereas they mimicked aerial alarm calls in response to aerial threat ($70 \pm 12\%$). However, they also mimicked aerial alarm calls in the absence of aerial threat when captured ($92 \pm 2\%$) and during nest disturbance ($71 \pm 5\%$). Thornbills were more likely to mimic aerial alarm calls, compared with mobbing alarm calls, during capture than during nest disturbance and terrestrial threat, but equally during capture and aerial threat ([Figure 3](#); [Table 4](#)). Furthermore, thornbills were more likely to mimic aerial alarm calls, compared with mobbing alarm calls,

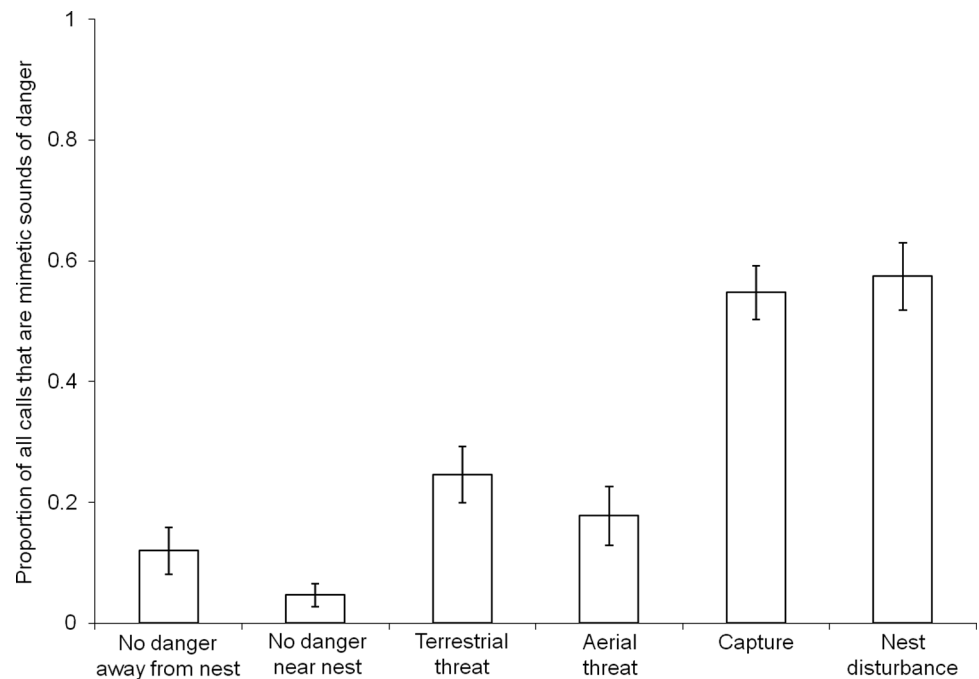


Figure 2 Proportion of total vocalizations that are mimetic sounds of danger (means \pm standard error) produced by brown thornbills in the absence of danger away from ($N = 30$) or near their nest ($N = 14$), and in response to terrestrial threat ($N = 20$), aerial threat ($N = 50$), mistnet capture ($N = 24$), and nest disturbance ($N = 22$).

Table 3 Differences between the proportion of mimetic heterospecific alarm calls from total vocalizations produced by thornbills across 6 contexts

Comparison	Estimate (SE)	Wald χ^2	P
No danger nest–capture	−3.64 (0.58)	−6.31	<0.001
No danger–capture	−2.00 (0.30)	−6.70	<0.001
Aerial threat–capture	−1.88 (1.11)	−1.69	0.49
Terrestrial threat–capture	−1.58 (0.28)	−5.71	<0.001
Nest disturbance–capture	−0.24 (0.28)	−0.86	0.95
No danger–no danger nest	1.62 (0.59)	2.78	0.05
Aerial threat–no danger nest	1.76 (1.22)	1.44	0.66
Terrestrial threat–no danger nest	2.05 (0.56)	3.65	<0.01
Nest disturbance–no danger nest	3.40 (0.53)	6.37	<0.001
Aerial threat–no danger	0.13 (1.11)	0.12	0.99
Terrestrial threat–no danger	0.42 (0.28)	1.51	0.62
Nest disturbance–no danger	1.77 (0.30)	5.91	<0.001
Terrestrial threat–aerial threat	0.29 (1.10)	0.27	0.99
Nest disturbance–aerial threat	1.64 (1.11)	1.48	0.64
Nest disturbance–terrestrial threat	1.35 (0.25)	5.42	<0.001

SE, standard error. Shown are estimates and Tukey Wald χ^2 tests ($\alpha = 0.05$) from a GLMM.

during aerial threat and nest disturbance compared with terrestrial threat, but equally during aerial threat and nest disturbance (Figure 3; Table 4).

