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Male Yellow Warblers Vary Use of Song Types Depending on Pairing Status and Distance from Nest

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Male birds use their songs in interactions with females and other males (for review, see McGregor 1991). Males normally use the same songs for both functions, but certain paruline warblers (and some species from other taxa) seem to divide their repertoire according to function (for review, see Spector 1992). For example, male Yellow Warblers (*Dendroica petechia*) sometimes sing one song type repeatedly (type I song), but at other times use a repertoire of several song types with little immediate repetition of each (type II song). Results from Spector (1991) and earlier studies (Ficken and Ficken 1965, Morse 1966) indicate that males use type I songs more in intersexual interactions, and type II songs more in intrasexual ones. Evidence that males direct type I songs toward females comes from the association between the use of this song type and both the male's proximity to his mate and his mating status.

Spector (1991) removed females from the territories of four pairs of Yellow Warblers and monitored the singing behavior of the male. All four females were incubating, a stage of the breeding season when type II singing normally predominates. Each of the four males increased the amount of type I song used after the removal of the female, but showed no corresponding increase in type II songs. Males that re-mated showed a rapid decline in type I singing.

In an attempt to replicate these findings, we performed a similar female-removal experiment using five pairs of Yellow Warblers. This is a small sample, but adequate when considered with four pairs studied by Spector (1991). Removal experiments are disrup-

tive to the birds, so we wished to keep the sample at a minimum.

We also investigated the relationship between song type use and distance from the nest. Spector found that male Yellow Warblers varied their song type use depending on the sex of the individual with which they were interacting; males were more likely to use type I songs when interacting with females, and type II songs when interacting with males. We were not able to identify with certainty the sex of the individual a male was interacting with. However, it is likely that distance from the nest, at least during incubation, was related to whether the male was interacting with his mate or with another male. Females rarely leave the nest at this stage, so when a male was close to his nest he was likely to be close to the female. For the same reason, males were less likely to be directing song toward their own mate when far from the nest (although they may have been directing it toward other females). It is at these greater distances from the nests that the most interactions with other males occurred.

Methods.—Subjects were six male Yellow Warblers from a population at Indian Point, St. Andrews, New Brunswick, Canada. The birds were color banded and their territories mapped during early June 1991. We found nests by following the female during nest building or following the male while the female was incubating (males feed females at the nest during incubation).

Once a nest was discovered and the female was incubating her clutch, we began tape recording the male. We visited each male's territory and recorded for a 10-min period, two to four times a day between 0700 and 1900 EST. Territories were visited in a similar order and, therefore, at similar times during each day of recording. We recorded two of the males (Figs.

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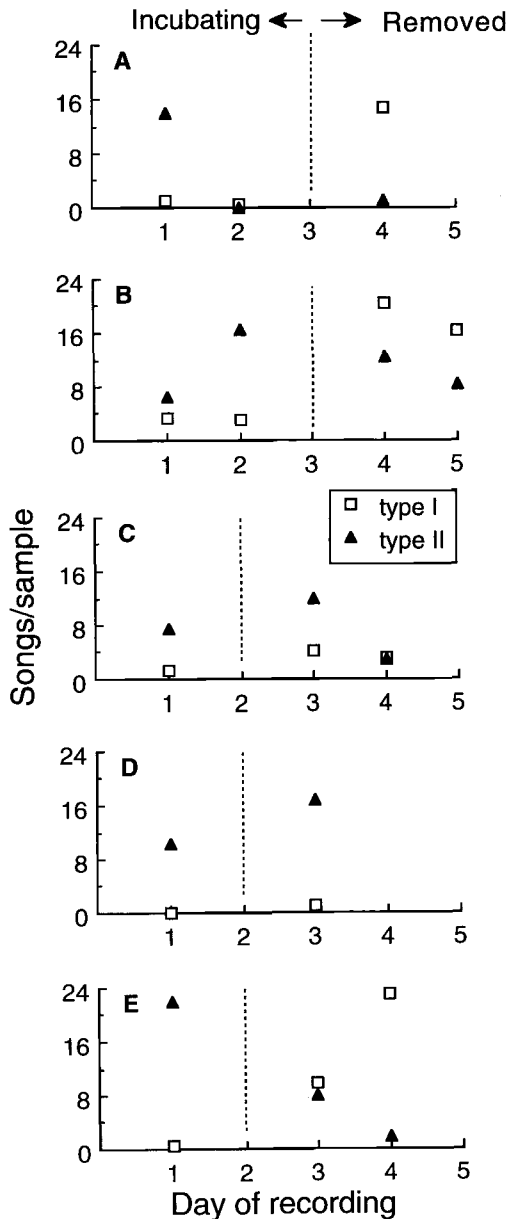


Fig. 1. Singing behavior of five male Yellow Warblers whose mates were removed from their territories during incubation. Males recorded two to four times/day for 10-min periods before and after the females removed ("incubating" and "removed" stages). Mean number of type I and type II songs recorded are shown.

1A, B) for two days before the female's removal, and the other three (Figs. 1C-E) for only a single day before removal.

Songs were tape recorded using a Marantz PMD

221 tape recorder, and a Sennheiser MD211 microphone mounted in a Dan Gibson parabolic reflector. Spectrograms of songs were generated using SoundEdit software and a Macintosh computer. Songs were classified as type I or type II on the basis of usage; only type I songs are sung repeatedly in long sequences (Spector 1991).

