GEOGRAPHICAL VARIATION AND FUNCTIONS OF SONG TYPES IN WARBLERS (PARULIDAE)

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Abstract.—Chestnut-sided Warblers (*Dendroica pensylvanica*) and Blue-winged Warblers (*Vermivora pinus*) sing different song types in different contexts. Local dialects exist in the "Unaccented Ending" songs (often termed the "Type II" song for the Blue-winged Warbler), but the "Accented Ending" songs (or the "Type I" songs) vary only slightly throughout the breeding ranges of the two species. The degree of geographical variation in song types suggests that intrasexual selection has promoted dialects in Unaccented Ending (Type II) songs, while intersexual selection may have played a greater role in maintaining the stereotypy of Accented Ending (Type I) songs. *Received 6 January 1981, accepted 21 April 1981.*

MOST male songbirds learn to sing (Thorpe 1958, Marler 1970, Kroodsma 1977), and limited dispersal from the site of learning (not necessarily the site of hatching) usually leads to micro-geographical variation in songs (Thielcke 1969, Baptista 1975). But whether the selective forces leading to these song dialects (where neighboring males have songs more similar to one another than to more distant yet local males) are primarily intrasexual or intersexual remains unclear. Local dialects in bird song could be maintained because shared song types are more effective in male-male countersinging over territorial rights; alternatively, the female, through mate choice, could maintain the homogeneity of song patterns within a confined geographical area (Marler and Tamura 1964; Nottebohm 1969; Thielcke 1969; Kroodsma 1974, 1979; Lemon 1975; Payne and Payne 1977; Baker and Mewaldt 1978).

Difficulty in clarifying this problem arises because most well-studied songbirds have multi-purpose songs that are used in a variety of contexts. On the other hand, many wood warblers (Parulidae) use different song types in different contexts (Ficken and Ficken 1962, 1965, 1967; Morse 1966, 1967, 1970; Lein 1972, 1978) and are therefore ideal subjects for studying the functions of geographical variation. In this paper I assess and discuss the relative degrees of geographical variation in the different song types of the Blue-winged Warbler (*Vermivora pinus*) and the Chestnut-sided Warbler (*Dendroica pensylvanica*).

METHODS

From the Library of Natural Sounds at the Cornell Laboratory of Ornithology, I obtained 59 cuts of Chestnut-sided Warbler recordings and 23 cuts of Blue-winged Warbler recordings. M. Ross Lein, University of Calgary, kindly loaned 19 recordings of representative Chestnut-sided Warbler songs. In addition, using a Uher 4200, 60-cm diameter parabola and Uher M514 microphone, I recorded songs from four Chestnut-sided Warblers and 10 Blue-winged Warblers at the Rockefeller University Field Research Center near Millbrook, New York. These males were unbanded but could be distinguished reliably from one another by singing locations or peculiarities of particular songs. Data collected here were then compared to data published by Lein (1978) on Chestnut-sided Warblers and Lanyon and Gill (1964) on Blue-winged Warblers.

Songs were analyzed on a continuous spectrum analyzer, and then selected examples were graphed on a Kay Electric Sona-Graph, Model 7029A, with wide-band filter (300 Hz). Because the Chestnut-sided Warbler recordings were quite noisy, ink tracings were made for Figs. 3–6.

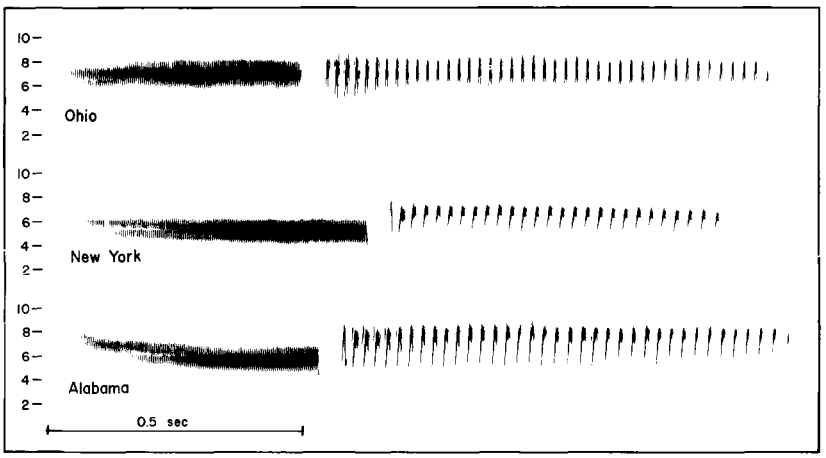

Fig. 1. Three representative examples of the Blue-winged Warbler Type I ("beee-bzzz") song from different parts of the breeding range. As in Figs. 2–7, the abscissa is time and the ordinate kHz. Exact location (and source) of the songs is as follows: Hocking Hills, Hocking County, Ohio (Cornell Cut 20 = CC20); Millbrook, New York (personal); Birmingham, Alabama (CC4).

