

LOSS OF FUNCTION IN TERRITORIAL SONG: COMPARISON OF ISLAND AND MAINLAND POPULATIONS OF THE SINGING HONEYEATER (*MELIPHAGA VIRESCENS*)

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ABSTRACT.—I studied vocal recognition in populations of Singing Honeyeaters (*Meliphaga virescens*) on Rottneest Island and the adjacent mainland of Western Australia through song-playback experiments. Morphological evidence suggested the island population had differentiated. I addressed the question of whether there was divergence in the vocal signaling system. I found significant loss of function of the territorial advertising song by comparing responses of the Rottneest subjects and those of subjects from the mainland Nedlands population. The low level of response by Rottneest birds to songs from the mainland was similar to the response by Rottneest birds to songs of the co-occurring Golden Whistler (*Pachycephala pectoralis*). On the mainland, Nedlands birds responded to the songs of another mainland population, located the same distance away as Rottneest Island, at an elevated level similar to their response to songs of their own Nedlands population. I conclude that there are population-specific vocal features in the songs of Rottneest Singing Honeyeaters that result from isolation. The isolation caused by the water barrier between Rottneest Island and the mainland is greater than isolation by distance through continuous populations on the mainland. I speculate that vocal recognition was probably lost as a result of an early colonization of Rottneest and the subsequent establishment of a new vocal tradition in the island birds. Received 31 July 1992, accepted 24 April 1993.

THE STUDY OF the differentiation of island forms from mainland source populations has contributed much to our understanding of evolution in birds (Lack 1947, Bond 1948, Amadon 1950, Raikow 1977). Numerous traits have been shown to diverge as a result of isolation on islands. Traits most commonly documented as diverging are morphological, and include beak length, body size, wing length, and plumage coloration (Murphy and Chapin 1929, Amadon 1953, Van Valen 1965, Grant 1965, 1968).

Rarely have isolated island populations of birds been examined for divergence in communicative signals. Although the classical cases of adaptive radiation in birds are satisfactorily explained by reference to ecological divergence (Amadon 1950, Grant 1986), the initial phase of differentiation and, particularly, the effects of subsequent new colonizations or recolonizations by the same or other forms may be influenced by reproductive signals involving territory defense and mate choice. Because many species of songbirds learn their songs, it might be expected that in such species the colonization of an island would lead to establishment

of a new vocal tradition through founder effect (Thielcke 1973, Baker and Cunningham 1985). This could have consequences for the isolation of gene pools (Carson 1971, Baker and Marler 1980, Kaneshiro 1980).

Previous work indicated that Singing Honeyeaters (*Meliphaga virescens*) of the Rottneest Island (Western Australia) population on average have a mass that is about 20% more than the adjacent mainland form (Wooller et al. 1985). Experienced birders also have noted that Rottneest Singing Honeyeaters are somewhat darker, with more streaked plumage on the underside of the body, than mainland individuals (Saunders and deRebeira 1985). I used tape recording and playback experiments to determine whether there was any loss of communicative function in the vocal signals of Singing Honeyeaters from the Rottneest Island and mainland populations.

MATERIALS AND METHODS

The Singing Honeyeater is one of 67 species belonging to the Meliphagidae, one of the most speciose families of Australian passerines (Thompson 1964). Many honeyeater species are abundant. Most feed principally on nectar. The Singing Honeyeater (20-30 g) is the most widely distributed honeyeater in

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Australia (Blakers et al. 1984) and seems to be especially successful in the abundantly flowered gardens of suburban areas. There are no published records of this species' vocalizations.

The Singing Honeyeater has a discrete dawn chorus that commences about 20 to 30 min before light, and lasts about 40 to 60 min. Typically, the male roosts overnight in a tree and sings from that location in the pre-dawn period. This song is heard infrequently at other times of the day. Along a residential street it is common to find a singing male nearly every 50 m in the trees along the verge and in the front gardens of the homes. A territory is defended physically and vocally, defense often being centered around nectar sources. Access to these nectar sources is contested frequently by the Red Wattlebird (*Anthochaera carunculata*) and the Brown Honeyeater (*Lichmera indistincta*). Vocal defense during daytime is usually not by song but by a number of different calls. These appear to indicate a range of motivational conditions from an initial "distant alarm," given when an intruder first enters the space of another male, to intense chattering and continuous multiple chirping when two birds are close together. Observations I made on two vocally distinct males over a period of several weeks suggest that the birds are monogamous. Most breeding commences in the Australasian spring (August-September) and ends in December-January. Males were singing persistently when this study was initiated on 1 October, but by mid- to late January singing had decreased considerably. Songs were heard occasionally on into March.