Females of four pairs (Figs. 1A-D) were captured (14-16 June) using a mist net and housed individually in cages (1 m³) with water and food (mealworms and wild arthropods) supplied *ad libitum*. Eggs were removed from the nest and kept at approximately 28°C. One female (Fig. 1B) was captured at 0900, but others were captured in the early afternoon. After 24 h the female was returned to the territory and released; the eggs also were returned to the nest. Two of the females (Figs. 1A, D) continued to incubate the eggs, which eventually hatched. The other two females were not seen again on the territory following release. A nest belonging to the fifth pair (Fig. 1E) was destroyed by a predator on 16 June and the female disappeared; thus, this fifth female was "naturally" removed.

We recorded all males on the day after the removal (before female was released). For the three males whose females deserted the territory (Figs. 1B, C, E), recordings were also performed on the following day. No female was seen on the territories during the removal period.

Results.—As illustrated in Figure 1, four of the five males sang somewhat more after the removal of the female (increase statistically significant comparing mean number of songs before vs. after female removal; paired $t = 2.43$, one-tailed $P = 0.036$). The five males sang mostly type II songs before removal, but each of these males showed at least some increase in the number of type I song used after removal. Although two birds showed only a slight increase (Figs. 1C, D), the effect across the five males was statistically significant (paired $t = 2.93$, 1-tailed $P = 0.021$). This increase in the number of type I songs used resulted in an increase in the proportion of type I songs to type II songs for all five males following the removal of the female (paired $t = 2.90$, 1-tailed $P = 0.022$). When these data are considered with those of Spector (1991), nine of nine birds from two study sites increased the proportion of type I songs used following the removal of the female.

The preremoval recordings of the five males considered above, and recordings from one other male at the same stage of breeding, were used to determine if there was a relationship between the type of song used and the singer's distance from the nest. Following each recording period, we measured the horizontal distance between the perch from which the male was singing and his nest. Males' songs were assigned to one of four different distance categories: (1) ≤ 10 m; (2) 11-20 m; (3) 21-30 m; (4) ≥ 31 m. All six males were recorded at each of the four distance categories, except for category 3, for which only five of the six

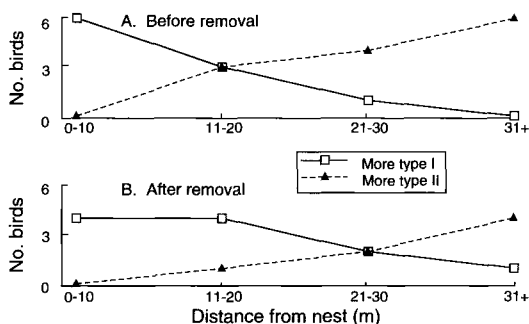


Fig. 2. Singing behavior of male Yellow Warblers in relation to singer's distance from his nest. (A) Singing before female removal, and (B) singing after female removal. Both panels indicate that, at distances of less than 10 m from the nest, males sang more type I songs than type II songs. In contrast, when males were 31 m or more from nest, they sang more type II than type I songs.

males were recorded. As illustrated in Figure 2A, when the birds were close to the nest (≤ 10 m), all tended to use type I songs (6:0, null expectation 3:3; binomial $P = 0.016$). When males were far from the nest (≥ 31 m), all used more type II songs (same probability as above). At intermediate distances the birds showed mixed usage of the two modes.

We replotted the relationship using data from the postremoval recordings of the five males used in the removal experiment. As illustrated in Figure 2B, the general pattern is the same in that males usually used type I song when near the nest and used type II song when distant from it. However, the effect of distance is less pronounced in these postremoval data, as more males used type I songs at greater distances from the nest. Given that we still find a relationship between song-type use and distance from the nest when no female is on the territory, it appears that this relationship is driven not only by the female's presence. Even when no female was present, males were likely to interact with other males some distance away from where nests were located. Yellow Warblers may also remember previous interactions that occurred at a location, and continue to sing songs appropriate to those interactions when returning to the same place (Morse 1966).

Discussion.—Our results agree with the findings of Spector (1991). Male Yellow Warblers showed at least some increase in their use of type I song after losing their mate. They also increased their use of type I songs when near their mate on the territory. These data, with those of Ficken and Ficken (1965), Morse

(1966) and Spector (1991), lend support to the idea that the two song modes of Yellow Warblers serve different functions. Specifically, our data support the interpretation that type I songs are directed toward females. Other supporting evidence is still missing. One element that would be particularly interesting is the female response to these song types. For example, is the sexual response of females to type I songs stronger than to type II songs?

Several other species of wood-warblers also have two song modes or types that may be homologous to the ones described for Yellow Warblers. For example, Chestnut-sided Warblers (*Dendroica pensylvanica*) sing the equivalent of type I songs early in the season and when unmated, while type II songs are used more during interactions with other males (Kroodsma et al. 1989). Kroodsma et al. also performed a female-removal experiment and found that the proportion of the functional equivalent of type I songs increased. Observational evidence indicates a similar pattern of song use relating to mating status and proximity to females in other species (see Spector 1992:table III).

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