RESULTS

BLUE-WINGED WARBLER

Type I, or "beee-bzzz."—As discussed by Lanyon and Gill (1964), this song of the Blue-winged Warbler can take several slightly different forms. Six of 15 males at Huntington, New York sang the typical "beee-bzzz" song, consisting of a frequency-modulated "beee" followed by a trill of repeated syllables (the "bzzz"—see Fig. 1). Seven other males inserted a brief (about 0.1 s) frequency-modulated note between the "beee" and the "bzzz," while two males sang only the frequency-modulated notes and omitted the "bzzz" entirely.

There is some variation within a population, but these variations represent most of the song forms that can be found in samples of recordings from other parts of the geographical range of this species. Thus, all 10 males at Millbrook, New York sang the typical "beee-bzzz," and the songs were indistinguishable from the "beee-bzzz" songs of Long Island (e.g. the median number of syllables/s in the "bzzz" portion of the song was 38.8 and "about 40" (Lanyon and Gill 1964; I measured 39.8 from their published sonagrams) in the Millbrook and Huntington samples, respectively.

Type II song.—The variation of Type II songs within and between populations provides a striking contrast to that of the Type I song. Lanyon and Gill (1964) found that all the males within their Huntington population had very similar songs: individual variation was limited to length and number of repetitions of different components and did not involve, as in the Type I songs, different combinations and sequences of the basic song components (Fig. 2). Males near Millbrook also had Type II songs that were very similar to one another. The populations near Millbrook and Huntington are approximately 175 km apart; the Type I songs did not vary over this distance, but the Type II songs are clearly different (Fig. 2). The greatest similarity occurs in the final frequency-modulated portion of the song, but even here the modulation rates differ significantly (a median rate of 85 and 59/s for Huntington and Millbrook, respectively, was significantly different at $P = 0.001$, two-tailed

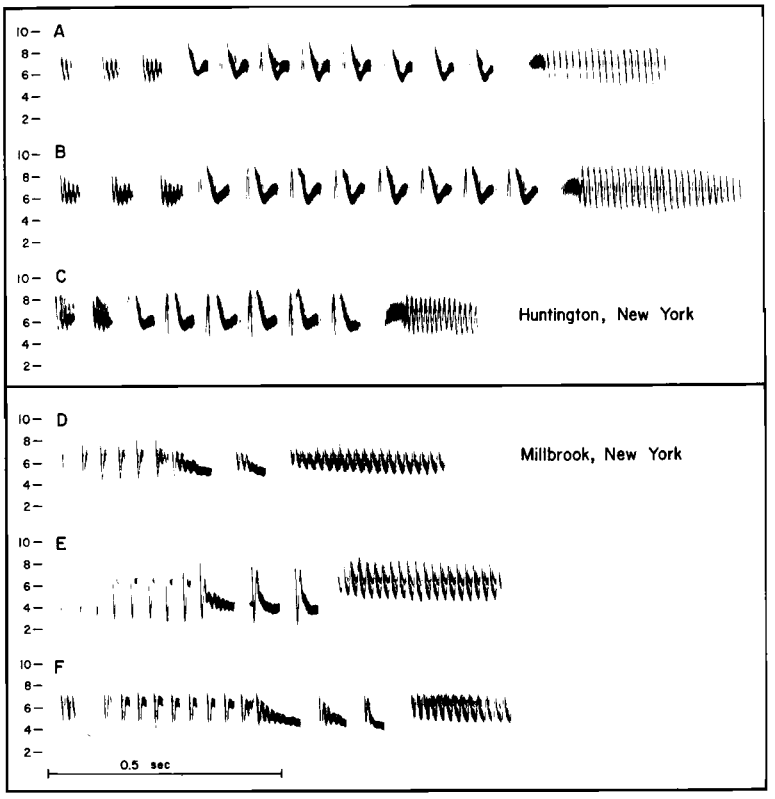

Fig. 2. Examples of Blue-winged Warbler Type II songs from the Kalbfleisch Field Research Station, Huntington, Long Island (courtesy of W. E. Lanyon) and from the Rockefeller University Field Research Station, Millbrook, New York. Members of a population share almost identical Type II songs.

