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Vocal mimicry in male bowerbirds: who learns from whom?

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Vocal mimicry is one of the more striking aspects of avian vocalization and is widespread across songbirds. However, little is known about how mimics acquire heterospecific and environmental sounds. We investigated geographical and individual variation in the mimetic repertoires of males of a proficient mimic, the spotted bowerbird *Ptilonorhynchus maculatus*. Male bower owners shared more of their mimetic repertoires with neighbouring bower owners than with more distant males. However, interbower distance did not explain variation in the highly repeatable renditions given by bower owners of two commonly mimicked species. From the similarity between model and mimic vocalizations and the patterns of repertoire sharing among males, we suggest that the bowerbirds are learning their mimetic repertoire from heterospecifics and not from each other.

Keywords: vocal mimicry; geographical variation; repertoire

1. INTRODUCTION

Songbirds typically learn their species-specific vocalizations as juveniles or young adults from conspecifics, but approximately 15 per cent of species also incorporate non-species-specific sounds into their song repertoires. Despite these impressive displays of learning and vocal production, the acquisition and the function of such mimicry remains unclear (Kelley *et al.* 2008). Although frequently assumed to serve some functional benefit to the mimic, it is plausible that songbirds acquire vocalizations from heterospecifics simply owing to some degree of imprecision in the process by which they learn vocalizations from conspecifics. Alternatively, individuals may deliberately learn sounds from their environment if mimicry serves a particular function, such as mimicking predators for defence (Dobkin 1979). Similarly, mimics may learn from their acoustic environment if the 'accuracy' of mimicry functions as an indicator of male age or quality, e.g. in sexual selection (Zann & Dunstan 2008). One way to investigate the acquisition and function of mimicry is to determine the entirety of an individual's mimetic repertoire to examine how this repertoire relates to possible sound

sources. To our knowledge, this has never been done in the wild.

Although better known for their bower building and bower decoration skills (e.g. Frith & Frith 2004), spotted bowerbirds *Ptilonorhynchus maculatus* are also proficient vocal mimics, typically mimicking over a dozen heterospecifics and other environmental noises. Males build bowers at least 1 km apart, far enough that they may not be able to hear each other's vocalizations when at their own bowers. However, they regularly visit each other's bowers to steal decorations and to destroy the bower. Such raids are usually directed at nearby bowers rather than those further away and thus the rate of bower-owning males' interactions with other bower owners is related to the distances between bowers (Madden *et al.* 2004). As territorial songbirds often share their repertoires with neighbouring males (Nicholson *et al.* 2007), it seems plausible that the mimetic repertoires of bower owners are also more similar the closer the neighbour. Mimetic repertoire sharing might come about in several ways: (i) birds mimic each others' vocalizations, either deliberately or owing to imperfect learning; (ii) birds mimic heterospecifics in their environment, which are likely to be similar species when bowers are closer together.

Here, we attempted to distinguish between these two alternatives by examining mimetic repertoire sharing among male spotted bowerbirds and the detailed structure of mimicry of two commonly mimicked models: the pied butcherbird *Cracticus nigrogularis* and the whistling kite *Haliastur sphenurus*. While acquisition from conspecifics or heterospecifics may both lead to local repertoire sharing, males learning directly from heterospecifics should demonstrate repeatable individual differences in renditions of their mimicry, whereas if males learn from each other, we would expect males to have both similar repertoires and renditions of mimicry.

2. MATERIAL AND METHODS

We recorded mimicry of 19 male bower-owning spotted bowerbirds in Taunton National Park (23.3° S, 149.1° E), Queensland, Australia, during 2007 and 2008. Individuals were identified by a unique series of colour bands on both legs. Males were recorded at their bowers using a Sennheiser ME66/K6 microphone and power supply onto a Sony TCD-D8 DAT recorder at a sampling rate of 44.1 kHz. Sampling effort was evenly distributed among bowers (time per bower per year 16.5 ± 1.5 h, mean $\pm$ s.e.). Interbower distances were measured using GPS coordinates, converted into kilometres and rounded to the nearest 10 m.

Recordings were converted into spectrograms using RAVEN PRO v. 1.3 (Charif *et al.* 2004) using a Hann window and a 512 pt. fast Fourier transform. Mimicry was identified using a CD-ROM of bird vocalizations (Simpson & Day 1999) alongside our field recordings of model vocalizations, and an experienced birder corroborated our identifications. None of our model sounds resembled those of other species found on the park. Mimicry usually comprised one repeated note that could be easily identified after a single note. When a phrase was composed of more than one note (figure 2a), we analysed only those recordings in which the entire phrase was present.

