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Fidelity of vocal mimicry: identification and accuracy of mimicry of heterospecific alarm calls by the brown thornbill

Branislav Igic*, Robert D. Magrath

Division of Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra, Australia

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Avian vocal mimicry has been studied for decades, but little is known about its function or requirements for accurate imitation. Furthermore, progress is hampered by the difficulty in identifying which vocalizations are indeed mimetic. We tested historical claims of vocal mimicry in the brown thornbill, *Acanthiza pusilla*, using a combination of human and computer methods to identify mimicry, followed by comparisons of acoustic similarity with model vocalizations. We recorded vocalizations of brown thornbills and sympatric heterospecifics while undisturbed and during mist net capture or the presence of natural or model predators. We then cross-validated human classification of mimicry with computer classification based on spectrographic measurements and spectral cross-correlation. Finally, we quantified the accuracy of the most common imitations. Brown thornbills predominantly imitated alarm calls given by heterospecifics towards aerial predators, which function in these models to provoke immediate flight by receivers. Human and computer-based methods produced consistent results when identifying and classifying mimicry. Mimicked aerial alarms were not perfect imitations of their corresponding model alarms, but did retain specific acoustic properties previously shown to be important for provoking immediate alarm responses. Although less accurate mimicry may reflect physiological constraints, we suggest that mimetic function, perhaps startling predators, only requires mimicry to retain features of model alarms that provoke immediate alarm responses by receivers. Understanding what factors influence the acoustic structure of mimetic vocalizations is essential in understanding the evolution of vocal mimicry, particularly with accumulating evidence that mimetic function does not always require perfect resemblance in other sensory modalities.

Mimics gain fitness benefits by being perceived as similar or identical to one or more organisms (models). Mimicry generally functions as a deceptive signal, benefiting the mimic at some cost to the receiver (Vane-Wright 1980); however, in some cases it can be honest and beneficial to both mimic and receiver (Kapan 2001; Coleman et al. 2007). Mimetic similarity can act on the visual (Igic et al. 2012), auditory (Nakano et al. 2010), olfactory (Meer & Wojick 1982) and tactile (Pekár & Král 2002) sensory systems, and close similarity between mimic and model generally implies a strong selection for mimetic accuracy (Dalziell & Magrath 2012).

Despite some mimics showing extreme similarity to their models, often mimics are different from models (Edmunds 2000). This imperfect mimicry can result from constraints on the evolution of accuracy (Zollinger & Suthers 2004), or weak selection for accurate mimicry (Harper & Pfennig 2007). Imperfect mimicry can be functional if receivers lack the ability to discriminate between model and mimic (Dittrich et al. 1993) or if the act of discrimination is too costly for receivers (Lorenzana & Sealy 2001). Indeed, there is increasing evidence that perfect resemblance is not always necessary for mimetic function (Dittrich et al. 1993; Kikuchi & Pfennig 2010).

Vocal mimicry presents an ideal opportunity to investigate how mimetic signals are structured because imitations are often learned, resulting in different individuals imitating different models at different levels of mimetic accuracy. Imitation of sounds produced by the environment or heterospecifics is widespread among songbirds, with an estimated 15–20% of species incorporating sounds from other sources into their vocal repertoires (Baylis 1982). Species can vary in both how often they mimic foreign sounds (Robinson 1974; Hindmarsh 1986) and the degree to which these imitations resemble the model sound (Hindmarsh 1986; Dalziell & Magrath 2012). Although mimetic vocalizations can be innate (Rowe et al. 1986; Langmore et al. 2008), for most songbirds

* Correspondence: B. Igic, Building 116, Division of Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra 0200, Australia.
E-mail address: brani.igic@gmail.com (B. Igic).

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they are considered to be learned (Kelley et al. 2008). The role of learning differentiates vocal mimicry from other types of mimicry, and can result in different models being mimicked by different individuals (Chu 2001b), differences in mimetic accuracy between individuals (Coleman et al. 2007), and even differences in mimetic accuracy between different imitations by an individual (Zollinger & Suthers 2004). The diversity of sounds mimicked allows us to examine how particular relationships between mimics, models and receivers shape the structure of particular mimetic signals.

Mimicry of heterospecific alarm calls is common (Goodale & Kotagama 2006; Kelley & Healy 2011), and presents a useful context in which to examine the requirements for mimetic accuracy because different acoustic features of alarm calls can affect different aspects of receiver alarm response. Alarm calls generally convey information critical to the survival of individuals (Caro 2005), implying that there may be strong selection for individuals to identify true dangers, and therefore discriminate between true alarms and deceptive mimetic alarms. However, failing to respond to alarm calls can result in death, a cost typically greater than the consequences of erroneously responding to false alarms (Koops 2004). This cost may lower the discrimination thresholds of receivers (Koops 2004; Wiley 2006), and in turn weaken selection for accurate mimicry of alarms. For example, alarm calls given to predators in flight (aerial alarms) signal immediate danger, and survival probably relies on rapid response rather than the ability to discriminate between alarm calls according to their fine acoustic structure. In support of this idea, superb fairy-wrens, *Malurus cyaneus,* flee to cover immediately according to simple features of alarm calls, such as call peak frequency, while the fine acoustic structure of signals subsequently affects how long individuals stay in cover (Fallow et al. 2011, 2013). If mimics benefit by provoking immediate alarm responses by receivers, then mimetic alarms may require similarity in only those acoustic features that prompt immediate flight, rather than accurate reproduction of all acoustic properties. Given that mimetic signals may not always require perfect accuracy to be functional, the process of identifying mimetic vocalizations can be problematic.

As it is often difficult to test how the intended receivers perceive mimetic signals, human assessment is typically used to identify mimetic vocalizations, yet this may introduce bias. Human assessment involves listening to recordings of mimic and model vocalizations, or comparing their spectrograms by eye, to identify mimetic vocalizations as those that are similar to model sounds. Although the human eye and ear are efficient in pattern recognition tasks, different individuals can vary in their ability to discern particular differences between vocalizations, such that multiple evaluators are required to offset variability (Jones et al. 2001). Human assessment is also difficult to standardize and therefore replicate across analyses or among different studies. Furthermore, avian hearing can be better at discerning fine-scale differences between similar avian vocalizations than human hearing (Lohr et al. 2006). There is also no certainty that differences seen on a spectrogram are indeed detected by bird hearing. Therefore, human-based methods may mistakenly exclude or overlook less accurate imitations that function mimetically, or fail to detect meaningful differences.

