

Research Program for Migratory Shore and Upland Game Birds, administered by the Central Management Unit Technical Committee and the Migratory Bird and Habitat Research Laboratory, U.S. Fish and Wildlife Service. The Oklahoma Cooperative Wildlife Research Unit has Oklahoma State University, Oklahoma Department of Wildlife Conservation, U.S. Fish and Wildlife Service, and Wildlife Management Institute cooperating. I thank P. A. Vohs for his advice and manuscript review, G. C. Iverson and D. C. Martin for assistance during fieldwork, and W. D. Warde for assistance with statistical analyses.—THOMAS C. TACHA, *Cooperative Wildlife Research Unit, 404 Life Sciences West, Oklahoma State Univ., Stillwater, Oklahoma 74078.* (Present address: *Cooperative Wildlife Research Laboratory, Southern Illinois Univ., Carbondale, Illinois 62901.*) Accepted 15 Dec. 1983.

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**Vocal mimicry of Nashville Warblers by Yellow-rumped Warblers.**—Many recent studies have emphasized the importance of learning in avian song development (surveyed by Kroodsma and Baylis, pp. 311–337 in *Acoustic Communication in Birds*, Kroodsma and Miller, eds., Academic Press, New York, New York, 1982). Birds are known to discriminate among potential song tutors (Marler and Peters, *Science* 198:519–521, 1977; West and Stroud, *Wilson Bull.* 95:635–640, 1983), yet misdirected song learning does occur (Baptista and Morton, *Auk* 98:383–385, 1981). Among the Parulinae, interspecific vocal learning has been demonstrated for only one species, the Common Yellowthroat (*Geothlypis trichas*) (Kroodsma et al., *Wilson Bull.* 95:138–140, 1983). This note describes a striking similarity between the songs of some Yellow-rumped Warblers (*Dendroica coronata*) and Nashville Warblers (*Vermivora ruficapilla*) in northern Michigan, which apparently arose from misdirected song learning by Yellow-rumped Warblers.

*Methods.*—The study area consisted of 37 islands (0.01–20.6 ha) at the northeastern tip of Isle Royale National Park, Michigan. The vegetation on these islands is typical boreal forest (Edwards, Ph.D. diss. Univ. Michigan, Ann Arbor, Michigan, 1978). During June 1983 I recorded singing warblers using a Marante PMD 200 tape recorder and an Audio-technica AT9100 directional microphone. Audiospectrograms of the recordings were made on a Kay Elemetrics Vibralyzer 6030-A at wide band setting (300 Hz). In this paper, a song “element” is defined as a sound that appears as an uninterrupted mark on an audiospectrogram; a series of elements of the same type is called a “phrase” (Wolffgramm and Todt, *Behaviour* 81:264–286, 1982). Songs of Nashville Warblers ordinarily consist of two phrases; those of Yellow-rumped Warblers consist of one to three phrases. Yellow-rumped Warblers which sing Nashville-type songs are termed “mimics” here.

I made two censuses of the breeding bird population on each island between 11 June and 12 July. The purpose was to assess the relationship between Yellow-rumped Warbler song characteristics and the abundance of singing Nashville Warblers in the immediate vicinity.

I made five measurements on each audiospectrogram: song duration (msec), maximum frequency (kHz), minimum frequency, and average time between elements within first and last phrases of the song. For Yellow-rumped Warblers with songs consisting of a single phrase, the latter two measurements were identical. These data were analyzed using Discriminant Function Analysis (Nei et al., *Statistical Package for the Social Sciences*, McGraw-Hill, New York, New York, 1975) to determine if the songs of typical Yellow-rumped and Nashville warblers could be distinguished by measures of frequency and tempo, and to predict the group membership of mimic Yellow-rumped Warblers by the same criteria. Two central assumptions of linear discrimination, homogeneity of variances among groups and