Males in three populations were tape recorded. One population was located in suburban Nedlands (Ned), near Perth, Western Australia. A second population was located 25 km west of Nedlands on the island of Rottneest (Rot) in the Indian Ocean. Rottneest was isolated about 6,500 years ago as the sea level rose near the end of the Holocene (Playford 1983). A third population was located 25 km east of Nedlands in the suburban areas on the western edge of John Forrest National Park (Jfp). Songs were recorded during the dawn chorus using a Marantz cassette recorder (PMD 201), Sennheiser microphone (MD 402-K) mounted in a 40-cm parabolic reflector, and TDK Type I tape.

Songs of five different males were randomly selected from each population and transferred to 20-s continuous-loop cassettes. These served as playback stimuli (Fig. 1), which were delivered at the rate of one song per 10 s for 5 min during each playback trial. A trial was initiated by locating a vocalizing Singing Honeyeater and placing the playback speaker (Perma Power S-610) within 5 m of the individual and under or beside a tree or bush. I activated the stimulus and retreated 5 to 10 m to make a record of events for 5 min on another cassette recorder.

I recorded the occurrence of vocalizations (vocals), flights, and hops as discrete countable events; also, I estimated the distance from the speaker to the subject

whenever there was a change of distance that resulted from movement initiated by the bird. In addition, a synthetic variable, *sumbeh*, was created by summing vocalizations, hops and flights to provide an index of the total activity. The distance estimates were aided by pacing between key features of the habitat in the vicinity of the speaker after the test was completed. For analysis, the distance estimates were averaged for the trial to give a single value of distance for that subject's response to the stimulus. Hops occurred usually where a subject remained within a single bush or tree for a period of time and changed locations without flying. Flights were usually between trees or bushes, and were frequently to and from the bush near the playback speaker. All types of vocalizations were summed in a single category. There was considerable variety in the vocal performance of subjects during tests, but the complexity was too great to make reliable categories of vocalizations. This would require a separate study. The kinds of vocalizations I heard during playback tests were the same as I heard during my observations of the aforementioned two territorial males during their normal day's interactions with intruder neighbors and other species.

In the playback tests on Rottneest, subjects heard songs of Singing Honeyeaters from Rottneest or from Nedlands or heard Golden Whistler (*Pachycephala pectoralis*; Gws) songs from Rottneest. The Golden Whistler stimuli were used to determine if the response to Nedlands stimuli was equivalent to the level of response given to heterospecific songs. The Golden Whistler occurs together with Singing Honeyeaters in many locations on Rottneest Island. Two different Golden Whistler songs were used as stimuli. Therefore, the statistical design consisted of three treatments (Rot, Ned, Gws) with five different stimulus songs within each of Rot and Ned treatments and two different stimulus songs within the Gws treatment. Forty subjects were tested (15 with Rot, 15 with Ned, 10 with Gws).

When evaluating the mainland population of Nedlands, subjects heard the same five Nedlands stimuli and five Rottneest stimuli as did the Rottneest subjects. In addition, I used five Jfp songs as stimuli. Forty-eight subjects were tested (16 each with Ned, Rot, and Jfp).

Data were analyzed by nested ANOVA (stimuli nested within treatments). Fisher's LSD (Carmer and Swanson 1973) was used to make multiple comparisons between pairs of treatments.

RESULTS

Rottneest subjects.—The experimental birds on Rottneest Island responded to the playback tests with behavioral reactions that indicated they clearly discriminated between classes of stimuli presented to them. Songs representing their own