Computer-based methods can overcome many of the shortcomings of human-based approaches to identify and categorize mimicry, and can be used to cross-validate human classification. A computer-based approach generally involves spectrogram analyses to measure acoustic characteristics of model and mimetic vocalizations, followed by a statistical analysis to quantify the level of acoustic similarity (Coleman et al. 2007; Zann & Dunstan 2008; Flower 2011; Kelley & Healy 2011; Dalziell & Magrath 2012). These approaches have the advantage of being repeatable, and the ability to quantify mimetic accuracy is potentially helpful in identifying which vocalizations are mimetic. Furthermore, sounds can be compared across a variety of different metrics (Ranjard et al. 2010), and analyses can be tailored to test how sounds differ in particular signal characteristics that affect the response by receivers (Fallow et al. 2011, 2013). However, even studies that use computer-based methods to quantify the accuracy of mimetic vocalizations still generally rely on human evaluation to select which mimic vocalizations should be compared with which models. This can introduce bias towards favouring mimetic vocalizations most similar to a particular model and excluding less accurate imitations. Computer-based methods may overcome this problem by systematically comparing relative acoustic similarity of putative mimicry with both nonmimetic and possible model vocalizations. Therefore, computer-based methods may be useful in cross-validating human evaluation.

The brown thornbill, *Acanthiza pusilla*, is claimed to use vocal mimicry, including heterospecific alarm mimicry, when humans disturb its nest (Chandler 1909; Hindwood 1933), or when it is captured in mist nets (B. Igic & R.D. Magrath, personal observation). However, there have been no formal assessments of its mimetic ability. The aims of our study were (1) to identify what sounds are imitated and quantify what proportion of these are heterospecific alarms, (2) to cross-validate the use of human assessment to identify mimicry with more objective and systematic computer-based methods of sound classification and (3) to quantify mimetic accuracy of the most regularly imitated alarms, and test which specific acoustic characteristics of model alarms are most accurately reproduced.

METHODS

Study Species and Study Site

We studied a colour-banded population of brown thornbills in the Australian National Botanic Gardens, Canberra, Australia (35°16′S, 149°6′E). The brown thornbill is a small passerine (6–8 g), common throughout southeastern Australia (Higgins & Peter 2002). It breeds in pairs and guards year-long territories of 0.4–3.1 ha against conspecific intruders (Green & Cockburn 1999). Both sexes sing throughout the year, although males are in general more vocal (B. Igic, personal observation). Mimicry has been reported to occur during human disturbance of nests, with parents imitating seven or eight heterospecifics in this context (Chandler 1909; Hindwood 1933). However, mimicry has also been noted away from nests (Waterhouse 1941), and most regularly when birds are captured in mist nets (B. Igic & R.D. Magrath, unpublished data).

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.

Recording Protocol and General Overview

We recorded vocalizations of brown thornbills and sympatric heterospecifics throughout the year in natural nonalarm contexts, in the presence of natural predators, and following model predator presentation. We followed and recorded individually identified foraging birds from 10–15 m away. We also used a stationary stuffed southern boobook owl, *Ninox novaeseelandiae*, model to incite mobbing alarms in brown thornbills and sympatric heterospecifics. These types of alarms are generally given towards terrestrial predators, or low threats, and can provoke nearby individuals to inspect the location of alarms or initiate mobbing behaviour (Curio et al. 1978). We presented the stuffed owl once to brown thornbill pairs ($N = 10$) in their territory, outside the

breeding season, and while they were foraging. To draw the attention of birds to the owl and prompt mobbing, we broadcast 20 s of white-browed scrubwren, *Sericornis frontalis,* mobbing alarms (mean ± SD = 187.7 ± 35.8 alarms/min) when the owl was first placed on the ground. We recorded vocal responses of both brown thornbills and any nearby heterospecifics provoked to mob the owl, from 15 m away. The owl model was presented to birds for an average of 260 ± 86 s. We also used a gliding model in the likeness of a collared sparrowhawk, *Accipiter cirrocephalus*, to incite aerial alarms (e.g. Magrath et al. 2007). These types of alarms are given to flying predators and generally cause others to flee immediately to cover (Magrath et al. 2007; Fallow et al. 2011). We also presented gliding models to brown thornbill pairs ($N = 10$) in their territory, outside the breeding season, and while they were foraging. Overall, we presented the gliding model five times per pair, and generally once per individual per day. We used recordings collected by previous studies at the study site, where gliding models were presented to heterospecifics to sample alarms produced by heterospecific species (Magrath et al. 2007, 2009; Fallow et al. 2011). In addition, we boosted this sample of model heterospecific alarms by making additional independent recordings of superb fairy-wren ($N = 7$), white-browed scrubwren ($N = 6$) and New Holland honeyeater, *Phylidonyris novaehollandiae* ($N = 2$) responses to the gliding model at our study site. We recorded vocal responses of focal individuals towards gliding models from within 10 m. Behaviour of birds returned to normal quickly after model presentations, or after hearing alarm calls of nearby individuals prompted by the models. Furthermore, a range of predators and large omnivores are common at our site, and regularly prompt alarm calls from brown thornbills and heterospecifics (Magrath et al. 2007). Therefore, the use of simulated predators in our study was unlikely to have any long-term detrimental impacts on birds tested. In total, we gathered 80 h of recordings of brown thornbills ($N = 55$ individuals) and a range of heterospecifics ($N = 26$ species) throughout the study. All recordings were made using a Sennheiser ME66 directional microphone connected to a Marantz PMD671 digital recorder, and saved in a wave file format of 44.1 kHz and 16 bits.

In addition to recording free-ranging birds, we recorded brown thornbills captured in mist nets during banding procedures. We used these recordings to identify what types of vocalizations are mimicked by brown thornbills while being extracted from mist nets. Birds were captured using mist nets set up at our study site between 0530 and 0900 hours and lured into them by using playback of conspecific vocalizations. Mist nets were continuously monitored after being set up, and captured birds were immediately extracted from nets when caught. Brown thornbills produce a large range of vocalizations in mist nets that are also produced during nest disturbances (B. Igic & R.D. Magrath, unpublished data). Recording birds in mist nets also produced recordings with good signal-to-noise ratios, and allowed us to measure acoustic parameters accurately. Furthermore, behaviour of birds during capture in mist nets may reflect behavioural responses of individuals when attacked or captured by predators (Norris & Stamm 1965; Stefanski & Falls 1972a, b; Conover 1994; Chu 2001a; Møller & Nielsen 2010). In total we recorded 55 birds during extraction from mist nets. Birds were recorded for an average of 3 ± 1.94 (SD) min from a distance of 20 cm. We recorded birds for the duration of their removal from mist nets, and released them back into their territory soon after morphometric measurements and banding procedures: birds were released 5–30 min after being caught in mist nets. To allow individual identification, birds were banded with a unique combination of a colour-anodized, numbered Australian Bird and Bat Banding Scheme aluminium band and a plastic colour band. Banded birds return to normal activity shortly after being released, suggesting no long-term stress effects. Furthermore, every individual banded was subsequently seen alive on a later date.