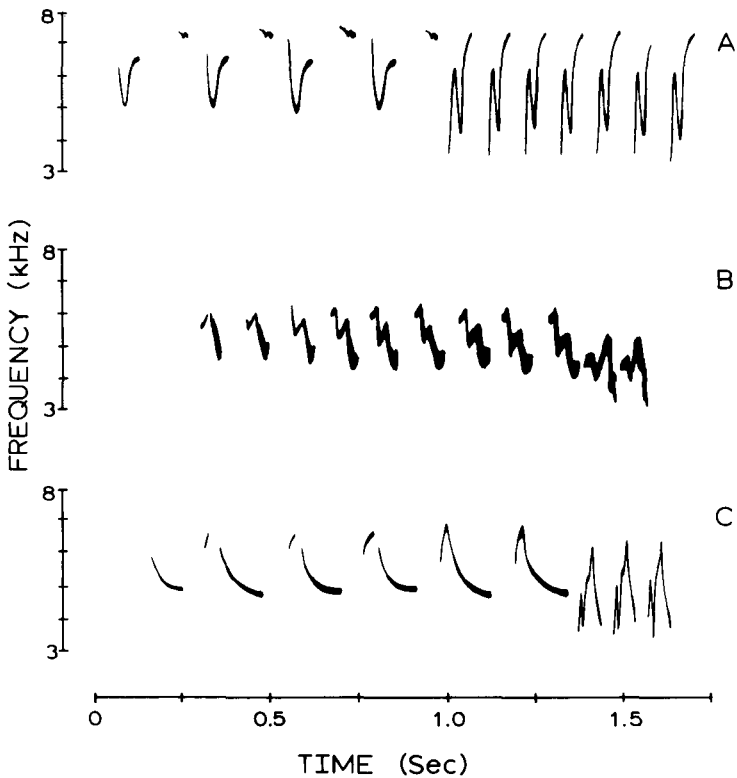


FIG. 1. Ink tracings of audiospectrograms of a typical Nashville Warbler (A), typical Yellow-rumped Warbler (B), and mimic Yellow-rumped Warbler (C). Nashville and mimic Yellow-rumped warblers differ from typical Yellow-rumped Warblers in their generally higher frequency and accelerating tempo.

normal distribution of observations, were tested with the  $F_{\max}$ -test for homogeneity of variances, and the  $G$ -test for goodness-of-fit (Sokal and Rohlf, Biometry, Freeman, San Francisco, California, 1981). The only violation consisted of significantly different variances between groups in the time between elements in the last phrase of the song ( $F = 3.29$ ,  $P < 0.01$ ). This single violation is less extreme than those in many ecological data sets used in discriminant analysis, and is not likely to have influenced the outcome of the analysis (Williams, Ecology 64:1283-1291, 1983).

I also sorted songs according to the similarity of their elements. The shape of each element was measured by the following procedure: (1) The element was divided into intervals within which the slope of the tracing was uniformly either positive or negative. For example, the elements in the last phrase of the song in Fig. 1A have three such intervals, while those in the last phrase of the song in Fig. 1B have four intervals. (2) For each interval, I measured the initial frequency, duration, and average width and slope (Hz/msec) of the mark. The width of the tracing on an audiospectrogram varies primarily with the range of frequency