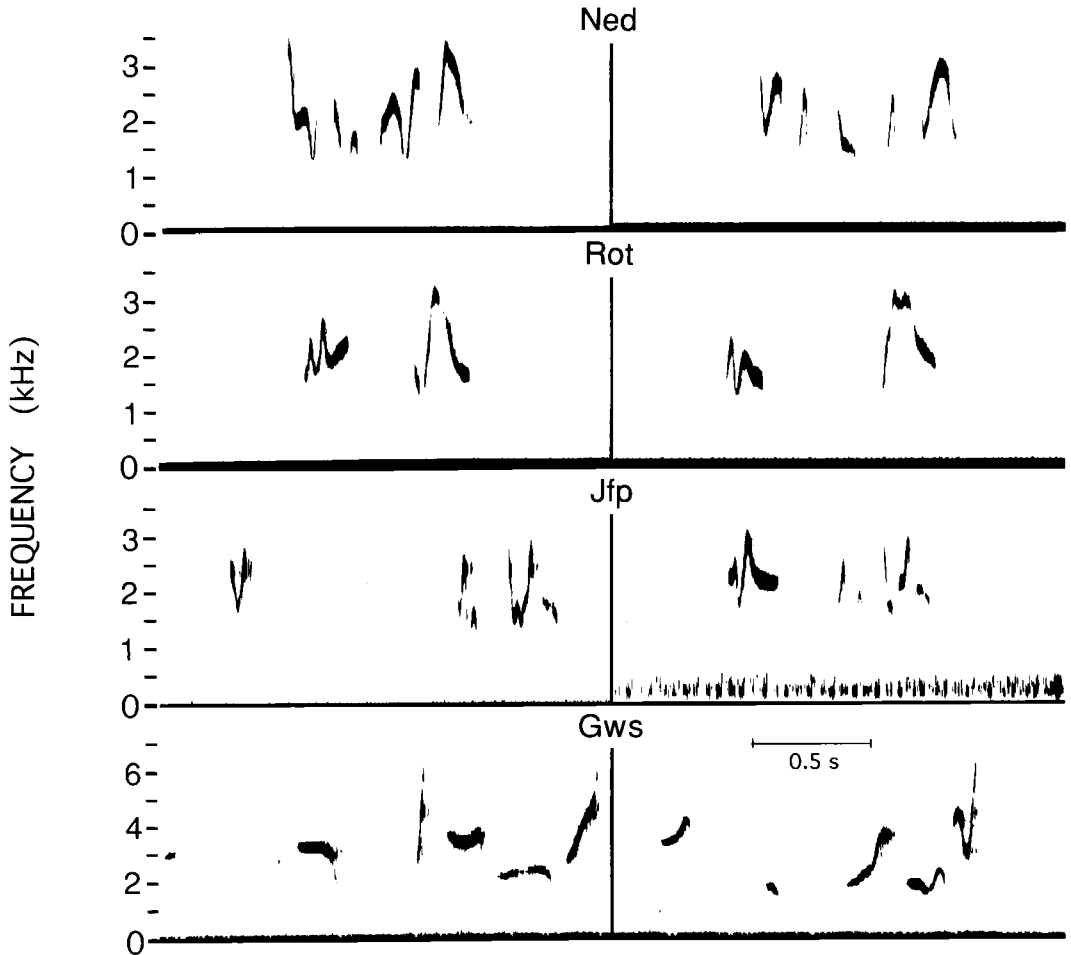


Fig. 1. Sound spectrograms of two examples of each class of songs used as playback stimuli. Population sources of songs are: Singing Honeyeaters from Nedlands (Ned), Rottnest Island (Rot), John Forrest National Park (Jfp); Golden Whistlers (Gws) from Rottnest Island.

Rottnest population elicited heightened levels of behavioral activity commonly seen in naturally occurring territorial interactions. All the dependent variables exhibited significant treatment effects and no significant effect of stimulus within treatment (Table 1). Multiple-comparison tests indicated that for the vocals, flights, hops and sumbeh variables Rottnest males responded more to Rot songs than to Ned or Gws songs (Fig. 2; $P < 0.05$). There was no difference between the responses to Ned and Gws. For the distance measure, response to Rot ($\bar{x} = 3.3 \pm \text{SE of } 0.4 \text{ m}$) was greater (approached closer to speaker) than to Ned ($\bar{x} = 12.2 \pm 3.1$; $P < 0.05$), but the responses to Rot versus Gws, and to Ned versus Gws ($\bar{x} = 7.8 \pm 1.7 \text{ m}$) did not differ.

Nedlands subjects.—The experimental birds in

the Nedlands population on the mainland also reacted to the playbacks in ways that indicated discrimination between the different kinds of songs used as stimuli. In general, Nedlands subjects showed elevated response to songs representative of their own Nedlands population and songs of the Jfp population in comparison to a lower response to songs from Rottnest Island. Significant treatment effects were present for the variables vocals, sumbeh and distance but not for hops or flights. There were no significant effects of stimuli within treatments for any variable (Table 1). Multiple-comparison tests indicated that for vocals, hops and sumbeh the subjects responded more to Ned than to Rot stimuli (Fig. 2; $P < 0.05$). There were no differences between Rot and Jfp or between Ned and

TABLE 1. Nested analysis of variance results for playback tests conducted on Singing Honeyeaters on Rottneest Island and in Nedlands, Western Australia.^a

