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Imitating the neighbours: vocal dialect matching in a mimic–model system

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Vocal mimicry provides a unique system for investigating song learning and cultural evolution in birds. Male lyrebirds produce complex vocal displays that include extensive and accurate mimicry of many other bird species. We recorded and analysed the songs of the Albert's lyrebird (*Menura alberti*) and its most commonly imitated model species, the satin bowerbird (*Ptilonorhynchus violaceus*), at six sites in southeast Queensland, Australia. We show that each population of lyrebirds faithfully reproduces the song of the local population of bowerbirds. Within a population, lyrebirds show less variation in song structure than the available variation in the songs of the models. These results provide the first quantitative evidence for dialect matching in the songs of two species that have no direct ecological relationship.

Keywords: vocal mimicry; dialect matching; cultural transmission; song learning; lyrebirds

1. INTRODUCTION

In the vast majority of songbird species studied to date, young individuals learn song only from other members of their own species. However, there are many examples where birds learn some components of their vocal repertoires from other species (reviewed in Bayliss 1982). Dialect matching in model and mimic songs, where intraspecific variation in mimicked song reflects the intraspecific variation in the model songs, has been reported in brood parasites that match the song types of their foster parents. For example, male straw-tailed whydahs (*Vidua fischeri*) mimic the songs of the local population of their host species, the purple grenadier (*Granatina ianthinogaster*; Payne *et al.* 2000), but the observed pattern of song variation suggests that most male whydahs actually learn the song from each other. Similarly, brood-parasitic village indigobirds (*Vidua chalybeata*) mimic the songs of their host species, the red-billed firefinch (*Lagonosticta senegala*). All males within a neighbourhood imitate the same set of firefinch song themes, but most male indigobirds learn their songs from other indigobirds (Payne 1990). Dialect matching is understandable where the mimic and model species share such a close association (host and parasite) and where accurate mimicry of the local host species may influence mate preferences in these host-specific brood parasites (Payne 1990). However, dialect matching has not yet been demonstrated in species that do not share such an intimate association.

Australia's lyrebirds are renowned for their complex songs that feature mimicry of numerous other bird species (Robinson & Curtis 1996). The display song of the male Albert's lyrebird (*Menura alberti*) is thought to function in female attraction and may contain mimicry of over 10 other bird species. Within each population, all male Albert's lyrebirds produce the same selection of mimicked songs in roughly the same sequence. Despite some 'imperfect repetition' in the sequence of sounds, these observations have been interpreted as clear evidence of cultural transmission (i.e. Albert's lyrebirds learn their songs from each other and not from their environment; Robinson & Curtis 1996).

Many of the model species whose songs are incorporated into the lyrebird display show geographical variation in song structure. For example, the advertisement song of the satin bowerbird (*Ptilonorhynchus violaceus*) is known to vary in structure among populations throughout its range along the east coast of Australia (Tack *et al.* 2005; Nicholls & Goldizen 2006), and is a common feature in lyrebird mimicry.

The satin bowerbird advertisement song and lyrebird imitations are ideal candidates for investigating song dialect matching. Here, we present the first detailed investigation into possible structural variation of individual mimicked song components within the stereotyped song sequence of the lyrebird, and investigate patterns of covariation in model and mimicked songs in these two species.

2. MATERIAL AND METHODS

(a) *Song recording*

We recorded the advertisement songs of male satin bowerbirds and mimicry of this song by male Albert's lyrebirds at each of six sites in southeast Queensland (153°E, 28°S), Australia, during 2004 and 2005. Sites were located at Binna Burra (A), Green Mountains (B), Springbrook (C), Tamborine Mountain (D), Gambubal (E) and Goomburra (F) (figure 1). Individuals of both species can be reliably located at known territories or regular display sites. Recordings of lyrebirds were obtained by stalking displaying individuals, while songs of bowerbirds were obtained using continuous recordings at their bowers. Songs were recorded using a Sennheiser ME67 microphone with K6 power supply, digitized at a sampling rate of 44.1 kHz and recorded uncompressed directly to hard disk using an iRiver iHP-140 hard disk recorder. For one site (B), additional recordings of bowerbirds from a previous study (Tack *et al.* 2005) were also used.

(b) *Acoustic analysis*

Sound spectrograms of all recorded songs were produced with Raven bioacoustics software (v. 1.2, Cornell Bioacoustics Laboratory), using a 512 pt fast Fourier transform and Hanning window. Imitations of bowerbird song always occur as isolated, discrete elements within the lyrebird sequence and can be easily edited for analysis. Frequency, time and amplitude parameters of each song were measured from the spectrograms. Measurements were taken on the fundamental harmonic of the main syllable, and included the start frequency, end frequency, minimum frequency, maximum frequency, peak frequency (frequency at the greatest amplitude), duration, the time to the minimum, maximum and peak frequencies (proportion of the duration) and the ratios of the maximum frequency to both the start and peak frequencies. It was also noted whether the song had a separate introductory syllable. Mean values were used where multiple recordings were obtained from one individual.

