

Aggressive Response of Red-winged Blackbirds to Mockingbird Song Imitation

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Vocal mimicry by birds has long received attention but is still not well understood. Several hypotheses have been advanced to explain its adaptive significance (Harcus 1977, Rechten 1978, Dobkin 1979, Krebs and Kroodma 1980). Proposed functions of mimicry include: (1) interspecific territorial defense, (2) increased size of song repertoire for mate attraction and/or intraspecific territoriality, (3) facilitation of individual recognition, and (4) increases in the apparent density of resident predators and/or competitors through deception. Both Dobkin (1979) and Rechten (1978) have suggested that, if the copied signal is to be used by the mimic in intraspecific interactions, then extremely accurate mimicry should not be selected for, as it would decrease the chance of the song being perceived as belonging to the mimic. One measure of the fidelity of the mimicked signal is whether individuals of the model species respond differentially to the presentation of imitation song and of true conspecific song.

Morton (1976) observed that, when he approached the nests of Thick-billed Euphonias (*Euphonia lanirostris*), they gave the alarm calls of other bird species nesting nearby and that these calls evoked mobbing by individuals of the model species while the euphonia remained still and continued mimicking. Lemaire (1975) found that Willow Warblers (*Phylloscopus trochilus*) and Chaffinches (*Fringilla coelebs*) did not distinguish between playback of conspecific vocalizations and of isolated imitations by Marsh Warblers (*Acrocephalus palustris*).

Mockingbirds (*Mimus polyglottos*) produce excellent imitations of several bird species (Bent 1948). It is unknown, however, whether individuals of the mimicked species can distinguish these copies from true conspecific signals. Using a previously established playback system with Red-winged Blackbirds (*Agelaius phoeniceus*) (Brenowitz 1981), I tested whether Mockingbird imitation of Red-wing song was of sufficient quality to deceive blackbirds.

From 2–5 July 1981 I conducted a series of experiments near Ithaca, New York in which I compared the strength of response of 10 territorial Red-wings to playback of conspecific song and to playback of a Mockingbird imitation. These songs are shown in Fig. 1. The mimic song was recorded by J. C. Glase in Reading, Pennsylvania on 19 June 1966 at a distance of about 15 m and is archived in the Cornell Library of Natural Sounds (catalog number 11117). The Mockingbird delivered three successive renditions of Red-wing song in a sequence of about 5 min of continuous song that included imitations of several other species. In the playbacks, one isolated Red-

wing copy was used. The Red-wing song used in the playbacks was recorded from a territorial blackbird near Ithaca using a Sennheiser MKH 815T condenser microphone and a Nagra IV-D recorder.

As can be seen from Fig. 1, the mimic song is of excellent quality. Like the true Red-wing song, it consists of a sequence of introductory notes followed by a pulsed trill. Both songs contain major energy from about 2.8 to 3.7 kHz. The temporal structure of the trills in both songs is quite similar. I have shown previously that the trill is both necessary and sufficient for species recognition in Red-wings (Brenowitz 1980, 1982).

The playback procedure used in the present experiment was the same as described in detail in Brenowitz (1981). Briefly, Red-wings were exposed to playback of Mockingbird imitation both before and after playback of conspecific song, either in early morning (0500–0800) or early evening (1900–2100). Each signal was presented at 15-s intervals for 3 min, followed by 1 min of post-playback observation. The birds' responses to these signals were quantified by five criteria: (1) the number of songs given during the 4-min playback period, (2) the number of song spreads given during the 4 min period, (3) the number of song spreads judged to be of high intensity, (4) the percentage of songs during the playback period that were accompanied by a song spread, and (5) the percentage of song spreads judged to be of high intensity. The song spread is a graded visual display that often accompanies song and that reflects a corresponding gradation of aggressive arousal (Orians and Christman 1968, Peek 1972, Yasukawa 1981). Data were tested with a Friedman two-way analysis of variance by ranks (Siegel 1956).

Table 1 presents summary data for 10 Red-wings. For all five response measures, there was no significant difference in strength of response to playback of true Red-wing song and of a Mockingbird imitation. Most of the blackbirds tested showed robust, strongly aggressive responses immediately upon presentation of the mimic song.

These results strongly suggest that Red-wings are unable to distinguish between conspecific song and isolated Mockingbird imitation. Mockingbirds could, therefore, potentially use their imitation of Red-wing song in interspecific territoriality directed at blackbirds. The fact that naturally occurring mimics learn Red-wing song indicates that these two species are sometimes sympatric. Support for this function of Mockingbird song mimicry comes from the observations that they are generalist feeders that are high-