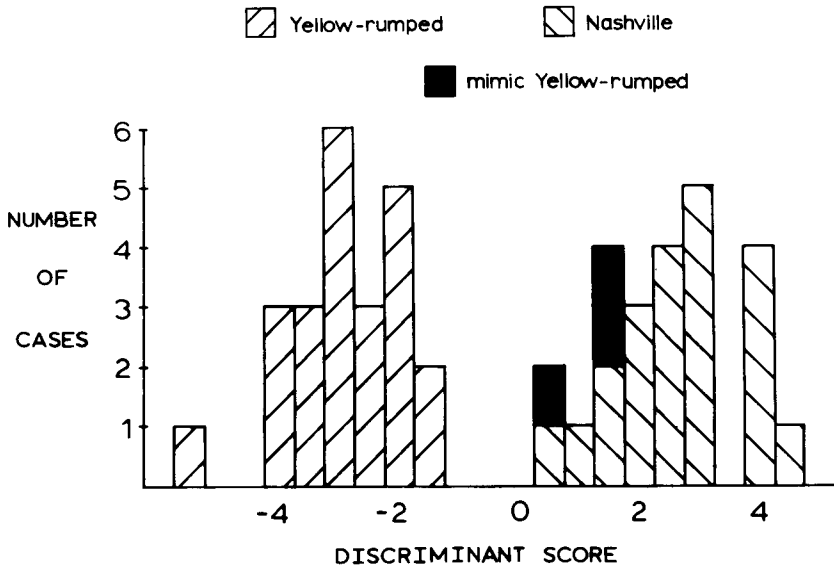


FIG. 2. Distribution of discriminant scores of warbler songs. Scores of typical Yellow-rumped and Nashville warblers do not overlap (group centroids: Yellow-rumped Warbler,  $-2.65$ ; Nashville Warbler,  $2.90$ ). Mimic Yellow-rumped Warbler songs are similar to those of Nashville Warblers, according to this analysis based on five measures of frequency and tempo.

being produced. For example, the elements in Fig. 1A are narrower than those in Fig. 1B because at any one time the acoustic energy in the elements of Fig. 1A is channeled into a narrower range of frequency. The measurement error in this analysis was minimized by measuring elements with a standard procedure on a 1-mm grid. The variation due to measurement error was small compared with variation due to real differences between songs. (3) I compared elements by comparing their intervals in sequence, weighting each of the four measurements equally. Similarities between songs were then found by weighting the similarities between pairs of their elements by the number of times each element was repeated in its respective song. The resulting song similarity matrix was analyzed using cluster analysis (Davis, *Statistics and Data Analysis in Geology*, John Wiley, New York, New York, 1973).

*Results.*—Three species comprised 61% of the breeding bird population of the study area: Yellow-rumped Warbler (0.69 pairs/ha on 26 islands), Song Sparrow (*Melospiza melodia*) (0.65 pairs/ha on 32 islands), and Nashville Warbler (0.38 pairs/ha on 11 islands). I observed Yellow-rumped Warblers singing mimic songs at six sites within the study area, including at least four individuals. Based on censuses of the 37 islands, roughly 8% of the Yellow-rumped Warbler population sang mimic songs. I was able to record three of these (Fig. 1). Clear audiospectrograms were obtained for 23 additional Yellow-rumped Warblers and 21 Nashville Warblers.

Discriminant analysis using the five measures of song structure correctly classifies all typical songs according to species (Fig. 2). Mimic Yellow-rumped Warbler songs fall within the region of typical Nashville Warbler songs (associated probabilities of misclassification