We approached our three aims as follows. (1) To identify what heterospecific vocalizations were mimicked, we compared vocalizations of brown thornbills in mist nets to those produced outside of mist nets and to vocalizations of sympatric heterospecifics. To quantify how often alarm calls were imitated, we compared vocalizations produced by thornbills with recordings of alarm calls of other species made during encounters with real or model predators. (2) To cross-validate the use of human assessment in identifying mimicry, we compared human categorization of brown thornbill imitations with categorizations made by two computer-based methods of sound classification. (3) To examine the accuracy of brown thornbill alarm call imitations, and identify which acoustic properties are most accurately reproduced, we used spectrogram analysis to quantify mimetic accuracy of the most common imitations, focusing on acoustic features of model alarms that affect response to alarm calls.

Identification of Mimicry

As a first step to identify mimicry we compared the acoustic similarity of brown thornbill mist net vocalizations to those of sympatric heterospecifics by listening to recordings and inspecting spectrograms by eye. We generated spectrograms of recordings using Raven Pro 1.3 (Charif et al. 2008), a Blackman window function with a 256 sample size, a temporal grid resolution of 0.499 ms with 91.4% overlap and a frequency grid resolution of 86.1 Hz. These spectrogram parameters were used throughout our analyses. We identified mimicry based on acoustic resemblance to vocalizations of sympatric species; brown thornbill vocalizations showing resemblance to vocalizations of heterospecifics were identified as mimetic, while brown thornbill vocalizations not showing resemblance to heterospecific vocalizations were assumed to be nonmimetic. We identified mobbing alarms as vocalizations predominantly produced when presented with a stationary stuffed owl, aerial alarms as those predominantly produced when presented with a gliding sparrowhawk model, and nonalarm vocalizations as those predominantly produced in the absence of these predator models or natural threats. We used published information to classify the species that brown thornbills imitate as harmless, or as either predators of small birds or aggressive towards them (Table 1; Higgins et al. 2006; Magrath et al. 2009). Where possible, we also used published information to identify the context in which mimicked heterospecific species use vocalizations (Table 1). We used the same criteria to identify brown thornbill nonmimetic alarm calls and nonalarm vocalizations. Inspection of recordings here was conducted by both authors.

Cross-validation of Human Assessment

We cross-validated three methods for classifying thornbill vocalizations based on similarity with model species' alarms: visual comparison of spectrograms by multiple human observers; discriminant function analysis based on time–frequency measurements from spectrograms; and discriminant function analysis of spectrogram cross-correlations.

Selection of vocalizations

We selected a subset of model species' aerial alarm calls, hereafter model alarms, because they share broad acoustic features with each other and the calls most regularly produced by brown thornbills in mist nets (Fig. 1, Table 1). We included buff-rumped thornbill, *Acanthiza reguloides*, aerial alarms ($N = 11$), white-

Table 1
Model species and vocalizations mimicked by brown thornbills during banding procedures ($N = 49$ brown thornbills)

Model species	Common name	Call type	Used in alarm contexts by model?	Number of brown thornbills	Source
Acanthiza reguloides	Buff-rumped thornbill	Aerial alarm	Yes	6	Fallow et al. 2011, gliding model presentation
Acanthorhynchus tenurostris	Eastern spinebill	Call	No	3	Higgins et al. 2001
*Anthochaera carunculata**	Red wattlebird	Call	No	4	Jurisevic & Sanderson 1994
Cormobates leucophaea	White-throated treecreeper	Call	Both alarm and nonalarm	4	Higgins et al. 2001, observation following hawk
Cracticus torquatus †	Grey butcherbird	Song/call	No	2	Higgins et al. 2006
Eopsaltria australis	Yellow robin	Mob alarm	Yes	1	Higgins & Peter 2002, stationary model presentation
Gymnorhina tibicen†	Australian magpie	Song	No	2	Higgins et al. 2006
Malurus cyaneus	Superb fairy-wren	Mob alarm	Yes	10	Higgins et al. 2001, stationary model presentation
		Aerial alarm	Yes	30	Fallow et al. 2011, gliding model presentation
		Seet alarm	Yes	27	Description for sister species in Greig & Pruett-Jones 2008, gliding model presentation
		Alarm song	Yes	27	Colombelli-Négrel et al. 2011, gliding model presentation
Pachycephala pectoralis	Golden whistler	Call	No	2	Higgins & Peter 2002
Pardalotus punctatus	Spotted pardalote	Song	No	1	Higgins & Peter 2002
Platycercus elegans	Crimson rosella	Alarm	Yes	10	Higgins 1999
Phylidonyris novaehollandiae	New Holland honeyeater	Mob alarm	Yes	9	Jurisevic & Sanderson 1994, stationary model presentation
		Aerial alarm	Yes	38	Magrath et al. 2009, gliding model presentation
Rhipidura albiscapa	Grey fantail	Call	Both alarm and nonalarm	2	Higgins et al. 2006, stationary model presentation
Sericornis frontalis	White-browed scrubwren	Mob alarm	Yes	9	Platzen & Magrath 2005, stationary model presentation
		Rapid chip alarm	Yes	15	Higgins & Peter 2002, stationary model presentation
Smicronis brevirostris	Weebill	Aerial alarm	Yes	7	Powys 1999, gliding model presentation
Strepera graculina †	Pied currawong	Song	No	5	Higgins et al. 2006
Turdus merula	Common blackbird	Mob alarm	Yes	1	Higgins et al. 2006, stationary model presentation
		Alarm rattle	Yes	1	Higgins et al. 2006

Identification of putative mimicry is based on acoustic and spectrogram similarity of brown thornbill vocalizations to recordings of sympatric species at the Australian National Botanic Gardens (judged by B.I., see text). Whether vocalizations are used by model species in alarm contexts was assessed using observations in alarm contexts, through presentation of simulated predators (stationary or gliding) and published literature. Predators and aggressive species were identified using published information.

* Aggressive species.

† Predators of adults and young.

browed scrubwren aerial alarms ($N = 19$), New Holland honeyeater aerial alarms ($N = 20$), superb fairy-wren seet alarms ($N = 7$) and superb fairy-wren aerial alarms ($N = 21$). These alarms all share similar acoustic space, apart from honeyeater alarms, which are lower in frequency. We included brown thornbill aerial alarms ($N = 12$) produced outside of mist nets as a type of conspecific 'model' alarm to allow for a null, nonmimetic outcome in our analyses. Not only are brown thornbill aerial alarms functionally equivalent to the heterospecific model alarms, but they also share a similar acoustic space (Fig. 1). Furthermore, they show the greatest acoustic resemblance of any brown thornbill vocalization to these heterospecific alarms, and therefore produce the most conservative estimates for which brown thornbill vocalizations are mimetic. Brown thornbills do not produce any nonmimetic vocalizations resembling honeyeater alarms, and therefore no appropriate vocalizations for a null outcome could be included. All these alarms are made up of repeated and stereotyped single elements (Fig. 1), show high signal-to-noise ratio on recordings, and the model species are abundant at our study site (B. Igic & R.D. Magrath, personal observation) allowing us to collect a sufficient number of independent recordings.

