SHORT COMMUNICATIONS

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"LEADER-FOLLOWER" SINGING IN RED-WINGED BLACKBIRDS

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The males of many songbird species sing species-typical songs at characteristic rates throughout the breeding season. These songs are correlated with establishment and maintenance of territory boundaries as well as with mate acquisition. Many male songbirds will sing regardless of whether or not conspecific males are nearby. However, the rate of song delivery is often strongly influenced by the presence of both conspecific males and females (Smith et al., unpubl. data; Dinsmore, Auk 86:139–140, 1969).

Red-winged Blackbirds usually nest in colonies, occupying contiguous territories. During a study of this species, we noticed that when a potentially intruding male sang, he was often "answered" by the resident male. We termed this phenomenon "leader-follower singing," the threatening male being the "leader" (A) and the resident, the "follower" (B). It usually occurred at disputed boundaries between territories. Throughout the breeding season, males sing short, stereotyped, "conc-a-ree" songs coupled with a visual display 1–9 times per minute. Males are often involved in conflicts with one another early in the breeding season when boundaries are being disputed. The data we discuss here were collected from a population of marked birds which we observed during the 1976 and 1977 breeding seasons, in Old Field, New York.

The interval between the songs of two male blackbirds sometimes varies predictably, in which case it may indicate to a threatening male that a particular resident male is "paying attention" to him.

A leader-follower singing relationship developed wherever a territorial boundary was threatened by a non-resident or by a neighboring territorial male. In order to standardize data collection, we defined a boundary encounter as a situation in which singing males were 10 m or less apart, separated by a boundary. To quantify this apparent interactive singing, we used a tone encoder system and noted the song delivery of the males and their territorial status. We plotted as a histogram the intervals between songs of males A and B (A → B) and those intervals between B's song and the following song of A (B → A). We predicted that if the songs were sung independently of one another, the intervals would be highly variable. Furthermore, this variability should equal that of birds singing at distances greater than 10 m apart.

In order to test this hypothesis, we computed a set of intersong intervals using the mean and variance of intervals between songs of each bird during an interactive singing period. We then examined the resulting distribution of the intervals, first assuming that the birds were singing independently. We measured intersong intervals and calculated means and standard deviations of these intervals for each male. We then computed two independent random song delivery sequences and plotted them onto the same time axis in order to compare the series of times. The computed A → B and B → A intervals were analyzed (Fig. 1, upper graph) and compared with the observed intervals (Fig. 1, lower graph). In the example shown, our computed interval histogram shows that the distributions of the A → B and B → A intervals are not significantly different from one another (t-test, two-tailed, $P > 0.3$). The interval histogram for the observed data, however, differs from that of the computed independent distributions. First, the

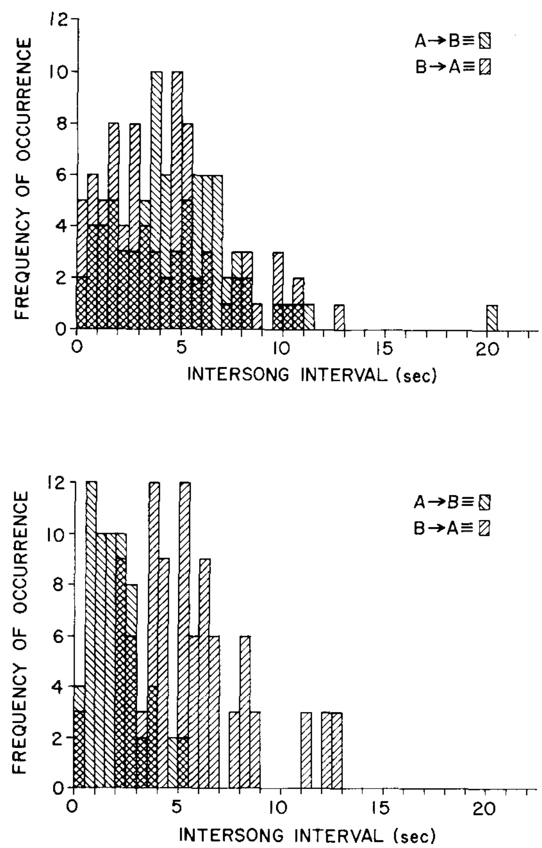

FIGURE 1. Upper graph: a histogram plot of computer-generated time intervals between the songs of two males singing independently. The computer generated these data using the mean and standard deviation of the song rate for each individual. Lower graph: a histogram plot of the observed intervals between songs of the same individuals during a territorial boundary encounter.

