



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

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ARTICLE INFO

Article history:

Received 11 September 2012
Initial acceptance 12 November 2012
Final acceptance 17 December 2012
Available online 21 January 2013
MS. number: 12-00699

Keywords:

Acanthiza pusilla
accuracy
alarm call
brown thornbill
imitation
imperfect mimicry
vocal mimicry

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.

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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 & Wojcik 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

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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; Dalziel & 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

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