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EVIDENCE OF INTRASPECIFIC VOCAL IMITATION IN SINGING HONEYEATERS (MELIPHAGIDAE) AND GOLDEN WHISTLERS (PACHYCEPHALIDAE)¹

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Vocal imitation, by which two or more individuals of the same species population come to share the same

¹ Received 29 March 1993. Accepted 22 June 1993. ² Present address: Biology Department, Colorado State University, Fort Collins, CO 80523. song patterns, is well known in birds (Kroodsma and Baylis 1982, Mundinger 1982). Such song sharing may be confined to small neighborhoods of a few individuals (Payne 1983) or encompass larger regions consisting of hundreds or thousands of individuals (Baker and Cunningham 1985). For functional interpretations of imitation it is important to determine whether members of a species regularly exhibit vocal convergence among neighbors or larger groups and how accurate is the vocal copying that occurs. Imitation has a number of interpretations and has led to several hypotheses that aid our understanding of social behavior and cul-

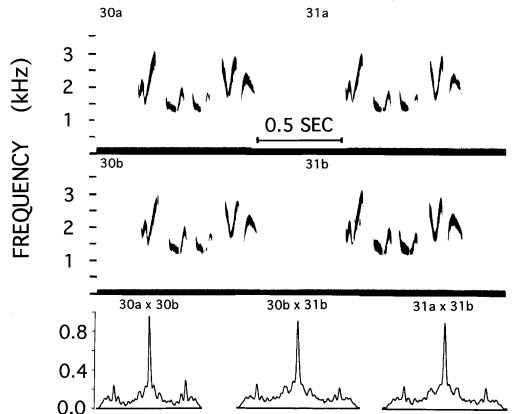


FIGURE 1. Neighboring male Singing Honeyeaters that matched songs. Songs 30a and 30b are separate utterances of one male; 31a and 31b are separate utterances of the neighboring male. Correlations within birds (0.951, 0.888, respectively) and between birds (0.899) are similar in magnitude.

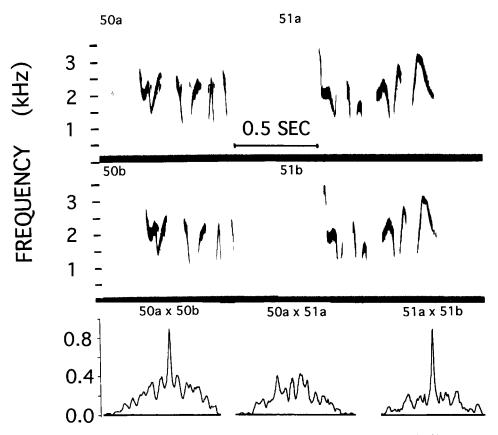


FIGURE 2. Neighboring Singing Honeyeaters that did not match songs. Songs 50a and 50b are separate utterances of one bird; 51a and 51b are separate utterances of the neighbor. Correlations within birds (0.887, 0.891, respectively) are higher than between birds (0.424).

tural evolution (Payne 1981, Mundinger 1982, Baker and Cunningham 1985).

The purpose of the present study was to document intraspecific vocal imitation (Type III vocal imitation: Kroodsma 1982) in natural populations of two Australasian species of birds, the Singing Honeyeater (*Meliphaga virescens*) and the Golden Whistler (*Pachycephala pectoralis*).

METHODS

Singing Honeyeaters and Golden Whistlers were tape recorded at locations in Western Australia from 5 October–8 November 1991 during the breeding season. Seventy Singing Honeyeaters were recorded in Nedlands, near Perth. Twelve Singing Honeyeaters and 10 Golden Whistlers were recorded in and adjacent to John Forrest National Park 25 km east of Nedlands. Twenty-five Singing Honeyeaters and 20 Golden Whistlers were recorded on Rottnest Island 25 km west of Nedlands in the Indian Ocean.