Song sharing between males was calculated using the number of model species a focal male shared with a particular bower owner, expressed as a proportion of the focal male's total repertoire. Mantel tests were used to test correlations between the proportion of repertoire shared and interbower distance in 2007 and 2008 separately, using 10 000 iterations on a full matrix without diagonals (Liedloff 1999).

We used recordings of butcherbird and kite mimicry to investigate individual differences in production of mimetic vocalizations. We

recorded from five to 10 recordings of butcherbird mimicry from each of 10 males and from two to 47 recordings of kite mimicry from each of five males. Spectrograms of these recordings were measured for start frequency, end frequency, minimum frequency, maximum frequency, peak frequency, duration and the time to maximum, minimum and peak frequency. We calculated the proportion of time to the minimum, maximum and peak frequencies, the ratios of the maximum frequency to peak frequency and frequency range, the ratios of the start frequency to end, peak and maximum frequency, the ratio of the peak frequency to frequency range and, for butcherbird mimicry, expressed the duration of the upward sweep at the end as a proportion of overall duration. Measurements that were highly correlated with other variables ($r > 0.7$) were dropped from further analyses.

Analyses of butcherbird and kite mimicry were carried out separately and discriminant function analysis was used to identify temporal or frequency measurements that classified individual bowerbird mimicry of each model. Means for each individual in canonical space were represented by group centroids and the squared Mahalanobis distances between each group centroid were used as a measurement of acoustic similarity between individuals. Matrices of these values and interbower distances were then used in a Mantel test to assess whether the mimicry of individuals with bowers closer together shared greater structural similarity than did individuals with bowers further apart. The repeatability (intraclass correlation coefficient) of the parameter that accounted for the most variation in mimetic production for each species was calculated based on among and within male variance components derived from a one-way ANOVA (Lessells & Boag 1987). Unless stated otherwise, all analyses were carried out using JMP (v. 7).

3. RESULTS

(a) Bower proximity and repertoire similarity

We identified mimicry of 16 different species of heterospecifics, including one example of human imitation. The average repertoire size of bower-owning males in 2007 was 3.7 ± 0.5 models and in 2008 was 3.2 ± 2.6 (range: 0–8, both years). The average nearest-neighbour distance among bowers was 1740 ± 700 m (range: 880–2830 m). In both years, males shared a larger proportion of their repertoire with males whose bowers were closer to their own bower than they did with males who had bowers further away (Mantel test, 2007: 17×17, $r = 0.246$, $p < 0.001$; 2008: 13×13, $r = 0.355$, $p < 0.001$; figure 1).

(b) Bower proximity and mimetic similarity

Discriminant function analysis revealed individual differences among renditions of pied butcherbird mimicry (Wilks' $\lambda = 0.023$, $F_{9,70} = 6.96$, $p < 0.0001$; figure 2) and whistling kite mimicry (Wilks' $\lambda = 0.26$, $F_{4,53} = 4.13$, $p < 0.0001$). For butcherbird mimicry, the first two canonical roots had eigenvalues greater than 1 and contributed over 76 per cent of the discriminatory power. The structural measurements that contributed most to the discriminant functions were duration, start frequency, end frequency, ratio of start frequency to maximum frequency and the proportion of time to maximum frequency. For kite mimicry, the first canonical root had an eigenvalue greater than 1 and contributed over 86 per cent of the discriminatory power. The spectral measurements that contributed most to the discriminant functions were the ratio between start and end frequency, minimum frequency, frequency range and the ratio of peak to maximum frequency.