Variable	Treatment		Stimulus within treatment	
	F-value	P	F-value	P
Rottneest Island				
Vocals	7.35	0.003	2.01	0.076
Hops	6.39	0.005	1.64	0.151
Flights	13.16	0.0001	0.33	0.958
Sumbeh	10.86	0.0003	1.92	0.090
Distance	5.18	0.012	1.37	0.246
Nedlands				
Vocals	4.12	0.025	0.88	0.569
Hops	3.00	0.063	1.28	0.271
Flights	1.43	0.254	0.57	0.848
Sumbeh	5.32	0.009	0.81	0.639
Distance	5.48	0.008	0.75	0.693

^a df = 2 for all treatments. df = 9 and 12, respectively, for evaluations of stimuli within treatments for Rottneest Island and Nedlands.

Jfp. For flights, there were no significant differences in any of the three pairwise comparisons. For the distance measure, subjects responded more (approached closer) to the Ned ($\bar{x} = 1.4 \pm 0.3$ m) and Jfp ($\bar{x} = 1.6 \pm 0.4$ m) stimuli than to Rot ($\bar{x} = 4.8 \pm 1.2$ m) stimuli (P

< 0.05). The distance measure did not differ for Ned versus Jfp.

DISCUSSION

I conclude that there are population-specific song features (or species-specific features in the case of the response to Gws) that are used as cues by Singing Honeyeaters for judging the appropriateness of an aggressive territorial response. In 8 of 10 comparisons, there were significant alterations in the behavioral response of the playback subjects caused by the three stimulus treatments. In none of the 10 was there significant variability caused by the different stimulus songs within a treatment (Table 1).

Subjects in both the mainland Nedlands population and the Rottneest Island population responded consistently more to songs of their own population than to songs representative of the other's population. This was true for the measures of vocals, hops, sumbeh and dist. The only exception was for the variable "flights" in the Nedlands population. Therefore, I conclude that the songs from the Nedlands population have lost significant function as territorial releasers for birds of the Rottneest Island population, and Rottneest songs function poorly in the Nedlands

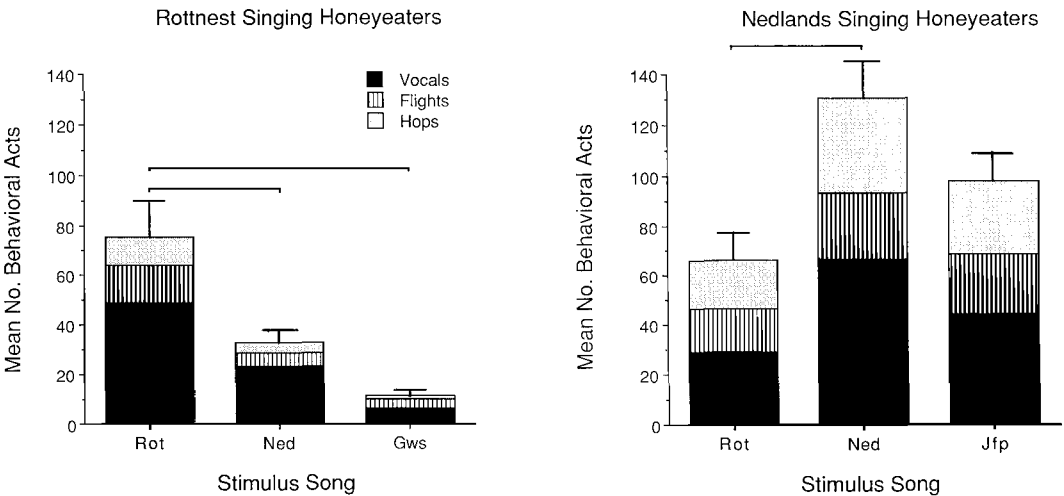


Fig. 2. Responses of Rottneest and Nedlands subjects to playback stimuli. Each histogram bar is stack of three separate response categories (vocals, flights, hops), and total bar height is their sum (sumbeh). Whisker indicates SE. Horizontal lines above graph connect pairs of stimuli that were significantly different. Responses of Rottneest birds to Rot stimuli were significantly greater than responses to Ned and Gws for all three response measures separately (vocals, flights, hops), as well as for composite sumbeh measure. Responses of Nedlands birds to Ned stimuli were significantly greater than responses to Rot for measures of vocals, hops and sumbeh, but not for flights.

population. For Rottnest birds, the degree of recognition of Nedlands songs was no different from the degree of recognition of Golden Whistler songs according to the nondistance measures of response. Thus, Rottnest birds treated songs of Nedlands birds as if they were those of another species. The close approach to speakers by Rottnest birds, however, suggests that the Golden Whistler song was recognized to a degree intermediate between Rottnest and Nedlands stimuli. Thus, Golden Whistler song may contain some features that tended to attract Rottnest Singing Honeyeaters, but once the subjects approached the stimulus they did not increase vocalizations, hops or flights.