Comparison of use of mimetic and nonmimetic alarm calls within and across alarm contexts

Thornbills used mimetic aerial and mobbing alarm calls in similar contexts to their nonmimetic equivalents, except during nest disturbance (Table 1; Figures 3 and 4). This comparison was restricted to cases in which both mimetic and nonmimetic alarm calls were used. As an overall pattern, the proportion of mimetic

alarm calls that are aerial alarm calls increased as the proportion of nonmimetic alarm calls that are also aerial alarm calls increased across contexts (Figure 4; Wald $F_{1,40} = 30.18$, $P < 0.001$), but less so within contexts (Figure 4; Wald $F_{1,37} = 3.17$, $P = 0.08$). More specifically, thornbills used mimetic aerial alarm calls in combination with nonmimetic mobbing alarm calls during nest disturbance, even though they typically used mimetic aerial and mobbing alarm calls similarly to nonmimetic equivalents in response to other threats (Supplementary Table 5; Figures 3 and 4; interaction effect: Wald $F_{3,66} = 11.11$, $P < 0.001$).

DISCUSSION

Brown thornbills changed their use of mimetic calls according to the behavioral context. They adjusted how often they mimicked alarm calls, as a proportion of total calls produced, and which types of heterospecific alarm calls they mimicked, in relation to different types of danger. They were most likely to include mimetic sounds of danger among their vocalizations when captured and during nest attack, less likely in response to terrestrial and aerial predator threats, and least likely in the absence of any threat. However, thornbills were only significantly more likely to mimic sounds of danger when captured and during nest attack than in the absence of danger, and more likely to mimic sounds of danger during terrestrial threat than in the absence of danger near their nest. When thornbills combined nonmimetic and mimetic alarm calls, they used nonmimetic and mimetic mobbing alarm calls when mobbing a predator, and nonmimetic and mimetic aerial alarm calls in response to a flying predator and when captured. However, during nest disturbance, they usually mimicked aerial alarm calls in combination with nonmimetic mobbing alarm calls. Our results suggest that thornbill alarm mimicry could have an antipredator function in contexts that pose extreme danger to callers or their offspring, where it potentially functions in deceiving predators.

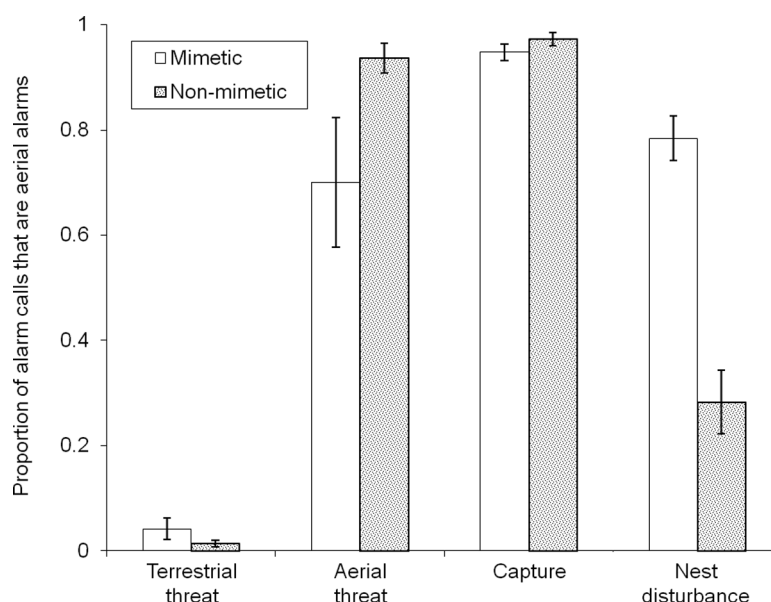


Figure 3

Proportion of mimetic alarm calls (means \pm standard error) that are aerial alarm calls (white bars) and proportion of nonmimetic alarm calls that are aerial alarm calls (shaded bars) produced by brown thornbills in response to 4 types of threat. Sample sizes are terrestrial threat ($N = 19$), aerial threat ($N = 11$), mistnet capture ($N = 23$), and nest disturbance ($N = 21$).