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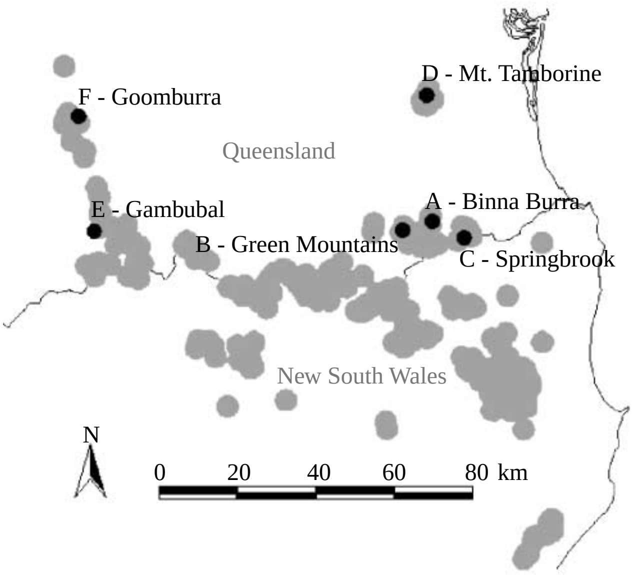

Figure 1. Locations of the six recording sites in southeast Queensland, Australia. Shaded areas represent the approximate current range of the Albert's lyrebird.

(c) *Statistical analysis*

Discriminant function analysis (STATISTICA v. 7.0, Statsoft, Inc.) was used to calculate functions that classified bowerbird advertisement songs based on site. The resulting classification functions were then applied to the equivalent parameters extracted from the lyrebirds' versions of the song. The similarity of patterns of variation between species was assessed by assigning individual lyrebirds to sites based on Mahalanobis distances and testing the classification success of predicted versus observed site groups. Within-site variation in song structure was assessed using a mixed-model ANOVA of Mahalanobis distances from group centroids versus species and site.

3. RESULTS

High-quality recordings were obtained for between four and nine individuals of each species at each site, with between 1 and 11 songs for each individual. In total, the songs of 38 bowerbirds and 34 lyrebirds were included in the analyses.

Discriminant function analysis revealed clear divergence in the structure of the bowerbird songs among sites (Wilk's $\lambda=0.000023$, $F_{60,102}=14.754$, $p<0.0001$; figure 2). The first three canonical roots had eigenvalues greater than 1 and contributed 99% of the discriminatory power. The structural song parameters that made the greatest contributions to the discriminant functions were the maximum frequency, the ratio of the maximum frequency to the starting frequency and the ratio of the peak frequency to the starting frequency. Sites A, B and C show considerable overlap in bowerbird song structure, but this is not surprising given their close geographical locations (all within a 7 km radius) and it is likely that bowerbirds regularly move among these sites. However, the other three sites are clearly separated by song structure reflecting their higher degree of geographical isolation (above 25 km). The mimicked lyrebird versions of the song cluster tightly with the bowerbird songs at each of the sites (figure 2). Across all six sites, 76% of lyrebird songs were correctly assigned to sites using the classification functions based on bowerbird songs. With sites A, B and C combined into a single group based on the similarity among bowerbird songs, classification success of lyrebird songs increased to 100%. Spectrograms illustrating the similar patterns of variation in song structure between species are provided in the electronic supplementary material.

Lyrebird songs showed significantly less individual variation than bowerbird songs across these sites (mixed model ANOVA of Mahalanobis distances from group centroids, species main effect, $F_1=8.497$, $p=0.032$), but this pattern was not consistent within all sites (species–site interaction, $F_5=2.775$, $p=0.025$). The pattern is particularly apparent for sites A, B and C, where the lyrebird songs cluster tightly together within a more diverse grouping of bowerbird songs (figure 2).

4. DISCUSSION

Each population of Albert's lyrebirds reproduces the song of the local population of satin bowerbirds, suggesting that lyrebirds copy their songs directly from the models at each site. To our knowledge, this is the first demonstration of dialect matching in mimicked and model songs in non-brood parasites. Similar patterns of variation have been reported in brood parasites that match the song types of their foster parents (Payne *et al.* 2000). Brood-parasitic species share long and intimate associations that facilitate the development of this pattern. In contrast, the only association between lyrebirds and bowerbirds is that they inhabit the same forest areas.