Before classification, we selected all vocalizations produced by brown thornbills in mist nets that shared the broad acoustic space of potential model alarms and brown thornbill aerial alarms. This selection was necessary to avoid reductions in statistical power resulting from comparisons of too many different vocalization categories with too few independent samples, and to avoid forcing classification on those thornbill vocalizations that were extremely different from model vocalizations (these methods force classification of all thornbill vocalizations with their most similar model vocalization, regardless of the degree of similarity). This was unlikely to overestimate mimetic accuracy because we selected all vocalizations that had a lowest frequency above 6 kHz, rather than similarity to any specific model. This included all model alarms (except honeyeater alarms; Fig. 1). We also included all brown thornbill vocalizations with a downward frequency sweep, irrespective of frequency, as this is the central feature of honeyeater alarms (Fig. 1). We included only one vocalization of each type for a particular individual. In total, we included 133 independent vocalizations produced by 49 brown thornbills in mist nets.

Human visual classification

We asked six researchers with experience in acoustic analysis of avian sounds to identify which model alarm they thought each brown thornbill vocalization resembled most on a spectrogram. For each of the independent 133 brown thornbill vocalizations and 90 model alarms, we selected the first alarm element that had a good signal-to-noise ratio. For each alarm element we generated a spectrogram using Syrinx software (J. Burt, http://www.syrinxpc.com) with the same frequency (2–12 kHz) and duration (0.22 s) axes. Researchers were given two sets of spectrograms: a set consisting of heterospecific and conspecific model alarms (47 spectrograms total, seven to eight per model alarm) and a set consisting of brown thornbill vocalizations (133 spectrograms total). Brown

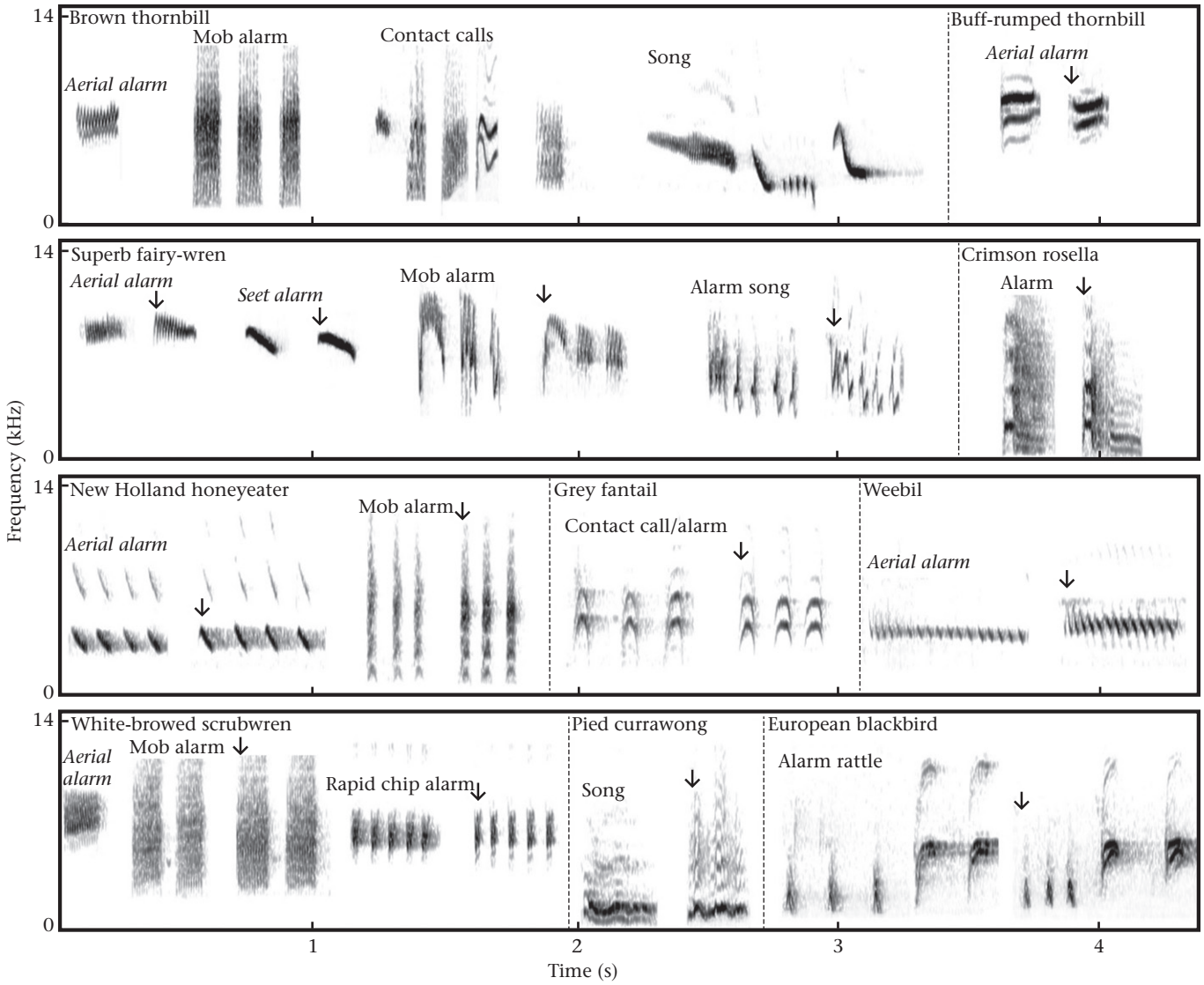

Figure 1. Spectrograms of brown thornbill species-specific vocalizations, heterospecific model species' vocalizations and corresponding brown thornbill mimicry (arrows). Vocalizations used in classification analyses are italicized.

thornbill vocalization spectrograms were presented to researchers in randomized order. Researchers chose the model alarm that they thought a brown thornbill vocalization most closely resembled. Finally, we pooled choices from all six researchers and used the most commonly chosen model alarm for each brown thornbill vocalization as its human-based classification. The survey was blind and researchers did not know which vocalizations were produced by which species.

Spectrogram measurements

Our first computer-based method involved comparing brown thornbill vocalizations and heterospecific model alarms using measured spectrogram time–frequency characteristics. We measured parameters that have been studied for these model species by Fallow et al. (2011), and spectrograms were generated in Raven Pro 1.3 (Charif et al. 2008). Prior to measurements each element was normalized and sound below 2 kHz was filtered out. For measurements we selected one to four alarm elements from each of the 133 independent brown thornbill vocalizations and each of the 90 independent model alarms, showing good signal-to-noise ratio. For each element we measured element duration (ms), modulation rate (the number of frequency modulations within an element/s, Hz), peak frequency (frequency with the maximum amplitude, Hz), and lowest frequency and highest frequency (the frequencies where the amplitude was 20 dB lower than at the peak frequency, Hz; Podos 2001). We measured frequency modulation as the number of complete frequency cycles per unit time visible on spectrograms, and excluded partial cycles at the beginning and end of elements (Magrath et al. 2007). For honeyeater alarms this included measuring frequency cycles, where present, about their downward-sweeping carrier frequency. Honeyeater alarms did not have frequency modulation about their carrier frequency, with the exception of one brown thornbill imitation, and therefore frequency modulation was usually zero. In total we measured 411 vocal elements. For sets of vocalizations where more than one element was measured, we calculated an average value for each measurement.

