

into two broad groups: (1) species in which the female sings and defends territory with the male and (2) species in which the female sings as well, or nearly as well, as the male, but the singing is concerned with pair-bond and/or family-group maintenance and not with the defense of territory. The results of the present study indicate that Black-headed Grosbeaks are another "group 2" species, since the singing of females has no territorial function. Previous studies indicate that such singing is important in the maintenance of the pair bond and of the family-group after fledging (Ritchison 1980).

Although females failed to respond to the songs of either neighboring or non-neighboring males, they did show a response when the songs of their mates were played back. Such a response indicates that female Black-headed Grosbeaks are able to recognize the songs of their mate. There have been several reports of such mate recognition in colonial seabirds (White, *Anim. Behav.* 19:125–131, 1971; Wooller, *Z. Tierpsychol.* 48:68–86, 1978; and others). However, mate recognition has rarely been documented in passerines.

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Vocal learning in the Parulinae.—Vocal learning is the ability to use auditory information, including feedback, to modify or enhance vocal development (Nottebohm, *Am. Nat.* 106:116–140, 1972). This learning is well documented in both humans and birds (e.g., Marler, *Am. Sci.* 58:669–673, 1970), and suspected in cetaceans (e.g., Payne and Payne, *Z. Tierpsychol.*, in press) and perhaps non-human primates (Green, *Z. Tierpsychol.* 38:304–314, 1975). Among birds, evidence for vocal learning now exists for over 300 bird species (Kroodsma and Baylis, in *Acoustic Communication in Birds*, Kroodsma and Miller, eds., Academic Press, New York, New York, in press) from the Psittaciformes, Apodiformes, Passeriformes, and perhaps even the Piciformes (Wagner, *Wilson Bull.* 56:65–76, 1944) and the Galliformes (Sparling, *Wilson Bull.* 91:618–621, 1979).

Most documented examples of avian vocal learning are from the oscines, however, and in this group the Parulinae (wood warblers) is one of the largest subfamilies for which solid evidence of vocal learning is still lacking. Evidence from micro-geographical variation suggests that some song types among warblers are learned (Kroodsma, *Auk* 98:743–751, 1981). Herein we verify through both experiment and observation that males of the Common Yellowthroat (*Geothlypis trichas*) and Chestnut-sided Warbler (*Dendroica pensylvanica*) are capable of vocal learning.

One male Chestnut-sided Warbler nestling at about 10 days of age was taken into the laboratory and then tutored from day 25 to day 100 with a Common Yellowthroat *witchity* song type (see Fig. 1A) and nine different song types of Yellow Warblers (*Dendroica petechia*). Yellow and Chestnut-sided warbler songs are rather similar and often confused by field biologists; hence, it was reasoned that, if Chestnut-sided Warblers do develop songs through imitation, then Yellow Warbler songs would be likely hetero-specific songs that would be learned. The Common Yellowthroat song was used both to tutor a male Common Yellowthroat in an adjacent cage and as an additional song model for the Chestnut-sided

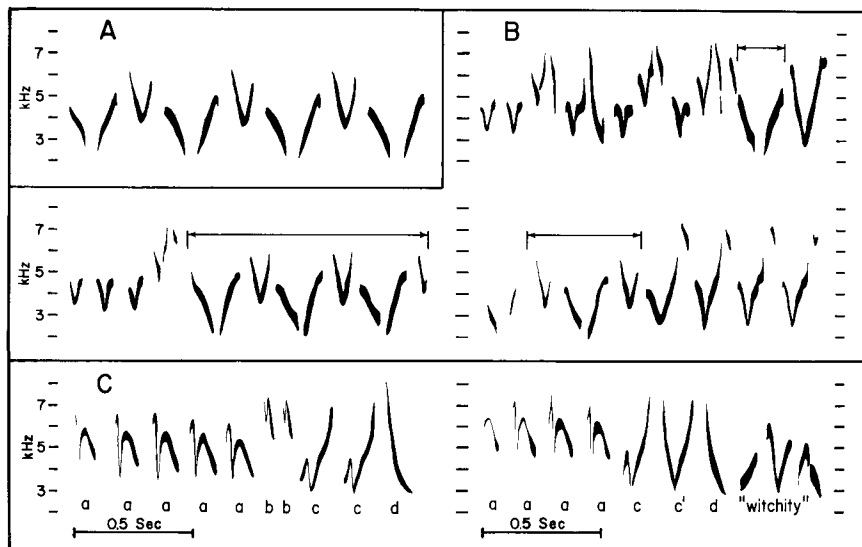


FIG. 1. Vocal learning by the Common Yellowthroat and the Chestnut-sided Warbler. A. Common Yellowthroat tutor song, the typical *witchity-witchity* of wild males. B. Three songs of a laboratory-reared Chestnut-sided Warbler which was exposed to both Yellow Warbler songs and the yellowthroat song in A. Arrows indicate clear imitations of the yellowthroat tutor song. C. On the left is a typical Chestnut-sided Warbler "accented ending type 2" *chee* variant (see Lein 1978), with song components labelled a, b, c, and d. On the right is a song of a Common Yellowthroat from Charlton City, Massachusetts. Homologous song components are labelled, and this Common Yellowthroat typically concluded his song with several renditions of the typical conspecific *witchity* (only one of which is illustrated). These spectrograms are ink tracings of sonagrams made on a Kay 7029A Sona-Graph with a 300 Hz filter (ordinate is kHz, abscissa time).