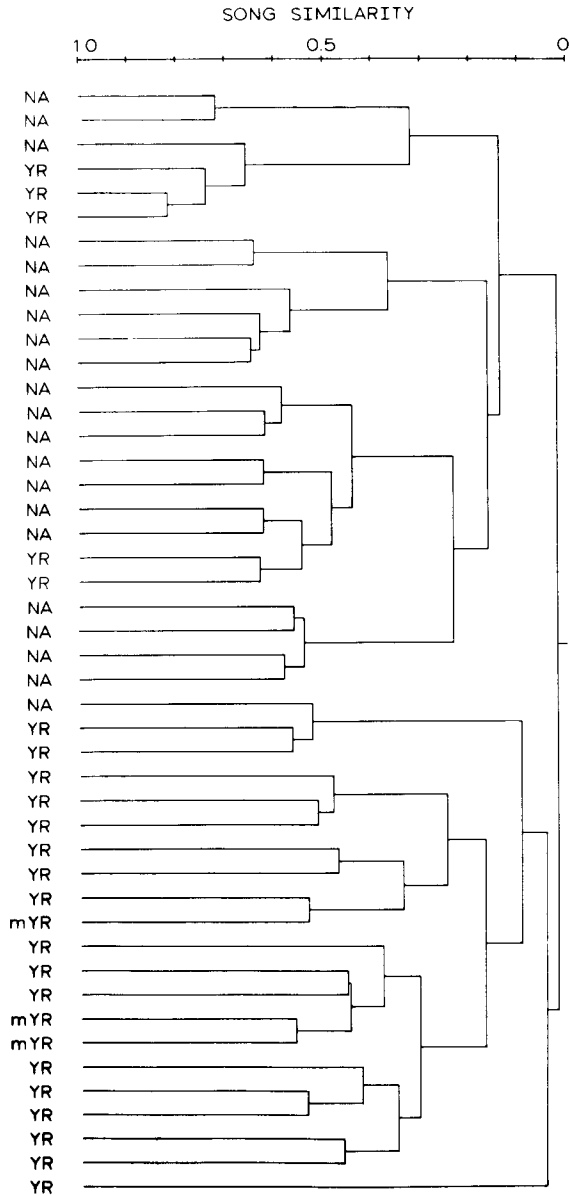


FIG. 3. Dendrogram of song similarity based on element shape. Mimic Yellow-rumped Warbler songs are composed of elements similar to those of typical Yellow-rumped Warblers. NA = Nashville Warbler; YR = typical Yellow-rumped Warbler; mYR = mimic Yellow-rumped Warbler.

are  $P < 0.001$ ,  $P < 0.001$ , and  $P < 0.10$ ). All five tempo and frequency variables contribute significantly to the discriminant function ( $P < 0.0001$ , Rao's  $V$ ); this function produces a highly significant degree of separation of groups (Wilks' Lambda = 0.1107,  $P < 0.0001$ ).

Classification of songs according to element shape gives imperfect distinction between species (Fig. 3). Two major clades are recognizable in the dendrogram of song similarity: the upper group contains 20 of the 21 Nashville Warblers and five Yellow-rumped Warblers; the lower group contains the remaining 21 Yellow-rumped Warblers and one Nashville Warbler. Song elements of mimic Yellow-rumped Warblers do not differ from those of typical Yellow-rumped Warblers by this analysis.

Censuses of breeding birds on all islands indicated that Yellow-rumped Warbler song characteristics were unaffected by the presence of nearby singing Nashville Warblers. There is no relationship between the discriminant scores of Yellow-rumped Warbler songs and the relative abundance of Nashville Warblers (no. Nashville/no. Yellow-rumped) on the islands at which they were recorded ( $r_s = 0.231$ ,  $N = 25$ ,  $P > 0.10$ ). In addition, at least one mimic Yellow-rumped Warbler bred on an island which contained no Nashville Warblers. These results suggest that Nashville song characteristics were not learned by mimic Yellow-rumped Warblers as the two species established territories together on their breeding islands.

*Discussion.*—Mimicry of Nashville Warblers occurs infrequently among Isle Royale Yellow-rumped Warblers, and consists of imitation of the general structure of Nashville songs (i.e., tempo and frequency; Fig. 2), but not of the configuration of song elements (Fig. 3). Yellow-rumped Warbler mimicry could result from misdirected song learning early in development. Imitation of Nashville Warblers apparently does not occur among adult Yellow-rumped Warblers, since high Nashville Warbler densities do not produce Nashville characteristics in the songs of nearby Yellow-rumped Warblers. Rather, incorrect song acquisition may result from the exposure of juvenile Yellow-rumped Warblers to Nashville Warbler song during their first summer, when song learning has been shown to occur (Marler and Peters 1977; Baptista and Morton 1981; Slater and Ince, *Ibis* 124:21–26, 1982). Exposure of juvenile birds to songs of allospecifics may be fairly extensive because both species are common in the study area.

We lack a sufficient understanding of the conditions under which normal song learning may take place. As yet there is no predictive model for assessing the outcome when these conditions are violated, even after 15 years of controlled experiments (Marler, pp. 231–244 in *Proc. XIV Int. Ornithol. Congr.*, 1967; Payne, *Anim. Behav.* 29:688–697, 1981). We are farther from an understanding of abnormal song learning in the field (Kroodsma et al. 1983). Studies such as this one increase our understanding of avian song learning by documenting conditions under which normal song development fails to occur.

