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Female preferences drive the evolution of mimetic accuracy in male sexual displays

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Males in many bird species mimic the vocalizations of other species during sexual displays, but the evolutionary and functional significance of interspecific vocal mimicry is unclear. Here we use spectrographic cross-correlation to compare mimetic calls produced by male satin bowerbirds (*Ptilonorhynchus violaceus*) in courtship with calls from several model species. We show that the accuracy of vocal mimicry and the number of model species mimicked are both independently related to male mating success. Multivariate analyses revealed that these mimetic traits were better predictors of male mating success than other male display traits previously shown to be important for male mating success. We suggest that preference-driven mimetic accuracy may be a widespread occurrence, and that mimetic accuracy may provide females with important information about male quality. Our findings support an alternative hypothesis to help explain a common element of male sexual displays.

Keywords: sexual selection; vocal mimicry; cross-correlation; repertoire size; multiple traits; bowerbirds

1. INTRODUCTION

In birds, interspecific vocal mimicry is often used by males in sexually selected displays (Baylis 1982), and is thought to be favoured by female preferences for large song repertoires—males can copy other species' songs to increase repertoire size (Baylis 1982). To date, however, studies investigating the relationship between vocal mimicry and female mate choice have provided little support for this hypothesis. In northern mockingbirds (*Mimus polyglottos*) and marsh warblers (*Acrocephalus palustris*), for instance, males' large (more than 100 spp.) mimetic repertoires may indirectly affect male mating success through their primary function in intraspecific competition (Howard 1974; Dowsett-Lemaire 1979), and in black-browed reed warblers (*Acrocephalus bistrigiceps*), a species with relatively small (2–5 spp.) mimetic repertoires, male repertoire size is not associated with male mating success (Hamao & Eda-Fujiwara 2004). Thus, the importance of female preferences in the evolution of vocal mimicry remains unclear. Here we investigate another aspect of vocal mimicry that may influence female choice: the accuracy with which model vocalizations are reproduced by displaying males.

It is possible that mimetic accuracy may contain important information for females in mate choice: by definition, mimetic vocalizations are learned display elements, and the accuracy of learned vocalizations can indicate a male's current (Garamszegi *et al.* 2005) and past (Nowicki *et al.* 2002) condition. Moreover, the production of accurate interspecific mimicry requires males to effectively modify their vocal motor patterns to match those of the model species (Zollinger & Suthers 2004), suggesting that mimetic accuracy may contain honest information regarding male physiological performance. Here we use cross-correlation sound analyses to test hypotheses about the importance of mimetic accuracy and repertoire size during courtship in satin bowerbirds (*Ptilonorhynchus violaceus*), a species where males have complex sexual displays (Borgia 1985) and produce vocal mimicry during courtship (Loffredo & Borgia 1986).

A previous study of vocal mimicry in this species suggested that mimetic call 'quality' may be important for male mating success, and that mimetic quality may inform females about male age (Loffredo & Borgia 1986), but that study did not compare mimetic calls with model calls. Here we test two hypotheses about the function of vocal mimicry in a natural population of satin bowerbirds. The mimetic accuracy hypothesis posits that females assess the accuracy of vocal mimicry while choosing their mates, and predicts a positive relationship between mimetic accuracy and male mating success. The repertoire size hypothesis posits that females assess mimetic repertoire size while choosing mates, and predicts a positive relationship between male mating success and the number of species mimicked.

2. MATERIAL AND METHODS

This study was conducted in 1997 at Wallaby Creek, NSW, Australia. From 1 September to 30 October, birds were captured; individuals were uniquely marked with coloured leg bands, morphometrics were taken and ectoparasites counted (see electronic supplementary material). During the mating season (1 November–20 December), automatically activated Hi-8 Sony Handycams equipped with 3 V electret condenser microphones recorded all mating-related behaviours/vocalizations at 29 males' bowers. Note that the sensitivity of these microphones, and the resolution of these video cameras, was superior to those used by Loffredo & Borgia (1986), thus allowing for this new study and revealing a more expanded mimetic repertoire than previously reported in this population. We recorded vocal mimicry in 123 courtships. For sound measurements and analyses, we used CANARY v. 1.2.4. Vocalizations were digitized at 16 bits with a sample rate of 22 kHz. For each male, mating success was calculated as the number of different mates. Male mating success was $\ln(Y+1)$ transformed to improve normality and homoscedasticity; all other variables were distributed normally among males.