Spectrogram cross-correlation

Our second computer-based classification method involved comparing brown thornbill vocalizations and heterospecific model

alarms using spectrographic cross-correlation and principal coordinate analysis (Cortopassi & Bradbury 2000). We used the batch correlation function in Raven to calculate cross-correlation coefficients between all 411 alarm elements. Cross-correlation produces a similarity matrix of all compared elements where values lie between 0 and 1; values close to 1 represent similar sounds and values close to 0 represent dissimilar sounds. We used principal coordinate analysis to recreate the correlation relationships between alarm elements as geometric distances in a lower dimensional space. Principal coordinate analysis was implemented using the cmdscale() function in R 2.14.0 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). The analysis created geometric coordinates for all elements in a 410-axis dimensional space, where the first axis represented the best approximation to original similarities between alarms and the 410th the worst. We selected the first 10 axes (64.3% of total variation) for subsequent analysis because eigenvalues reached an asymptote and additional axes did not explain much additional variation (Cortopassi & Bradbury 2000). For vocalizations for which more than one element was measured, we calculated an average value for each axis.

Computer-based classification

We used either spectrogram time–frequency measurements or spectrogram cross-correlation output in combination with regularized discriminant function analysis to generate classification rules using model alarm data, and used these classification rules to identify mimicry in the brown thornbill vocalizations. Regularized discriminant function analysis performs better than conventional linear discriminant function analysis when data are collinear and when the number of variables is greater than the number of observations (Friedman 1989). Discriminant analysis was implemented using the rda() function of the klaR package (Weihs et al. 2005) in R. Lambda and Gamma coefficients were set to minimize apparent error (Friedman 1989), at 0.1 and 0, respectively. Prior probabilities were equal for all model alarms. To estimate classification error rates, we calculated the apparent error rate (the rate of reclassifying model alarms incorrectly) and estimated bias using bootstrapping methods (Efron 1983), which we implemented using the boot() function of the boot package (Canty & Ripley 2012). The final error rates for reclassifying model alarms using our discriminant rules were estimated as 1.6% for classifications using spectrogram measurements and 0.01% for classifications using spectrographic cross-correlation. Lastly, we used these two classification rules to classify each of the 133 brown thornbill vocalizations as a type of model alarm based on respective similarity in spectrogram measurements or similarity in spectrographic cross-correlations to model alarms.

Quantification of Mimetic Accuracy

To quantify mimetic accuracy of brown thornbill mimicry, we used multivariate and univariate statistics to compare acoustic features of brown thornbill vocalizations with model alarms. In the multivariate approach we reduced the dimensionality of the spectrogram measurement data and 10 axes from spectrographic cross-correlation analysis using principal component analysis on the correlation matrix. The analysis reduced the full 15 variables to 10 axes that explained 98.7% of the original variance. We divided brown thornbill vocalizations into model alarm groups as classified by the six researchers. We compared acoustic structure of imitations to corresponding model alarms across all 10 axes simultaneously using MANOVA contrast F tests. We excluded vocalizations identified as white-browed scrubwren aerial alarm mimicry because of a small sample size ($N = 2$). In the univariate approach we used t tests to compare mimicry of honeyeater aerial alarms and mimicry of superb fairy-wren aerial alarms to their corresponding model alarms across spectrogram measurements. Honeyeater aerial alarms and superb fairy-wren aerial alarms were selected because they respectively showed the most and least overlap between human-based and computer-based classification methods (97% versus 47%), and had the largest and smallest P values in contrast F tests from MANOVA. A single sample of superb fairy-wren aerial alarm mimicry was excluded from analysis as it was found to be an extreme outlier. We used t tests with unpooled variance to adjust where groups had unequal variance. We tested whether differences in frequency range result from differences in lower frequency when comparing mimicry of honeyeater alarms, using a generalized linear model created using restricted maximum likelihood, frequency range as response, and lowest frequency and mimicry versus model as fixed effects. Mimetic accuracy analyses were conducted using JMP 9 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

Identification of Mimicry

Brown thornbills mimicked a large range of heterospecific vocalizations but predominantly heterospecific aerial alarms (Fig. 1, Table 1). Brown thornbills in mist nets imitated 23 different vocalizations, from 17 different model species at our study site. From 55 captured thornbills, 49 vocalized in mist nets and 47 included mimicry. Birds that vocalized produced an average of 4.47 ± 2.14 SD different mimetic vocalizations belonging to 3.02 ± 1.47 SD model species, with a range of 0–10 mimetic calls, from up to six model species (mean recording period $\pm$ SD $= 3 \pm 1.94$ min). A large proportion of all call types imitated by thornbills were heterospecific alarms (mean $\pm$ SD $= 0.92 \pm 0.14$, $N = 47$ birds), and a large proportion of mimicked alarm elements were heterospecific aerial alarms (mean $\pm$ SD $= 0.97 \pm 0.06$, $N = 24$ birds). Brown thornbills also frequently produced nonmimetic alarms in mist nets. The most common type of alarm produced towards gliding predator models (nonmimetic aerial alarm; Fig. 1) was also produced by 49 of 55 captured birds, and the most common type of alarm produced towards the stationary stuffed owl was produced by 16 of 55 captured birds (nonmimetic terrestrial alarm; Fig. 1). Nonmimetic songs (Fig. 1), which are frequently produced by brown thornbills while foraging or in territory disputes with neighbours, were produced by only three of 55 birds captured in mist nets. Males and females were equally likely to vocalize in mist nets (proportion males $= 0.86$ versus females $= 0.85$; Fisher's exact test: $P \approx 1$) and to use mimicry if they did vocalize (proportion males $= 0.95$ versus females $= 0.94$; Fisher's exact test: $P \approx 1$).