Table 4

Differential use of mimetic alarm call types

Comparison	Estimate (SE)	Wald χ^2	P
Aerial threat–capture	−2.62 (1.25)	−2.10	0.13
Terrestrial threat–capture	−7.40 (0.44)	−13.74	<0.001
Nest disturbance–capture	−2.11 (0.44)	−4.81	<0.001
Terrestrial threat–aerial threat	−4.78 (1.22)	−3.90	<0.001
Nest disturbance–aerial threat	0.51 (1.18)	0.43	0.97
Nest disturbance–terrestrial threat	5.28 (0.38)	13.94	<0.001

SE, standard error. Differences are calculated as the proportion of mimetic aerial alarm calls from total mimetic aerial and mobbing alarm calls produced by thornbills across 4 contexts of danger. Shown are estimates and Tukey Wald χ^2 tests ($\alpha = 0.05$) from a GLM.

Production of mimetic vocalizations during predator capture and nest disturbance has been suggested to function in attracting other individuals to help captured callers or prevent nest predation (Morton 1976; Chu 2001a). A function in attracting aid has been tested in phainopeplas (*Phainopepla nitens*), which also regularly use vocal mimicry when captured in mist nets (Chu 2001b) and possibly also in nest defense (Crampton et al. 2004). Recordings of captured phainopeplas (a mixture of nonmimetic distress calls and mimetic heterospecific vocalizations) are better at provoking nearby heterospecifics to mob predators than recordings where mimicry was digitally altered (Chu 2001a). However, it is unclear how mimicry was digitally altered in this study and therefore whether heterospecific behavior was affected by modifying recordings or exclusion of mimicry (Kelley et al. 2008). Although attracting aid is a plausible function for vocal mimicry during capture or nest defense, it is yet to be clearly demonstrated.

We suggest that deterring or startling predators is a more likely function than attracting aid for mimetic aerial alarms produced by thornbills when captured and during nest defense (Wise et al. 1999; Igic and Magrath 2013). Aerial alarm calls generally function in

provoking individuals to flee in the presence of aerial predators, and therefore, mimetic versions are unlikely to provoke aid from other individuals (Flower 2011). Thornbills produced these mimetic aerial alarm calls in the absence of aerial danger, thereby providing inaccurate and potentially deceptive information to receivers (Munn 1986). Indeed, thornbills produced mimetic aerial alarm calls in combination with nonmimetic mobbing alarm calls during nest disturbances, even though mimetic aerial alarm calls were generally used like nonmimetic aerial alarm calls in other contexts, further suggesting deceptive signaling. If the predator attacking the thornbill, or its nest, is itself vulnerable to predation from other larger aerial predators, then the thornbill's mimetic aerial alarm calls may startle the predator into releasing the caller or its offspring, providing an opportunity for escape (Wise et al. 1999; Igic and Magrath 2013). The next step is verifying that thornbills also mimic aerial alarms in response to natural predators during nest defense and capture.

Studies of other species show that aerial alarm calls, including mimetic versions, can be deceptive. Kleptoparasitic species often use aerial alarm calls deceptively to startle other individuals and steal their resources (Munn 1986; Möller 1988). Aerial alarm calls are particularly startling signals because they signal the presence of dangerous predators from whom survival requires receivers to flee immediately (Caro 2005). If true and false alarm calls are indistinguishable, the costs of ignoring true alarm calls, such as injury or death, can outweigh the costs of erroneously responding to false alarm calls, such as the loss of a meal, and ensure that receivers keep responding to false alarms (Koops 2004). Mimicking other species' aerial alarm calls in deception may be advantageous because it prevents receivers from being able to identify and habituate to deceptive alarms (Flower 2011). Our results suggest that predators, and not just competitors with food, could be targets of deception (Igic and Magrath 2013).

Although thornbills mimicked sounds of danger in contexts of danger, they also produced some mimetic sounds of danger when recorded away from nests in the absence of predator models.