Warbler. This experimental Chestnut-sided Warbler was maintained on natural daylengths and then recorded as it came into song the next spring.

This Chestnut-sided Warbler developed four stable song types, three of which contained unmistakable elements of the Common Yellowthroat song type (Fig. 1B). In spite of the apparent similarity of the Yellow and Chestnut-sided warbler songs to the human ear, none of the Yellow Warbler songs or song elements were imitated. By default, all songs would be classified as "Unaccented," for at no time did this male sing any typical "Accented Ending" (Fig. 1C; see also Figs. 1-3 in Lein, *Can. J. Zool.* 56:1266-1283, 1978).

Interspecific vocal learning was also documented in the Common Yellowthroat, but this time in the field. Meservey discovered near Charlton Center, Massachusetts, a male Yellowthroat singing both a typical Common Yellowthroat *witchity* song and an excellent copy of the "Accented Ending Type 2," *chee* variant of the Chestnut-sided Warbler (Fig. 1C; see also Fig. 2 in Lein 1978). This male typically sang the Chestnut-sided Warbler song first, followed immediately by two to four repetitions of the conspecific song syllable. This particular song type of the Chestnut-sided Warbler varies little throughout the geographical range of the species, but some individuals do omit or deemphasize song component "b" in their

song types (e.g., Fig. 2D in Lein 1978 and Fig. 4B in Kroodsma 1981), just as this male Common Yellowthroat did. Other than the slightly modified "c" note (song component c' in Fig. 1C), this is a perfect copy of a Chestnut-sided Warbler Accented Ending song type.

Other suggestive evidence of vocal learning as a normal process in the Common Yellowthroat comes from song development in the nestling male which was tutored simultaneously with the experimental Chestnut-sided Warbler male discussed above. This male developed a highly abnormal, simple song syllable, which was repeated in typical Common Yellowthroat fashion. The repeated song component consisted of a single note, however, not the typical three to six note syllable of wild birds (Borror, *Living Bird* 6:141-161, 1967). Such simplification of song syllables typically occurs in isolated birds where conditions for vocal learning are not sufficient for the normal complex song of the species to develop (e.g., Kroodsma, *Anim. Behav.* 25:390-399, 1977).

Other than the micro-geographical variation of Unaccented Ending songs (or Type II songs) in the Chestnut-sided Warbler and the Blue-winged Warbler (*Vermivora pinus*) (Kroodsma 1981), the only other possible evidence of vocal imitation in the Parulinae had involved disputed examples of interspecific mimicry by the Yellow-breasted Chat (*Icteria virens*) (Grinnell et al., *Univ. Calif. Publ. Zool.* 35, 1930; but compare Saunders, pp. 592-593 in Bent, *U.S. Natl. Mus. Bull.* 203, 1953). The evidence in our report is unequivocal, however, and confirms the presence of vocal learning in the Parulinae. Such vocal learning among species where different song types are used in different contexts raises interesting questions not only about what males learn to sing but also about how they come to use these learned signals in an intriguing vocal communication system.

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Factors affecting the performance of flight songs and perch songs in the Common Yellowthroat.—Flight songs have been reported for 11 species of wood warblers (Parulinae) (Ficken and Ficken, *Living Bird* 1:103-121, 1962; Meanley, *Wilson Bull.* 80:72-77, 1968), including the Common Yellowthroat (*Geothlypis trichas*). The flight songs are given as the singer ascends to 10 m above the ground in slow, bobbing flight. The ascent is accompanied by a series of sputtering notes ending with a portion of the perch song; the descent is silent (Bent, *U.S. Natl. Mus. Bull.* 203, 1953). Hann (*Wilson Bull.* 49:145-237, 1937) presents data showing that most flight-singing by the Ovenbird (*Seiurus aurocapillus*) occurs late in the day and late in the season, and other workers have described a similar tendency in yellowthroats (Bent 1953; Stewart, *Wilson Bull.* 65:99-115, 1953; Hofslund, *Proc. Minnesota Acad. Sci.* 27:144-174, 1959). In this paper I examine factors influencing the relative frequencies of yellowthroat flight song and perch song, and suggest a possible function for the flight song in this species.

Yellowthroat singing behavior was studied on two oldfield study areas located in northern Bartholomew Co., Indiana, from 26 April-22 July 1970, and from 28 April-19 Sept. 1971. In 1970 these areas supported seven yellowthroat territories and in 1971, six territories. In 1970 temperature and wind velocity 1 m above the ground were measured during observation periods, and all songs were counted. Notes on behavior were taken during both field seasons.

Data from 1970 yielded 92 hour-long periods during which songs were counted. Multiple