Cross-validation of Human Assessment

Human and computer-based classification produced very similar results in identifying which brown thornbill vocalizations were mimetic, although there were slight disagreements in classifying which specific model species' alarm calls were imitated (Table 2). From all brown thornbill vocalizations above 6 kHz or having downward frequency sweeps, 63% were identified as mimetic by human visual inspection, 63% by time–frequency spectrogram measurements and 73% by spectrogram cross-correlation; the rest were identified as brown thornbill aerial alarms. Furthermore, elements identified as mimetic by human inspection were also classified as a type of mimicry 96.5% of the time by both computer-based methods. There was also good agreement in which specific model alarm calls were imitated. There was an overall 70.4% overlap in classification of imitation type by the three methods,

Table 2
Proportion of elements showing overlap between classification by visual inspection of spectrograms and classification of elements using two computer-based methods

Human classification	Computer-based classification						
	BT	BF	FWA	FWS	NH	SW	Different
BT	0.61	0	0	0	0	0.04	0.35
	(30)	(0)	(0)	(0)	(0)	(2)	(17)
BF	0	0.83	0	0	0	0.17	0
	(0)	(5)	(0)	(0)	(0)	(1)	(0)
FWA	0	0	0.47	0.07	0	0	0.47
	(0)	(0)	(7)	(1)	(0)	(0)	(7)
FWS	0	0	0	0.72	0	0	0.28
	(0)	(0)	(0)	(18)	(0)	(0)	(7)
NH	0	0	0	0	0.97	0	0.03
	(0)	(0)	(0)	(0)	(34)	(0)	(1)
SW	0.75	0	0	0	0	0.25	0
	(3)	(0)	(0)	(0)	(0)	(1)	(0)

BT = brown thornbill aerial, BF = buff-rumped thornbill aerial, FWA = superb fairy-wren aerial, FWS = superb fairy-wren seet, NH = New Holland honeyeater aerial, SW = white-browed scrubwren aerial and Different = classified as two different element types by the two computer-based methods (Fig. 2 for further details). Total number of elements is indicated in parentheses.

where human inspection and spectrogram measurements had 85.2% overlap, spectrogram measurements and spectrographic cross-correlation 75.6% overlap, and human-visual inspection and spectrographic cross-correlation 74.8% overlap. There was even greater agreement among methods when considering only those vocalizations identified as mimetic by human inspection: 81.7% were classified as mimicry of the same model species' calls by both computer-based classification methods, and 79.3% were classified as mimicry of the same model species calls by all three methods.

Quantification of Mimetic Accuracy

Mimetic aerial alarms were most similar to their corresponding model vocalizations (Fig. 2), but their acoustic structure did not always perfectly match model alarms (Table 3). MANOVA contrast tests found that mimicry of honeyeater aerial alarms ($F_{1,203} = 0.42$, $P = 0.52$) and fairy-wren seet alarms ($F_{1,203} = 0.51$, $P = 0.48$) were acoustically similar to their corresponding model vocalizations, while mimicry of buff-rumped thornbill aerial alarms ($F_{1,203} = 6.07$, $P = 0.02$) and fairy-wren aerial alarms ($F_{1,203} = 12.74$, $P < 0.0001$) were different from their corresponding model vocalizations. Although mimicry of scrubwren aerial alarms was similar to model scrubwren alarms (Fig. 2.), this comparison is based on a small sample of mimetic elements ($N = 2$) and may not be a reliable measure of acoustic similarity. Brown thornbill aerial alarms produced at mist nets were acoustically indistinguishable from aerial alarms prompted by gliding predator models away from mist nets ($F_{1,\ 203} = 0.94$, $P = 0.33$). Univariate analysis of honeyeater aerial alarm mimicry found that mimetic alarms were similar in peak frequency, highest frequency and element duration to the model's

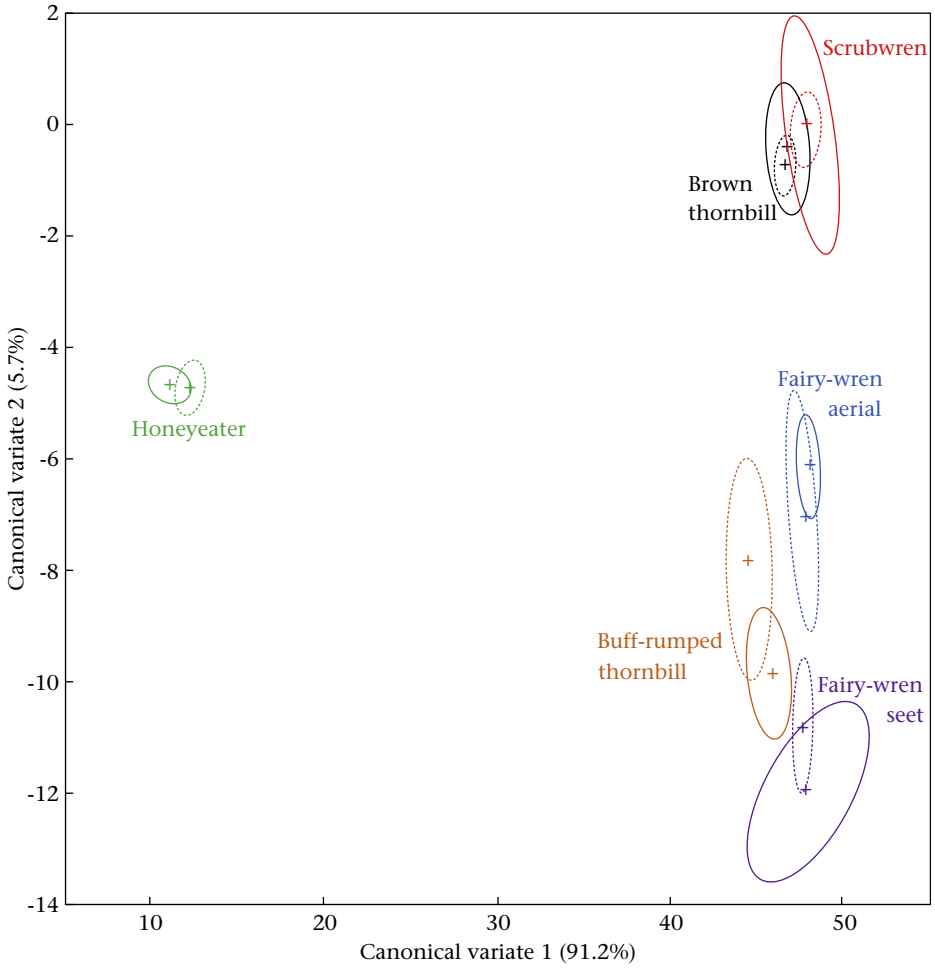

Figure 2. Canonical variates plot of model vocalizations and corresponding brown thornbill mimicry used in classification analyses. The plot was generated using measured spectrogram parameters and spectrographic cross-correlation as explanatory variables, and classification of spectrograms by six researchers as the grouping factor in a regularized discriminant function analysis. Ellipses represent 95% confidence intervals around group centroids (+) for heterospecific model vocalizations (full) and brown thornbill mist net vocalizations (dashed).