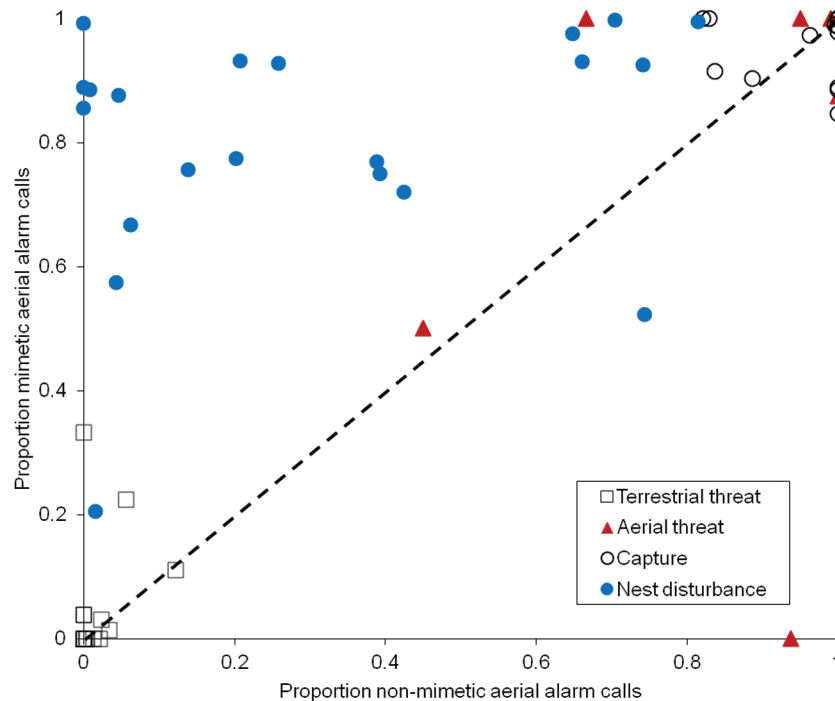


Figure 4

The relationship between the proportion of mimetic aerial alarm calls from total mimetic alarm calls produced and the proportion of nonmimetic aerial alarm calls from total nonmimetic alarm calls produced across 4 contexts of danger. The dotted line represents a one-to-one relationship between the proportion of mimetic aerial alarm calls produced and proportion of nonmimetic aerial alarm calls produced. Points above the line represent recordings where mimicry contained a disproportionate number of aerial alarm calls compared with the proportion in nonmimetic alarm calls.

This meant that such mimicry did not differ significantly during terrestrial and aerial threat and the absence of danger away from the nest. We suggest that thornbills may have regarded our presence when following and recording them away from their nest as a type of terrestrial threat. In support of this explanation, thornbills were less likely to mimic sounds of danger in the absence of threat near their nest, when the observer was stationary and hidden from view. Alternatively, mimetic sounds of danger produced by thornbills during foraging may have been provoked by threats that were not seen by the observer. It is also possible that short flight periods of our gliding predator models (mean duration \pm standard error: 1.9 ± 0.07 s) may have reduced the opportunity for thornbills to incorporate mimicry with nonmimetic alarm vocalizations during our aerial threat context. This implies that thornbills prioritize non-mimetic alarm calls when warning others of aerial predators.

Thornbills generally mimicked “appropriate” heterospecific alarm calls in response to stationary and flying predators when they used mimicry. For example, they mimicked mobbing alarm calls when mobbing a perched avian predator and mimicked aerial alarm calls in response to a flying predator. Although presenting thornbills with heterospecific mobbing alarm calls during the terrestrial threat context may have provoked them to mimic mobbing alarm calls, thornbills often mob predators together with other species in their environment, and therefore the presence of heterospecific mobbing alarm calls in these contexts is a common occurrence. Furthermore, they often mimicked species that were not present during our owl presentations (Igic B, personal observation), implying they do not merely copy sounds they can hear. The simple presence of an auditory cue is also unlikely to explain why thornbills preferentially mimicked mobbing alarm calls in this context because auditory cues were also present in other contexts

of danger, such as heterospecific aerial alarm calls during aerial threats and nestling distress calls during nest disturbances. Indeed, we observed similar behavior by thornbills to real predators: mimicry of mobbing alarm calls in response to the presence of perched pied currawongs (*Strepera graculina*) and laughing kookaburras (*Dacelo novaeguineae*), and mimicry of aerial alarm calls in response to flying collared sparrowhawks (*Accipiter cirrocephalus*), grey butcherbirds (*Cracticus torquatus*), and pied currawongs (Igic B and Magrath RD, personal observation). Like thornbills, greater racket-tailed drongos also selectively mimic heterospecific mobbing alarm calls when mobbing terrestrial threats (Goodale and Kotagama 2006). Therefore, it is possible that mimicking heterospecific alarm calls in appropriate contexts is more common among avian mimics than currently believed (Kelley et al. 2008).