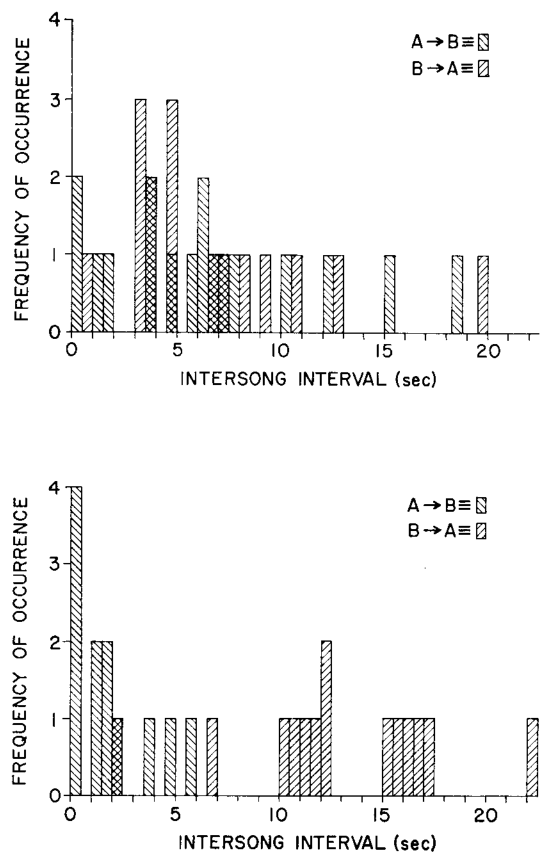

FIGURE 2. Upper graph: a histogram plot of two territorial males A and B singing independently on their territories. There is considerable variation in the intersong intervals between males. Lower graph: a histogram plot of the same two males in a leader-follower situation. There is virtually no overlap in the intervals between A's song and B's as compared to those between B's song and A's. These data represent a single encounter in which A sang 12 songs and B, 14 songs.

A → B and B → A interval distributions differ significantly from each other (*t*-test, two-tailed, $P < .001$); this indicates that the interval histogram for the observed data differs from that made by a random model. Second, the distribution of the A → B intervals differs significantly between the computed and the observed intervals (*t*-test, two-tailed, $P < .001$). The mean duration of the A → B interval and the variability about this mean have decreased dramatically in the observed data, suggesting that B's song is following A's at a regular delay.

This same analysis can be performed by comparing the rate of song delivery between two neighboring birds when they are closer than 10 m and when they are relatively far apart. Figure 2, upper graph shows the distribution of intervals between the songs of neighboring males, male A and male B, which by our operational definition were singing without regard to one another. When recorded, the birds were 50 m apart. The distribution of intervals from A's song to B's is statistically similar to that from B's song to A's (*t*-test, two-tailed, $P > 0.3$). However, the same individuals show an entirely different singing relationship when within 10 m of one another. Figure 2, lower graph shows the histogram plot of the intervals between the two males' songs. These data show that B delivered his song at a relatively constant and short pause after he heard A's song. The opposite was not true; the intervals from B's song to A's were much longer and more variable. We conclude that in this situation B's song delivery was controlled by A's song.

We have noted this leader-follower singing relation during two Red-winged Blackbird breeding seasons. We recorded 13 boundary encounters involving two males. Only one male of each pair showed this consistently low variation in interval and short pause. In 12 of 13 cases where we recorded leader-follower singing it was the threatened resident who adopted the follower role. We defined a threatening male as the one who first approaches a boundary and the threatened male as the one who flies to the proximity of the boundary, apparently in response to the presence of the threatening male. The leader-follower singing relationship might inform a threatening male or intruder that the resident male is responding directly to the threat of intrusion.

It would be interesting to record interactions of individuals of known status in other species to determine whether leader-follower singing is widespread.

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