During courtship, individual males in our populations mimicked five sympatric bird species: laughing kookaburra (*Dacelo novaeguineae*); Lewin's honeyeater (*Meliphaga lewinii*); Australian raven (*Corvus coronoides*); sulphur-crested cockatoo (*Cacatua galerita*); and yellow-tailed black cockatoo (*Calyptorhynchus funereus*). To test the mimetic accuracy hypothesis, we quantified the similarities between model species' calls and each male's mimetic renditions of these calls. Spectrograms revealed clear qualitative differences between 'high-accuracy' and 'low-accuracy' mimicries (figure 1). Thus, we used spectrographic cross-correlation (SPCC; Clark *et al.* 1987) to quantify

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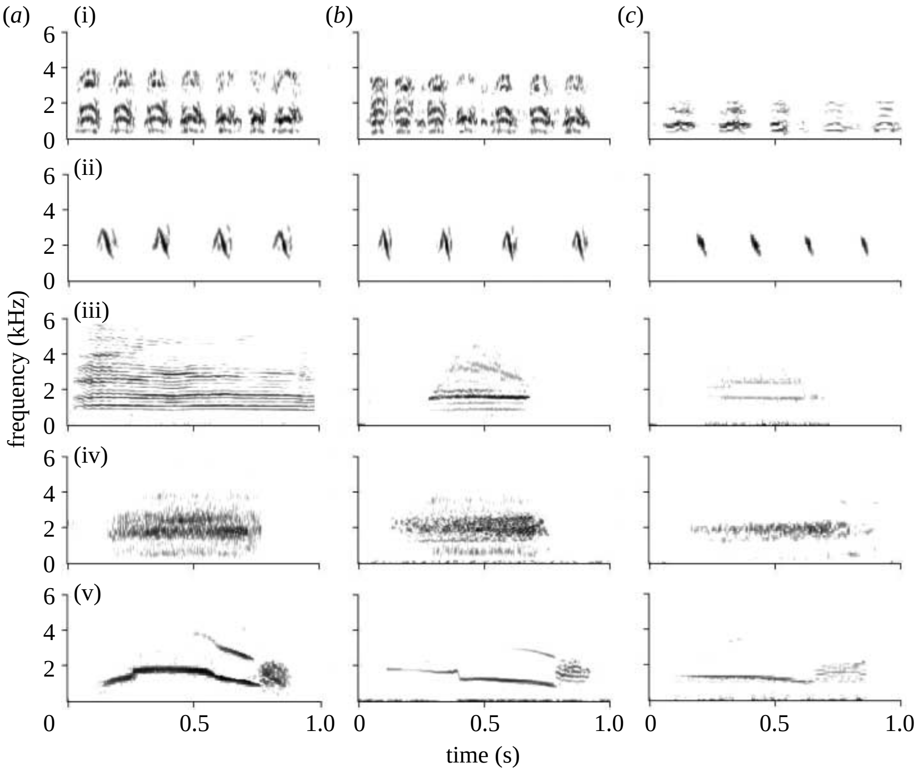

Figure 1. Spectrograms of (*a*) model species' calls, (*b*) high-accuracy and (*c*) low-accuracy mimetic calls. (i) *D. n.*, *Dacelo novaeguineae*; (ii) *M. l.*, *Meliphaga lewinii*; (iii) *C. c.*, *Corvus coronoides*; (iv) *C. g.*, *Cacatua galerita*; (v) *C. f.*, *Calyptorhynchus funereus*.