Thornbills did not simply mimic acoustically similar calls in similar contexts, implying that they learn the context in which to produce other species’ alarm calls. Although both learning (Magrath and Bennett 2012) and acoustic similarity (Fallow et al. 2011) can enable individuals to respond appropriately to other species’ alarm calls, acoustic similarity cannot explain why thornbills mimicked acoustically diverse alarm sounds in similar contexts (Figure 1; Igic and Magrath 2013). For example, thornbills mimicked superb fairy-wren (*Malurus cyaneus*) and New Holland honeyeater (*Phylidonyris novaehollandiae*) aerial alarm calls in similar circumstances and mimicked superb fairy-wren and New Holland honeyeater mobbing alarm calls in similar circumstances, regardless of large acoustic differences (Figure 1). Thornbills might learn the context of production directly from heterospecifics or indirectly from other conspecifics. It is less likely that they merely adjust which sounds they mimic based on how receivers respond (trial-and-error learning; Langmore et al. 2008). This is unlikely because 1) thornbills

selectively mimicked heterospecific aerial alarm calls during predator capture, even though these are presumably rare events and often result in death, and 2) thornbills selectively mimicked aerial alarm calls in nest defense even if nesting for the first time (Igic B, personal observation).

Mimicking “appropriate” alarm calls in response to aerial and terrestrial threats may benefit thornbills by facilitating interspecific alarm communication with other prey species. Mimicking mobbing alarm calls when mobbing predators may improve the thornbill’s ability to provoke heterospecifics to also mob (Goodale et al. 2014; Wheatcroft and Price 2013), which in turn may reduce the risk of mobbing behavior for the thornbill (Pettifor 1990). Mimicking aerial alarm calls in response to a flying predator may improve the thornbill’s ability to provoke heterospecifics to flee (Fallow et al. 2011), which in turn could cause mass movement and may reduce the predator’s hunting success (Caro 2005). However, given thornbills were not more likely to include mimetic alarm calls among their vocalizations in response to aerial threats than in the absence of danger, mimicry may not have an important function in this context. Any potential benefits to using mimicry in response to predators still need to be tested by examining how heterospecifics respond to these mimetic alarms.

Context-specific usage might simply reflect how thornbills learn mimetic alarm calls, and therefore, alarm mimicry may not be functional in all contexts. Thornbills may categorize heterospecific alarm calls in relation to the level of danger experienced during learning and then mimic those alarm calls that are relevant to the current level of danger experienced (Kelley and Healy 2011, 2012). Indeed, this may explain why thornbills generally mimicked alarm calls that are associated with immediate danger (e.g., aerial alarm calls) in contexts of immediate danger (aerial threat, capture, and nest disturbance) and alarm calls that are associated with nonimmediate danger (e.g., mobbing alarm calls) in the presence of nonimmediate danger (terrestrial threat). Although this may imply that context-specific mimicry is nonfunctional (Kelley and Healy 2011, 2012), it is also possible that such a learning mechanism facilitates mimicry of particular heterospecific alarm calls in contexts where they serve a function. A nonfunctional explanation seems particularly unlikely for contexts where mimicry outnumbers nonmimetic vocalizations, such as during nest disturbance and capture.

We conclude that thornbills adjust how they use vocal mimicry in relation to different types of danger. When mimicry was used, thornbills mimicked appropriate heterospecific alarm calls in response to aerial and perched avian predators, which may facilitate interspecific alarm communication with other prey species, and mimicked aerial alarm calls when the caller or offspring were in immediate danger, which may function in deceiving predators to release caught callers or offspring. Although alarm mimicry could have different functions in different contexts, our results suggest thornbill alarm mimicry is most likely to have a function during capture by predators or during nest defense. However, it is still necessary to test how intended receivers respond to mimetic alarm calls to identify the contexts in which they provide an adaptive benefit. Thornbills did not always use mimetic alarm calls interchangeably with comparable nonmimetic alarm calls, suggesting that different mechanisms control production of mimetic and nonmimetic alarm calls.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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