A final caveat—this analysis has ignored the multiple song types sung by many parulines, including the Yellow-rumped Warbler (M.R. Lein, pers. comm., cited in Kroodsma, *Auk* 98:743–751, 1981). Morse (*Nature* 226:659–661, 1970), Lein (*Can. J. Zool.* 56:1266–1283, 1978), and Kroodsma (1981) have shown that warblers use different songs in different contexts: the Type I song of Kroodsma (1981) is used in male-female interactions, whereas the Type II song occurs in intrasexual confrontations. A second group of studies has suggested that song repertoires in density limited populations may serve to repel newcomers by creating the false impression that many birds occupy the territory of a single male ("Beau Geste" hypothesis; Krebs, *Anim. Behav.* 25:475–478, 1977; Krebs et al., *Nature* 271:539–542, 1978; Yasukawa, *Anim. Behav.* 29:114–125, 1981; but see Dawson and Jenkins, *Behaviour* 87:256–269, 1983). An evaluation of the function of mimic songs in the Isle Royale Yellow-rumped Warbler population is not possible without knowing whether the songs were male- or female-directed. However, my observations indicate that mimic Yellow-

rumped Warblers may not sing multiple song types. Two of the four mimic Yellow-rumped Warblers were observed regularly through June and early July; neither bird was heard singing a typical song or an unfamiliar mimic song.

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**Misdirected displays by a solitary bird of paradise in an oropendola nesting colony.**—On 19 March 1979 we spent the day roaming the forest on Little Tobago Island, a 113-ha hilly islet lying 2 km off the northeast coast of Tobago. Our objective was to track down any surviving remnants of a colony of about 50 Greater Birds of Paradise (*Paradisaea apoda*) transported from the Aru Islands off New Guinea as a conservation measure by W. Ingram in 1909 and 1912 (Ingram, *Avic. Mag.* 18:142–147, 1911; 23:341–351, 1917). Roldan George, the government-employed conservator for the islet and its seabird colonies thought that one male and possibly one female remained, and steered us to the south end of the island where he felt the male might be found. Here, in two tall palm trees (*Roystonea oleracea*) emerging above the 15-m canopy of deciduous trees a dozen or more Crested Oropendolas (*Psarocolius decumanus*) were singing and displaying noisily, among their long, pendulent nests. In the midst of the group was a single adult male bird of paradise, in full display. This bird was clearly a member of the displaying group, and we watched for an hour through the screening canopy as the bird displayed, repeatedly throwing its body and wings forward with plumes fanned upwards in typical *P. apoda* display patterns (Wallace, *The Malay Archipelago*, Harper, New York, New York, 1869; Gilliard, *Natl. Geogr. Mag.* 114:428–440, 1958; Dinsmore, *Auk* 87:305–321, 1970). Dominance and territorial relationships were difficult to determine, but the bird of paradise clearly maintained a central position in the colony and was rarely, if ever, displaced during an hour of almost continuous displaying.

Ingram's colony, despite evidence of successful breeding in early decades, has declined continuously with one or more catastrophic drops (Dinsmore, *Carib. J. Sci.* 10:93–100, 1970). Baker (*Bird-Lore* 25:295–302, 1923) observed 15 or 16 birds in one tree in the early 1920's, but other observers in that period were less successful. On a 3-week visit in 1958, Gilliard (1958) recognized 15 different individuals and estimated that as many as 35 birds might still be present. However, a hurricane in 1963 destroyed much of the forest habitat on the island and no more than nine birds have been counted since that time. Dinsmore (1970), in his intensive 9-month study of the birds in 1965–66, found only seven birds: four males and three female-plumaged (female or juvenile) birds. Four males and one female were still present in 1968 (Dinsmore 1970) but records since 1970 have been limited to an occasional sighting of a single bird (R. George, pers. comm. to Dinsmore). Residents of Speyside, a coastal town directly opposite the islet, continue to propagate rumors of one or two birds, but Richard French of Pointe-a-Pierre, Trinidad, an active ornithologist who contacts many of the ornithological visitors to the area, has been unable to confirm these