Recording was accomplished with a Marantz cassette recorder (PMD 201), Sennheiser microphone (MD 402-K) mounted in a 40 cm parabola, and TDK Type I tape. Analysis of the recordings was done with a digital signal processor (Kay Elemetrics DSP 5500) and a Macintosh II computer implementing Canary software (version 1.0, Cornell Laboratory of Ornithology, Bioacoustics Research Program). For spectrographic display of vocalizations of Singing Honeyeaters, I used DSP settings of DC-4kHz frequency range and 200 Hz transform size. For Golden Whistlers, I used DSP settings of DC-8 kHz frequency range and 234 Hz transform size.

Correlations between spectrograms were done with Canary software. The process of correlating two sound spectrograms can be visualized as follows (Clark et al. 1987): (1) imagine two separated spectrograms sharing the same frequency by time axes, one to the left and one to the right as you observe them, (2) in stepwise increments of time, gradually move one of the spectrograms across the other, (3) at each increment, calculate a correlation coefficient between the two spectrograms. A peak correlation value results when the two spectrograms are overlaid in a way that they are most similar. This peak value can be used as an index of similarity.

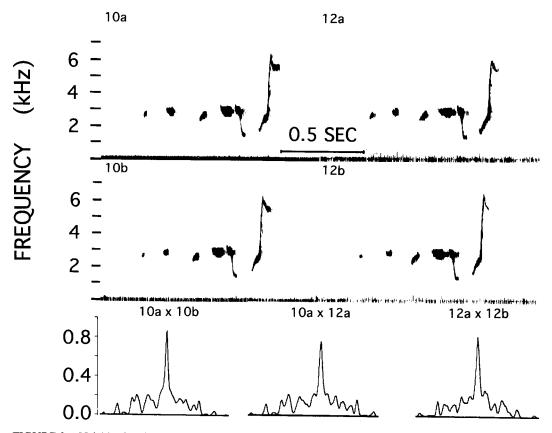


FIGURE 3. Neighboring Golden Whistlers that matched songs. Songs 10a and 10b are separate utterances of one bird; songs 12a and 12b are separate utterances of the neighbor. Correlations within birds (0.873, 0.820, respectively) are slightly greater than between birds (0.759).

Because birds were not color-banded, I selected neighboring birds that were interacting aggressively and counter-singing in close enough proximity to allow recording of both. Singing Honeyeaters were very abundant, and I could often hear other neighbors matching in addition to the two being recorded. My impression was that neighborhoods of 2-5 birds with matching songs were common in this species. Golden Whistlers occupied larger territories than did Singing Honeyeaters, and I rarely could hear clearly more than two birds at a time.

RESULTS

Song sharing between neighboring Singing Honeyeaters and between neighboring Golden Whistlers was apparent to the unaided ear. Spectrographic analyses revealed the detail and accuracy of vocal similarity. Twenty-five cases of two counter-singing neighboring Singing Honeyeaters were recorded. In 11 cases no matching occurred, and in 14 cases matching was observed during countersinging episodes. Seven cases of two counter-singing neighboring Golden Whistlers were recorded. In three cases no matching occurred, and in four cases matching was observed during counter-sing-ing episodes.

Correlational analyses of spectrograms (Clark et al. 1987) revealed the accuracy with which some neighbors matched their songs and how different were the songs of neighbors that did not match. Matching and non-matching of neighbors were judged in relationship to the similarity of repetitions of songs within individuals.

Songs of neighboring Singing Honeyeaters that matched appeared highly similar spectrographically and correlational analyses supported this subjective impression (Fig. 1). Non-matching neighbors sang structurally differing songs and correlation values for neighbor's songs were about half the magnitude of the correlations within birds (Fig. 2).