'mimetic accuracy' by comparing the mimetic calls of each male in our population with the calls of the model species. SPCC quantifies call similarity by 'sliding' the spectrograms of two calls across each other in time. The maximum degree of overlap between the two spectrograms (measured as the peak cross-correlation value) reflects their structural similarity (Clark *et al.* 1987). For each male, we calculated the mean peak cross-correlation value for the calls it mimicked, and we used this mean as a measure of its mimetic accuracy. Despite criticisms of SPCC (Khanna *et al.* 1997), Cortopassi & Bradbury (2000) found that it performed well for harmonically rich calls, such as the kookaburra, and for calls with background noise. However, broadband 'noisy' calls, such as those produced by the raven and sulphur-crested cockatoo (figure 1), are not amenable to SPCC analyses; relatively few ($n=17$) males produced the black cockatoo call. Thus, we used only the relatively tonal and common kookaburra and honeyeater calls in assays of mimetic accuracy. We visually inspected mimetic sequences, and for each male, selected a single element based on its visual similarity to a pre-selected element from both model species. To control for differences in courtship duration, we recorded mimetic sequences in only the first bout of mimicry (also eliminating any confounds related to variation in female mate search behaviour), and in all cases, females remained in the bower throughout the mimetic bout. Also, mimetic calls are produced early and sequentially in courtship, in one distinct bout; thus, variation in overall courtship length should not affect the production of mimetic sequences.

3. RESULTS

Supporting the mimetic accuracy hypothesis, we found positive relationships between male mating success and the accuracy of males' laughing kookaburra and Lewin's honeyeater calls ($b_{novaeguineae}=0.67$, $p<0.001$; $b_{lewinii}=0.51$, $p=0.002$; $r^2=0.55$, $F_{2,23}=14.27$, $p<0.0001$). When we calculated the mean accuracy of each male's laughing kookaburra and Lewin's honeyeater calls, we found a highly significant relationship between mean mimetic accuracy and male mating success ($r^2=0.73$, $F_{1,23}=26.89$, $p=0.004$; figure 2*a*); this measure of mean mimetic accuracy is used in all subsequent tests involving mimetic accuracy.

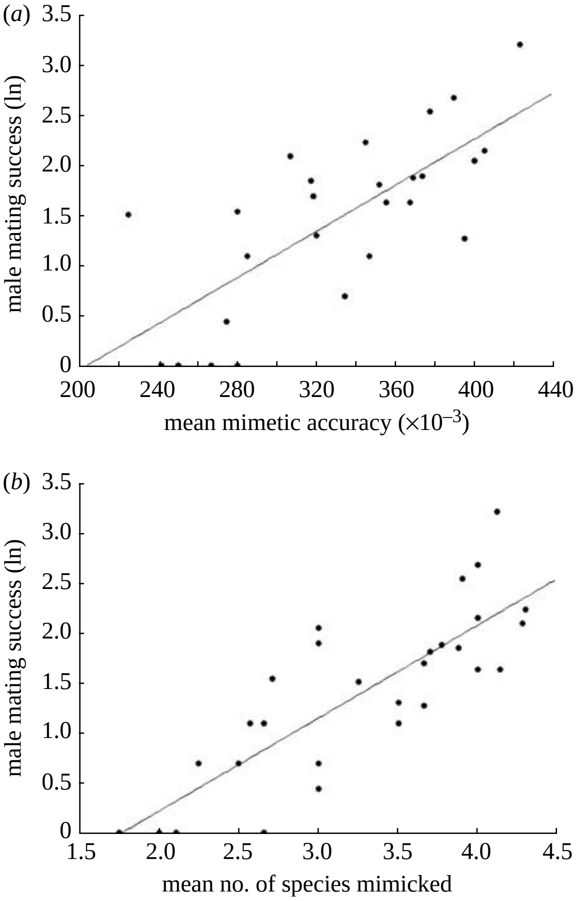

Figure 2. Scatterplots showing the linear regressions of male mating success on (*a*) mean mimetic accuracy and (*b*) mean number of species mimicked.