Table 3
Comparison of acoustic measurements of brown thornbill aerial alarm call mimicry with the corresponding heterospecific model alarms

Model species		Lowest frequency (Hz)	Highest frequency (Hz)	Frequency range (Hz)	Peak frequency (Hz)	Element duration (ms)	Modulation rate (Hz)
New Holland honeyeater	Model	3220.11	4923.80	1703.69	3929.8	48.00	
	SD	±168.47	±240.05	±231.38	±225.24	±4.89	
	Mimicry	3375.18	4903.07	1527.90	3914.11	50.80	
	SD	±239.55	±366.68	±235.63	±269.71	±11.65	
	t	2.55	−0.23	−2.68	−0.22	1.02	
	(*df*)	(53)	(53)	(53)	(53)	(53)	
	P	0.01	0.82	<0.01	0.83	0.31	
Superb fairy-wren	Model	8391.11	10218.18	1827.06	9128.01	103.50	102.68
	SD	±165.90	±414.33	±389.89	±239.19	±28.80	±18.86
	Mimicry	7935.38	9287.91	1629.34	8600.83	113.74	78.95
	SD	±603.07	±619.97	±417.54	±639.55	±22.71	±11.57
	t	−2.94	−5.95	−3.82	−3.58	2.82	−6.78
	(*df*)	(15.59)	(33)	(33)	(33)	(33)	(33)
	P	0.01	<0.01	<0.01	<0.01	<0.01	<0.01

All measurements were made on spectrograms using spectrogram parameters and measurement methods described in the text. The table shows acoustic measurements (mean ± SD) on New Holland honeyeater aerial alarm call elements produced by models ($N = 20$) and brown thornbills ($N = 35$), and superb fairy-wren aerial alarm call elements produced by models ($N = 21$) and brown thornbills ($N = 14$). We used *t* tests with unpooled variance where group variances were significantly different.

alarm, but had a higher lowest frequency and a smaller overall frequency range compared with the model. The frequency range was smaller even when controlling for lowest frequency (GLM *t* test: $t_{32} = -3.94$, $P < 0.01$). Univariate analysis of fairy-wren alarm mimicry found that mimetic alarms had an overall lower frequency structure (lowest, highest and peak), a smaller frequency range, longer element duration and a lower modulation rate compared with model fairy-wren alarms. However, the peak frequency of mimetic fairy-wren alarms (8.6 kHz) was within the peak frequency range that prompts fairy-wrens to flee (below; Fallow et al. 2011, 2013).

DISCUSSION

Our study provides the first formal evidence of vocal mimicry in the brown thornbill. Brown thornbills caught in mist nets imitated a large range of heterospecific vocalizations, but most commonly alarm calls, and in particular aerial alarm calls. We found consistency between human classification of mimicry and computer classification using spectrogram measurements or spectral cross-correlation. To our knowledge this is the first study to use systematic cross-validation of human and computer-based methods to identify mimetic vocalizations. Imitations of aerial alarms were similar, but not acoustically identical, to their corresponding model species' alarms. However, imitations retained those acoustic parameters previously shown to be important in provoking alarm responses in a heterospecific. These findings suggest that mimicry of heterospecific alarms may not require perfect accuracy, as long as particular acoustic features of model alarms are retained.

Identification and Possible Function of Mimicry

Brown thornbills imitated a great diversity of heterospecific vocalizations (Table 1, Fig. 1), which is remarkable for a 6–8 g bird. They imitated a range of taxonomic groups, including similarly sized birds such as superb fairy-wrens (10 g), and large predators such as pied currawongs, *Strepera graculina* (300 g). Mimicked vocalizations also varied greatly in acoustic structure: both high and low frequency vocalizations were regularly imitated (e.g. superb fairy-wren aerial alarm, 8.6 kHz peak frequency versus crimson rosella, *Platycercus elegans*, alarm, 2.7 kHz peak frequency). Imitations included both alarms with repeated elements of the same type (e.g. superb fairy-wren aerial alarm) and alarms with multiple different elements imitated in their correct sequence (e.g. blackbird, *Turdus merula*, alarm rattle; Fig. 1). Despite this diversity, brown thornbills primarily mimicked other species' aerial alarm calls.

We suggest that brown thornbill mimicry may function to startle predators. There are three primary functional explanations for mimicking sounds associated with alarm: (1) to attract aid from heterospecifics (Chu 2001a); (2) to distract heterospecifics and steal resources (Flower 2011); or (3) to deter or startle predators (Kelley & Healy 2011). (1) For mimetic alarms to attract aid, they need to be attractive alarms, such as mobbing alarms. However, many of the alarms recorded in mist nets were heterospecific aerial alarms, which generally cause individuals to flee (Magrath et al. 2007), and therefore attracting aid is unlikely. (2) Production of aerial alarms in the absence of aerial threats has been linked to kleptoparasitism (Flower 2011), but brown thornbills were never observed to steal food from heterospecifics during our study. Furthermore, kleptoparasitism is an unlikely explanation for mimicry used when an individual is restrained. (3) Mimicry of aversive sounds, such as predator sounds and alarm calls, may deter or startle predators during attack (Rowe et al. 1986; Kelley & Healy 2011). In addition to imitating aerial alarms, brown thornbills also imitated predators and aggressive species such as Australian magpies, *Gymnorhina tibicen*, pied currawongs, grey butcherbirds, *Cracticus torquatus*, and red wattlebirds, *Anthochaera carunculata* (Higgins et al. 2006; Magrath et al. 2009), although not as commonly. As mist net capture may simulate a circumstance of being caught by a predator (Conover 1994; Møller & Nielsen 2010), we suggest aerial alarm and predator mimicry may function to startle the predator into releasing caught brown thornbills, a function similar to that proposed to explain why captured birds produce distress calls (Conover 1994; Wise et al. 1999). Mimicry of aerial alarms may be particularly effective in startling the brown thornbill's predators if the attacking predator is prey to other predators. Indeed, Australian magpies, pied currawongs and grey butcherbirds are all prey to raptors (Marchant & Higgins 1993), and might therefore use heterospecific aerial alarms as signals of approaching danger. Production of multiple types of mimetic alarms by the brown thornbill may produce particularly strong distractions to these predators because more threatening flying predators often cause simultaneous production of alarms by multiple different prey species (B. Igic & R.D. Magrath, personal observations). However, any possible function for brown thornbill mimicry requires investigation of predator responses.

Mimicry of vocalizations associated with alarm, or danger, may also suggest how brown thornbills acquire heterospecific

vocalizations. Mimicry of sounds associated with alarm has been reported in many avian mimics (Morton 1976; Chu 2001b; Goodale & Kotagama 2006; Flower 2011; Kelley & Healy 2011). Recently it has been suggested that increased stress during dangerous circumstances may facilitate learning of sounds associated with alarm (Kelley & Healy 2011), and even prompt the production of these sounds during other stressful occasions (Kelley et al. 2008; Kelley & Healy 2012). However, the role of stress in learning and production of vocal mimicry is yet to be investigated, and stress-induced learning does not necessarily mean mimicry is nonfunctional, as sometimes suggested (Kelley et al. 2008). Stress-induced learning could instead be a mechanism that underlies an adaptive function, particularly when alarm mimicry is frequently used in dangerous circumstances. Brown thornbills appear to mimic heterospecific aerial alarms less frequently when foraging undisturbed compared with circumstances involving threat (B. Igic & R.D. Magrath, unpublished data). However, comparing which vocalizations are mimicked in circumstances of alarm and nonalarm by brown thornbills is beyond the scope of the current study and requires further investigation.