The nondistance measures of response by Nedlands subjects suggest that the songs of Jfp elicited an intermediate degree of recognition compared to Nedlands and Rottnest songs. Although Jfp songs elicited as much response as Nedlands songs, Jfp songs also did not elicit a response significantly different from that given to Rottnest songs. The distance measure, however, suggests that Jfp songs were as stimulating to Nedlands subjects as Nedlands songs were, and that both these classes of songs were discriminated from Rottnest songs. Therefore, the data from the mainland populations indicate that the 25-km distance between Nedlands and John Forrest Park does not lead to a major loss of song function. Together with the results from the Rottnest subjects, I conclude that isolation by distance through continuous populations of Singing Honeyeaters is not as effective in causing loss of vocal recognition as is isolation by the water barrier between Rottnest Island and the adjacent mainland of Western Australia.

There are no experimental data concerning the method by which song features are transmitted across generations of Singing Honeyeaters. Previously, the only evidence that learning is involved in the acquisition of song in any species in the Meliphagidae rested upon an anecdotal report of the Parson Bird (*Prosthemadera novaeseelandiae*) mimicking nonavian sounds (Gilliard 1958). My observations (Baker 1993) suggest vocal learning is involved in song development in Singing Honeyeaters because of the existence of local song neighborhoods. In these song neighborhoods, a few neighboring males have very similar songs and these differ markedly from other nearby groups of neighbors. This type of vocal convergence at the microgeographic scale is usually taken as strong

circumstantial evidence of a role for imitation in song development (Kroodsmma 1982).

Other comparisons of island-island or island-mainland vocal recognition in birds are rare in the literature. A number of studies compared song structure of island and mainland populations (e.g. Lack and Southern 1949, Marler and Boatman 1951, Marler 1960), but did not conduct experiments to determine if the differences were discriminated by the birds (reviewed in Miller 1982). An exception is the island-island comparison of responses to playback by Galapagos finches. Five species of *Geospiza* were tested in seven between-island comparisons of response to song playback (Ratcliffe and Grant 1985). The general pattern of results showed that in most comparisons the subjects exhibited some degree of discrimination; they responded more to songs from their local population than to songs representing another island population (Ratcliffe and Grant 1985).

Finding a significant loss of recognition of conspecific songs raises questions about the possible consequences for population processes. In particular, the immigration of a Rottnest male into the Nedlands population, or vice versa, presumably would not be met with any excess aggression by a resident male. Instead, it might initially be ignored. The immigrant's song would not be an effective keep-out signal for territory establishment. Morphologically, the birds of Rottnest and Nedlands are similar enough that it seems likely an immigrant, when seen by the resident, would elicit an aggressive reaction. In turn, this response might trigger an adoption of the local song traits by the immigrant or the acquisition of perceptual recognition by the resident of the immigrant's song features. The former hypothesis could be tested by experiments on captive birds and the latter hypothesis might be tested by extended-time playback experiments on territorial residents. Such occurrences of immigration, however, may be quite rare. On nearby Carnac Island, 8 km from the mainland, 70 days of continuous monitoring of immigrants revealed no Singing Honeyeaters, and only one immigrant Singing Honeyeater was found during the period 1934-1977 (Abbott 1978).

Loss of recognition by males could imply a similar loss by females and this suggests a further consequence for gene flow. Perhaps an immigrant male would have trouble attracting a mate, assuming that the song of the Singing

Honeyeater has a role in this process. Results of female preference tests in several species suggest that loss of recognition by females might occur (Baker et al. 1987a, b, Balaban 1988, Baker and Baker 1990), although experiments on Singing Honeyeaters are needed to examine this possibility.

Conceivably, there is sufficient genomic divergence between Rottnest and mainland Singing Honeyeaters to cause hybrid breakdown in the event of matings between the populations. This speculation is based upon the morphological divergence of the Rottnest population (Saunders and deRebeira 1985, Wooller et al. 1985) that earlier led Milligan (1911) to describe the Rottnest form as a new species. Increased understanding of this problem could be achieved by a description of the genetic structure of the populations, as well as by further experimentation on the reproductive communication system of these birds.

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