Supporting the repertoire size hypothesis, we found a significant relationship between the number of species mimicked and male mating success ($r^2 = 0.83$, $F_{1,26} = 56.30$, $p < 0.001$; figure 2*b*); this relationship was not confounded by the duration of mimicry, which was not correlated with the number of species mimicked ($r_P = -0.22$, $p = 0.25$) and was a poor predictor of male mating success ($r^2 = 0.12$, $F_{1,26} = 3.77$, $p = 0.08$). In addition, we found that mimetic accuracy and repertoire size were positively associated: males that produced high-accuracy mimicry mimicked more model species than those with low-accuracy mimicry ($r_P = 0.56$, $p = 0.002$). Multiple regression analysis showed that the number of species mimicked explained more of the variation in male mating success than mimetic accuracy, but both traits contributed independently to the variation in male mating success ($b_{\text{accuracy}} = 0.38$, $p = 0.008$; $b_{\text{spp. mimicked}} = 0.58$, $p = 0.0002$; $r^2 = 0.75$, $F_{2,23} = 34.47$, $p < 0.0001$).

As in many species where males have multifaceted sexual displays, correlations among multiple male display traits may be important for male mating success (Andersson 1994). Male satin bowerbirds build specialized stick structures, called bowers, where courtship and copulation take place, and they decorate the areas in front of their bowers with objects collected from the environment (Borgia 1985). Previous studies have shown that the number of decorations and bower quality are important for male mating success (Borgia 1985). Thus, we tested for correlation between mimetic accuracy, number of species mimicked, bower quality and number of bower decorations. We found that mimetic accuracy was positively associated with the number of decorations, and that the number of species mimicked was positively associated with the number of bower decorations and with bower quality (electronic supplementary material, table 1). Multiple regression analysis showed that mimetic accuracy and the number of species mimicked explained significant amounts of the variation in male mating success, while the number of decorations and bower quality did not ($b_{\text{accuracy}} = 0.42$, $p = 0.007$; $b_{\text{spp. mimicked}} = 0.68$, $p = 0.0004$; $b_{\text{decorations}} = -0.14$, $p = 0.39$; $b_{\text{bowerquality}} = -0.07$, $p = 0.67$; $r^2 = 0.77$, $F_{4,21} = 17.22$, $p < 0.001$). We did not find any relationship between male mimetic accuracy and either ectoparasite load or body condition (see electronic supplementary material).

4. DISCUSSION

Vocal mimicry is widespread in male sexual displays (Baylis 1982), yet the functional and evolutionary significance of interspecific vocal mimicry in mate choice remains unclear. We show that female preferences may drive both the accuracy and complexity of males' mimetic displays. Supporting the mimetic accuracy hypothesis and the repertoire size hypothesis, we found that both mimetic accuracy and number of species mimicked contributed independently to male mating success. Moreover, we found correlations between these two traits and other male display elements previously shown to be important for male mating success. These correlations suggest that males that are the best mimics also build the best bowers and maintain the most attractive decoration displays. Multivariate analyses revealed that relative to bowers and bower decorations, mimetic accuracy and complexity may be particularly important for male mating success.

Previous studies of vocal mimicry, which have typically focused on evaluating how repertoire size affects male mating success, have provided largely equivocal results (Howard 1974; Dowsett-Lemaire 1979; Hamao & Eda-Fujiwara 2004). We found evidence that female satin bowerbirds prefer males with large mimetic repertoires. While female preferences for large mimetic repertoires may reflect general preferences for complex male displays, the evolution of female preferences for accurate mimicry is less clear. Because vocal mimicry is a learned element of male displays, and the production of accurate mimicry requires males to modify their vocal motor patterns to match those of the model species (Zollinger & Suthers 2004), the accuracy with which a male produces mimicry may indicate how well a male learned and refined display as a juvenile. While here we did not find relationships between mimicry and measures of male quality—measured as ectoparasite load and body condition—accurate age and juvenile body condition data were unavailable for this study. The hypothesis that the quality of adult males' displays indicates learning efficacy of juveniles has been supported in several songbirds (Nowicki *et al.* 2002), and is plausible in satin bowerbirds as other aspects of adult males' displays reflect juvenile health (Borgia *et al.* 2004); future studies are needed to explicitly test this hypothesis. In this study, SPCC provides evidence that female preferences drive the evolution of highly accurate vocal mimicry. We suggest that preference-driven mimetic accuracy may be a widespread occurrence, supporting an alternative hypothesis to help explain a common element of male sexual displays.

This research complies with the regulations of the ABBBS and the NSW National Parks and Wildlife Service.

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