Songs of neighboring Golden Whistlers that matched appeared similar by visual inspection of sonagrams, and the correlation values supported this interpretation (Fig. 3). There was, however, a consistent trend of slightly less accuracy of neighbor matching than was the case for Singing Honeyeaters. When neighboring

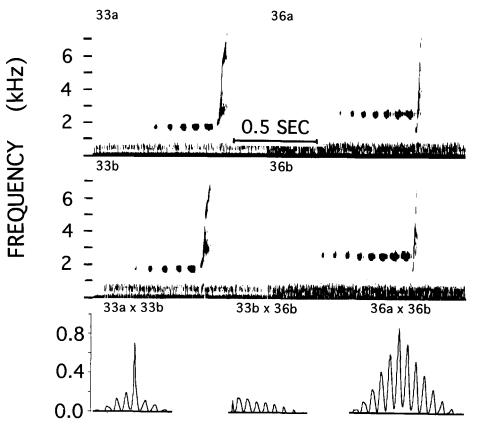


FIGURE 4. Neighboring Golden Whistlers that did not match songs. Songs 33a and 33b are separate utterances of one bird; songs 36a and 36b are separate utterances of the neighbor. Correlations within birds (0.709, 0.879, respectively) are higher than between birds (0.156).

pairs of Golden Whistlers did not match songs (Fig. 4), the degree of mismatch was large by correlational analysis. The example shown in Figure 4 is instructive because a cursory visual examination of the neighbor's songs suggests they are more similar than the correlation value indicates. This impression results from the more obvious temporal pattern similarities and the less apparent major differences in frequency of the two songs.

DISCUSSION

The main conclusion drawn from this study is that Singing Honeyeaters and Golden Whistlers are capable of modifying their songs to achieve matching with neighbor's songs. The general pattern of convergence in song structure among neighboring birds is generally accepted as indirect evidence of song learning (Kroodsma 1982). Experiments on learning have not been carried out in these species, however, nor has the process of vocal modification from the pre-convergence song structure to the matching structure been documented. Therefore, the conclusion is tentative. The history of the individuals recorded in the present study was unknown. Thus, such potentially important factors as the ages of the birds involved in sharing songs, the time course of vocal convergence, or the sites of origin of the individuals could not be used to suggest hypotheses on how or why vocal convergence occurred.

There are anecdotal reports of other species in these two Families mimicking vocalizations of other species. Chisholm (1946) identified interspecific vocal imitation by two species of the Pachycephalidae, the Shriketit (*Falcunculus fronatus*) and the Gray Shrike-thrush (*Collurichincla harmonica*). Gilliard (1958) noted the common occurrence of imitation of human voice by a member of the Meliphagidae, the Parson Bird (or Tui, *Prosthemadera novaeseelandiae*). These subjective reports were not documented with spectrographic evidence, but it seems unlikely that the observations were vastly misunderstood. In spite of these early observations, however, there have been no follow-up studies.

A more recent report (Bruce 1988) indicates the existence of dialects in the songs of Yellow-throated Honeyeaters (*Lichenostomus flavicollis*) in Tasmania. However, the documentation of vocal variation and spatial scale of song similarity was inadequate for comparisons to the Singing Honeyeater patterns reported here.

In applying the Canary software to this analysis, an important point is raised. When differences in two songs are primarily a result of an offset in the frequency axis but the shapes of the elements are similar, the resulting low correlation seems somewhat misleading. This is a consequence of applying a visual analysis to the two spectrograms rather than hearing the two songs. The latter perception makes the difference more apparent. In any case, the question of how the birds perceive similarity and difference is an experimental issue that can be addressed by manipulation of features of songs and presentation of the altered stimuli via the playback paradigm (e.g., Baker 1991).

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NOVEL METHOD FOR ESTIMATING HOURS OF OVIPOSITION, ILLUSTRATED BY DATA ON GRAY CATBIRDS'

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Key words: Hour of egg-laying; oviposition; Gray Catbird; Dumetella carolinensis.

The hour of egg-laying has been studied less than many other features of nesting, e.g., clutch size or incubation period. Lack of information on the hour of laying may be due to the difficulty of obtaining precise records. Without mechanical devices, such as used by Haftorn (1966) to determine laying times of *Parus* spp., most investigators have relied either on two daily visits to a nest that bracketed egg-laying (Skutch 1952, Brackbill 1958), or on observations on the arrival of a female at her nest to lay (Nolan 1978, Muma 1986) and her departure after laying (Muma 1986). These procedures are time-consuming. Also, because some species lay inconveniently close to sunrise, few investigators of life histories routinely record the hour of laying. This is unfortunate because there is much interspecific vari-

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