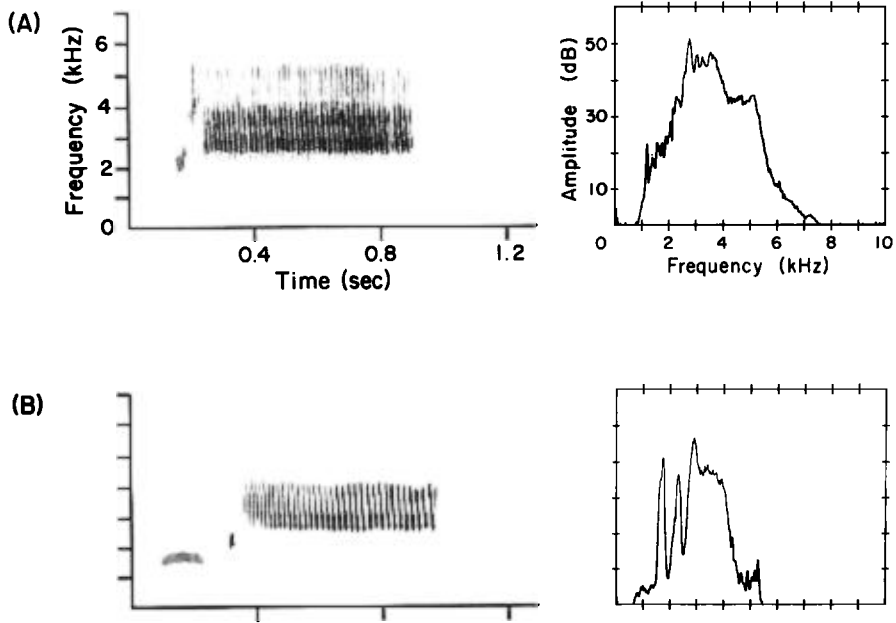


Fig. 1. Red-winged Blackbird song (A) and Mockingbird imitation of Red-wing song (B) used in playbacks. Wide-band sound spectrograms in left column, power spectra in right column.

ly aggressive toward a large number of species (Moore 1978) and that they imitate the songs of many of their competitors (J. Baylis pers. comm. to Krebs and Kroodsma 1980). One additional point that is of related interest is that, while making the original Mockingbird recordings, Glase noted that when a Common Flicker (*Colaptes auratus*) landed nearby and called, the Mockingbird responded by mimicking it. This also happened when an American Robin (*Turdus migratorius*) approached and "scolded." The

present study does not, of course, prove that Mockingbird mimicry functions in interspecific territoriality. Additional research is needed to resolve this question.

The results presented in this report demonstrate that Mockingbirds are able to produce imitations of extraordinary fidelity. Further experiments might be conducted to examine the response of Red-wings to mimicked blackbird song presented in the context of complete Mockingbird song. Also, it would be in-

TABLE 1. Responses ($\bar{x} \pm SD$) shown by Red-winged Blackbirds to playbacks of Mockingbird imitation of Red-wing song both before and after playback of true Red-wing song. $\chi^2 r$ values computed with Friedman two-way analysis of variance; $n = 10$ for all tests; * indicates $P > 0.05$.

	Mockingbird imitation	Red-wing song	Mockingbird imitation
Number of songs	16.1 \pm 7.0	13.2 \pm 7.5 $\chi^2 r = 4.85^*$	13.7 \pm 6.2
Number of song spreads	15.1 \pm 8.4	12.6 \pm 8.2 $\chi^2 r = 3.15^*$	12.9 \pm 7.1
Number of high-intensity song spreads	13.3 \pm 9.4	11.9 \pm 8.9 $\chi^2 r = 2.16^*$	10.9 \pm 7.6
Percentage high-intensity song spreads	60.4 \pm 43.5	81.8 \pm 32.8 $\chi^2 r = 1.05^*$	72.6 \pm 34.2
Percentage songs accompanied by song spread	74.9 \pm 37.7	88.6 \pm 21.3 $\chi^2 r = 0.35^*$	85.1 \pm 31.6

interesting to know whether other mimicked species are similarly unable to distinguish the copied from the model vocalization.

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Reproductive Synchrony and Predator Satiation: an Analogy Between the Darling Effect in Birds and Mast Fruiting in Plants

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Breeding synchrony characterizes many taxa. Some factors impose or select for synchrony, while others entrain it on a more immediate, proximate basis. Observed synchrony in a population represents a compromise between synchronizing and desynchronizing factors. Avian ecologists trace discussion of synchrony to F. Fraser Darling (1938), who proposed that, in gulls, synchrony was adaptive in minimizing predation on young. He assumed that a predator has a finite appetite and that there is no recruitment of predators (Gochfeld 1980: 256). As long as the number or biomass of young was below this predation threshold (a term he did not use), all might be consumed. Synchronous hatching would yield a superabundance of young for a brief period,

allowing some to survive as predators became satiated. Darling's model is attractive in linking evolution and ecology (selection via reduced predation) with behavior and physiology (social facilitation in large groups enhancing neuroendocrine stimulation leading to increased synchrony). Despite this attractiveness, few studies have found support for the model. A relation between synchrony and group size or improved productivity is demonstrable in some studies (Hall 1970, Collias et al. 1971, Burger 1979, Gochfeld 1979), while Nisbet (1975) found evidence for timing and predator satiation. Some studies have found no evidence for the model (Oriani 1961, MacRoberts & MacRoberts 1972).

The complexities of studying these interrelated