Previous work on the advertisement song of the satin bowerbird (Nicholls & Goldizen 2006) has shown that the geographical variation in bowerbird song reflects the acoustic properties of their local habitats. However, the variation apparent among populations in this study is independent of the effect of habitat acoustics, since all recordings of both species were obtained in similar rainforest habitats with similar acoustic properties. The observed dialect matching is a result of local cultural adaptation rather than local acoustic co-adaptation.

In addition to the clear separation among groups of both species based on site, there appears to be some small divergence in song structure between the two species within sites (figure 2). One possible explanation for this is signal degradation; lyrebirds' reproductions of song must be based on what they hear after the original signal has been attenuated and degraded during transmission over variable distances in dense rainforest habitats (Hansen 1979). Alternatively, this small divergence may be a result of cultural drift (Lynch 1996; Bentley *et al.* 2004) of the lyrebird songs away from the model songs at each site.

The highly stereotyped sequence of mimicked song elements within the lyrebird's display has been used as evidence that the song is culturally transmitted among lyrebirds rather than learnt directly from the models (Robinson & Curtis 1996). Cultural transmission of song among lyrebirds is also consistent with observations that a population of superb lyrebirds (*Menura novaehollandiae*) introduced to

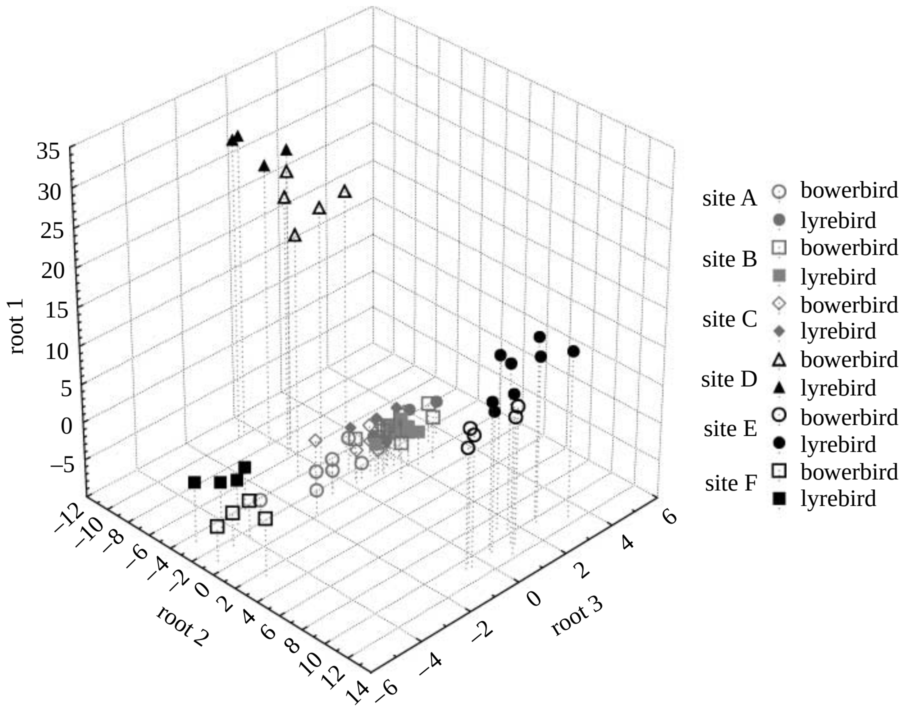

Figure 2. Variation in song structure among sites and between species illustrated by the first three canonical roots resulting from the discriminant function analysis. Open shapes represent bowerbird advertisement songs, while matching closed shapes represent the lyrebird imitations from the same sites.

Tasmania continued for several decades to imitate model species that were no longer present in their environment following the translocation (Robinson & Curtis 1996). We propose that male lyrebirds may indeed learn the sequence of elements within their song from other male lyrebirds, but learn the individual elements within that sequence either from other lyrebirds or directly from the models.

The reduced structural variation within sites in the songs of the lyrebirds compared with those of the bowerbirds suggests that the lyrebirds may copy their mimicry from other lyrebirds as well as directly from the models. Albert's lyrebirds are terrestrial rainforest specialists with modest flying capabilities and limited dispersal ability (Higgins *et al.* 2001). It is unlikely that individuals move between recording sites, and extremely unlikely that all of the individuals recorded at site A originated from sites B or C. Further research is required to investigate whether these patterns of variation could be influenced by different singing rates or singing seasons of the two species. Satin bowerbirds are also accomplished mimics (Loffredo & Borgia 1986) and there is the intriguing possibility that the similarity in song between these two species may involve cultural coevolution.

These results thus suggest that this single element in lyrebird song may be learnt from two separate sources. The matching of song dialects among sites suggests that lyrebirds learn songs from the models, while the reduced structural variation in the lyrebird imitations within sites suggests that these song types are also culturally transmitted among lyrebirds. It is not yet clear how these two learning paths may interact or whether they occur at different stages in the song development process.

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