Cross-validation of Methods to Classify Vocal Mimicry

Computer-based and human-based sound classification consistently identified which brown thornbill vocalizations were mimetic, and usually agreed regarding which specific model vocalization was imitated. Ninety-seven per cent of vocalizations identified as mimicry by humans were also identified as mimicry by both computer methods, with 75–85% agreement between human and computer methods on the specific type of call imitated. These results show that human classification of brown thornbill mimicry is comparable to more systematic computer-based classification methods. Cross-validation of methods showed in particular that human assessment agreed more with classification based on spectrogram measurements than that based on spectral cross-correlation. This difference may have resulted because spectrogram cross-correlation overestimated similarity between sounds with similar background noise.

The similarity between human and computer classification of thornbill vocalizations is reassuring because, although computer-based methods are commonly employed in the study of vocal mimicry, human evaluation is still predominantly used in identifying vocalizations that are possible imitations, and in choosing their corresponding model (Coleman et al. 2007; Zann & Dunstan 2008; Flower 2011; Kelley & Healy 2011; Dalziell & Magrath 2012). Human-based methods are often difficult to eliminate entirely from studies of animal acoustic communication, and their complete exclusion may even be inappropriate (Janik 1999). We suggest that the best approach is to use computer-based techniques to cross-validate human evaluation of mimetic vocalizations, as this allows estimation of reliability for human classification, which may differ according to the vocalizations studied. Furthermore, these computer-based techniques are readily available, replicable across different studies and study systems, and can be tailored to evaluate similarity based on fine acoustic structure.

Mimetic Accuracy

Imitations produced by the brown thornbill were similar but not identical to their corresponding model vocalizations, which could reflect vocal constraints on accurate mimicry. Vocal signals can have constraints associated with their production (Podos 1997, 2001), and for mimics this can impede the ability to imitate a large range of acoustically different heterospecific sounds accurately (Zollinger & Suthers 2004). Although thornbills can imitate a diversity of different vocalizations, they may lack the vocal machinery to accurately imitate vocalizations that are outside their normal species-specific vocal range (typically between 1 and 7 kHz peak frequency). This may explain why honeyeater aerial alarms (4 kHz natural peak frequency) were more accurately imitated than superb fairy-wren aerial alarms (9 kHz natural peak frequency). However, this does not explain why imitation of fairy-wren seet calls was accurate ($P = 0.48$) while buff-rumped thornbill aerial alarm imitation was not ($P = 0.02$), as both have a peak frequency of 8.5 kHz. The latter has a more complex acoustic structure (Fig. 1), which might make imitation more difficult. There can also be vocal constraints on temporal acoustic structure. For example, bill morphology can affect the ability to produce rapid frequency sweeps (Podos 2001), which might explain why the lowest frequency and frequency range of honeyeater aerial alarms were not perfectly reproduced.

Although vocal constraints might affect the accuracy of imitations, mimicry of heterospecific alarms might not require perfect resemblance for function. Visual mimicry, for example, does not always require perfect resemblance to be functional (Dittrich et al. 1993; Kikuchi & Pfennig 2010). If intended receivers lack the sensory capabilities to detect fine-scale differences between models and inaccurate mimics (Dittrich et al. 1993; Kikuchi & Pfennig 2010), then selection for accuracy would be weak and imperfect mimicry could persist. Discrimination between true and false alarms could also be costly because aerial alarm calls require immediate responses for survival, and the act of discrimination itself can increase overall reaction time (Wickelgren 1977). In support of this prediction of a speed–accuracy trade-off, superb fairy-wrens flee immediately to cover according to the peak frequency of aerial alarm calls, a simple call feature, while the detailed acoustic structure of calls affects the delayed response of how much time is spent in cover (Fallow et al. 2011, 2013). Assuming that the peak frequency is in general a key feature of aerial alarms, brown thornbill mimicry may only require sufficient accuracy in this feature of model alarms to prompt response by receivers. Brown thornbills accurately imitated the peak frequency of honeyeater alarm calls (both 3.9 kHz), despite other differences. Furthermore, the peak frequency of fairy-wren alarm imitations approached that of model alarms (8.6 versus 9.1 kHz), and although lower, it is within the range of alarm call peak frequencies that prompts fleeing by superb fairy-wrens (Fallow et al. 2011, 2013). This suggests that even though imitations are imperfect, they may maintain acoustic properties necessary to provoke immediate responses by receivers. However, accurate imitation of other model alarm call features may still have some functional importance because although imitations were different from model alarms in fine acoustic structure, they did retain an overall level of similarity to model alarms (Fig. 1).

Imitating a number of different alarms may also reduce selection for perfect accuracy if it reduces the exposure of receivers to particular imitations relative to their model counterparts. For example, greater abundance of the model can reduce requirements for mimetic accuracy in visual Batesian mimicry systems (Harper & Pfennig 2007). Reduced relative exposure may limit the ability of receivers to fine-tune their ability to discriminate between true model and false mimetic alarms (Flower 2011). This may also explain why fairy-wren alarm mimicry is less accurate than honeyeater mimicry. Fairy-wrens are more abundant at the study site than honeyeaters, and fairy-wren groups give alarm calls at a much higher rate than honeyeater groups (5 versus 0.7/h; Magrath et al. 2009). More frequent exposure to true model alarms may weaken the selection for accurate imitations of fairy-wren alarms as opposed to rarer honeyeater alarms (frequency-dependent benefits; Lindström et al. 1997).

Our research confirms that brown thornbills mimic other species' vocalizations, often their aerial alarm calls, but they do so with variable accuracy. Inaccurate mimicry might reflect vocal constraints or could imply that alarm mimicry does not always require perfect imitation to be functional. The strength of selection for accuracy may vary between different model alarms, and possibly reflect the relationships between model and receiver. However, the next step in testing these predictions is a bioassay of the response by intended receivers to alarm mimicry (e.g. Flower 2011), with an emphasis on examining how imitation of different heterospecifics' alarms, and the level of mimetic accuracy, affect alarm response. Alternatively, developing perceptual models of avian hearing, similarly to those used in studies of visual mimicry (e.g. Igic et al. 2012), may prove useful for testing how receiver perception shapes signal structure. Examining mimicry from intended receiver perspectives becomes particularly important with accumulating evidence showing that perfect mimicry is not always a requirement for mimetic function (Sherratt 2002). Alarm mimicry is particularly interesting because alarm signalling can play a fundamental role in both cooperative and exploitative relationships among and within species (Munn 1986; Krams et al. 2008; Goodale et al. 2010; Flower 2011), such that alarm mimicry may have both deceptive and cooperative functions.

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