A Mantel test using group centroids and interbower distance matrices revealed that there was no relationship between the measured acoustic characteristics of
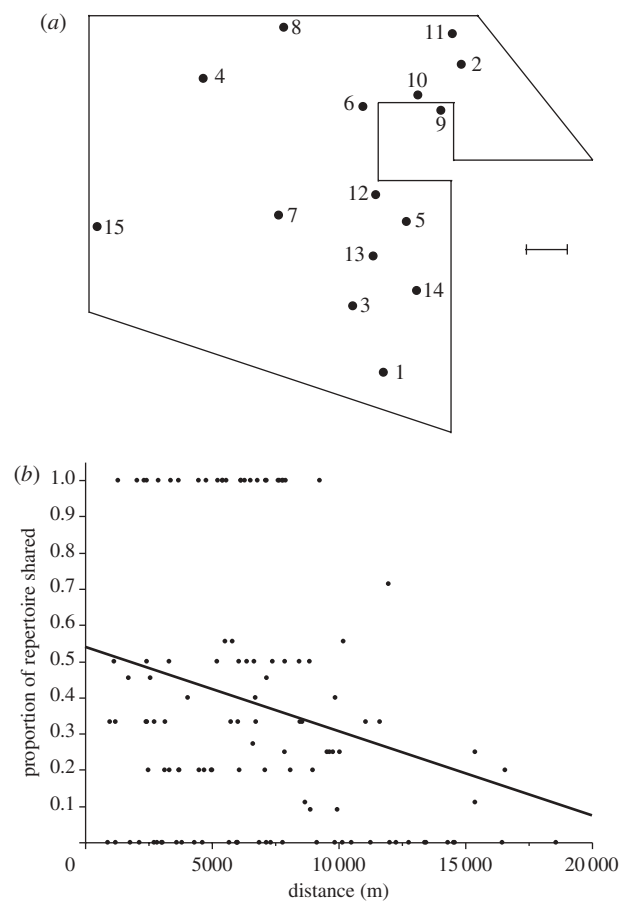

Figure 1. (*a*) Map of Taunton National Park showing the distribution of bower sites, represented by numbered dots. Bower 16 and 17 (used in 2007 analysis only) are not shown and are 5.1 and 7.9 km, respectively, outside the park boundary. Scale bar, 1 km. (*b*) The proportion of repertoire shared against interbower distance for all pairs of males in 2007, line represents best fit.

mimicry and distance between bowers for either butcherbird or kite mimicry (butcherbird: 10×10, $r = -0.13$, $p = 0.71$, $n = 10$; kite: 5×5, $r = 0.495$, $p = 0.15$, $n = 5$). Repeatability analyses on the measurement that explained the most variation in mimetic structure revealed that these vocalizations were highly repeatable within individuals (butcherbird: duration $r = 0.79$; kite: ratio of start to end frequency $r = 0.42$).

4. DISCUSSION

Males with bowers closer together had more similar mimetic repertoires than did males with bowers further apart. However, variation in the reproductions of the sounds of two of the most commonly mimicked species was not explained by interbower distance. Moreover, individuals were highly repeatable in aspects of these vocalizations.

Our finding that males were more likely to share the contents of their repertoire the closer they were to another bower owner is consistent with the birds learning from either conspecifics or heterospecifics. However, closer inspection of two of these shared sounds shows that the detailed structures of the
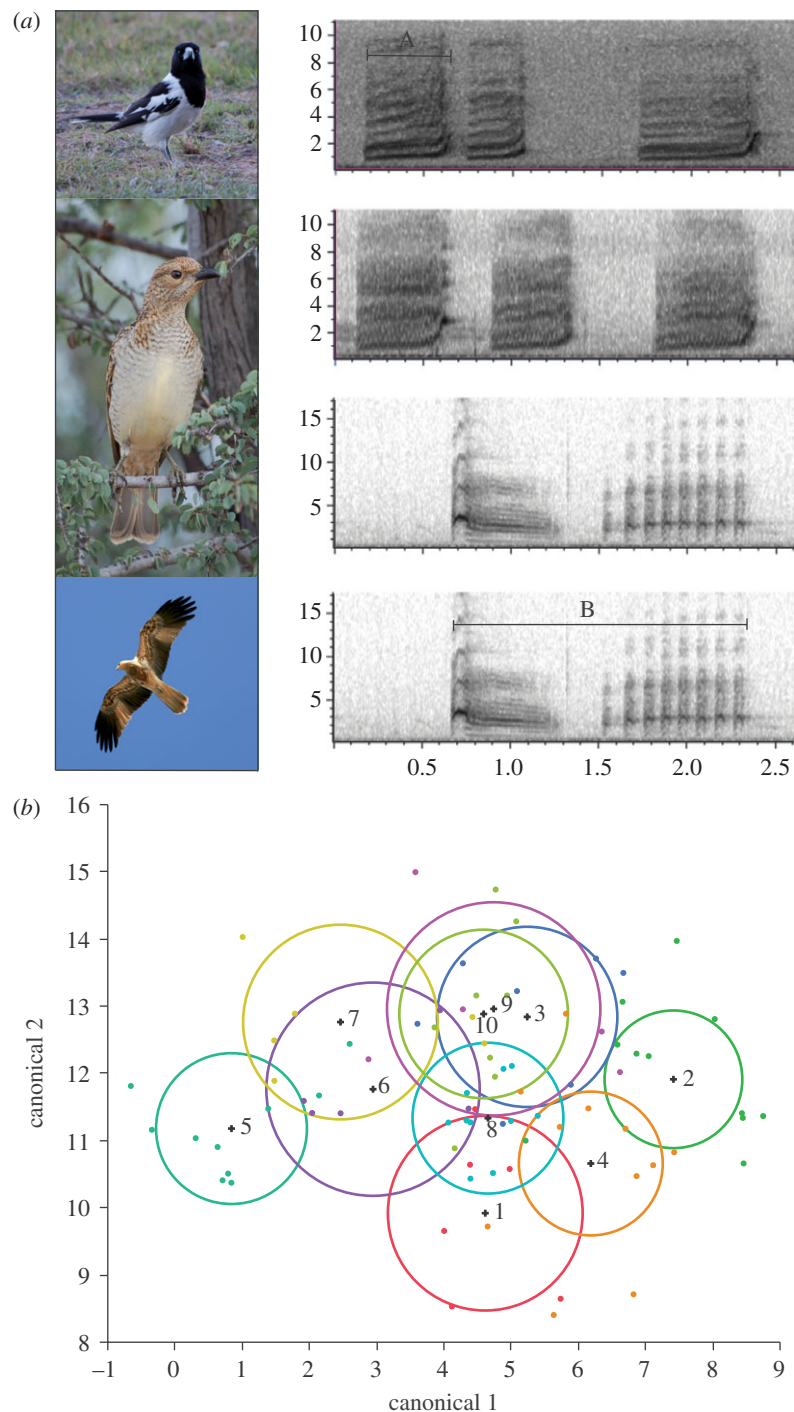
Figure 2. (*a*) Top to bottom: a pied butcherbird with spectrogram of its species-specific vocalization (one phrase denoted by A, three phrases shown on spectrogram), a male spotted bowerbird with spectrograms of butcherbird and kite mimicry; a whistling kite with spectrogram of species-specific call (one phrase, denoted by B). Sound files for these spectrograms are in the electronic supplementary material. (*b*) Discriminant analysis of pied butcherbird mimicry. Each point represents one mimetic recording and each colour represents a different individual. Circles are 95% confidence intervals for each individual's mean centroid value (individuals numbered 1–10). Non-intersecting circles indicate that individuals produced significantly different mimetic sounds.

mimicry are not explained by spatial proximity. Instead, the high among-male variability in butcherbird mimetic structure suggests that learning directly from heterospecific models is more likely. As kites have large territories, multiple bower owners are likely to hear calls of a single kite whereas a butcherbird, with a relatively small territory, will be heard by fewer, or a single, bowerbird. A more definitive test would require recordings from individually identifiable models, allowing variation within and among model vocalizations to be assessed. Given the difficulty of collecting such data, it is perhaps not surprising that this remains an unexplored avenue of research.

To our knowledge, only one other study on vocal mimicry has examined geographical variation in

structure across mimics: Albert's lyrebird males *Menura alberti* also appear to learn their mimicry directly from a heterospecific (satin bowerbirds *Ptilonorhynchus violaceus*), as geographically discrete populations of male lyrebirds faithfully reproduce the structurally distinct songs of the corresponding local population of satin bowerbirds (Putland *et al.* 2006). Unlike the spotted bowerbirds, there is less variation in the structure of mimicry within populations of lyrebirds than there is in the structure of the vocalizations of the local satin bowerbird models. This may mean lyrebirds may copy each other and not models directly. It seems likely that a spatial analysis of content and mimetic structure would determine if this was the case.

Birds copying the vocalizations of heterospecifics provide some of the most striking examples of animal mimicry, yet we know remarkably little about its adaptive significance, if any. Tests of sexual selection on repertoire size, or vocal mimicry as a defensive adaptation, have proved equivocal at best (Kelley *et al.* 2008). Moreover, in stark contrast to more conventional song learning in birds (e.g. Catchpole & Slater 2008), we know next to nothing about how vocal mimicry develops mechanistically. Here, we have at least begun the process of studying both mechanism and function by identifying the probable models for, and the sources of variation in, spotted bowerbird vocal mimicry.

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