Mann-Whitney *U*-test). Three recordings of Type II songs from the Cornell Laboratory of Ornithology (Cuts 3, 5, and 23) were also unique and verify the marked geographical variation in this song type.

Chestnut-sided Warbler

The male Blue-winged Warbler has only two song types in his repertoire, but the repertoire of the Chestnut-sided Warbler is much larger. Males have three forms of accented ending songs and three forms (plus variations) of unaccented ending songs.

Accented Ending Type 1 (AE-1) song type.—This song type is probably the one most frequently heard and the one most readily associated with the Chestnut-sided Warbler. It is distinguished from the other song types by the very characteristic and emphatic two-note ending (Notes D and E, Fig. 3, the "beecher" or "wee-chew" of the literature). I examined 30 recordings of the AE-1 song variant from New York (13), New Hampshire (5), Tennessee (3), Virginia (3), North Carolina (2), Maine (2), Ohio (1), and Maryland (1), and 12 representative songs are depicted in Fig. 3.

Twenty-eight of the 30 songs (e.g. Fig. 3a–k) began with an alternation of note type A and note type B, while the remaining two songs lacked the A element (e.g. Fig. 3l). The center portion of the song consisted of one of two basic types of C

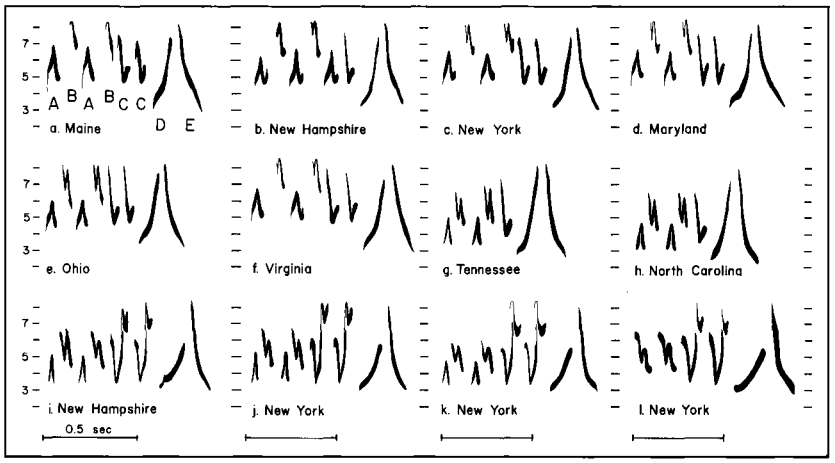

Fig. 3. Geographical variation in Accented Ending Type 1 songs of the Chestnut-sided Warbler, showing songs from 12 locations throughout the geographical range. In "a" are labelled notes A–E, which are discussed in the text. For display here, each song was shortened by deleting several A and B notes from the introduction. Exact location (and source) of the songs is as follows: a. Moosehorn Refuge, Calais (Cornell Cut 27 = CC27); b. Errol (CC25); c. Monkey Run, Tompkins County (CC52); d. Maple Glade Road, Garrett County (CC21); e. Columbus (CC55—this bird was undoubtedly a migrant); f. Shenandoah National Park (CC10); g. Collins Gap, Great Smoky Mountains (CC45); h. Clingman's Dome Road, Great Smoky Mountains (CC41); i. South Lyndeboro (M. R. Lein); j. Newfield (CC58); k. Little Simon Pond (CC8); l. Millbrook.

notes; 20 songs contained the "reverse check" illustrated in Fig. 3a–h, while 10 songs had the slightly more complex note as depicted in Fig. 3i–l.

One apparent regional difference involved several parameters that seemed to covary with this more complex C note (Fig. 3i–l). Ten songs with this element occurred at six locations in New York and New Hampshire, and, when these 10 songs were compared to the other songs of New York, New Hampshire, or other portions of the geographical range (e.g. Fig. 3a–h), several consistent differences were found. The maximum frequencies of the final Note A (the final one was chosen because frequencies of introductory syllables often decline progressively), the final Note B (measured at the peak before the last frequency drop), and Note D were consistently lower for those New York and New Hampshire songs typified by Fig. 3i–l (5.0 vs. 6.3 kHz, 5.9 vs. 8.0 kHz, and 5.7 vs. 7.3 kHz, respectively; all median differences significant at $P < 0.0001$, two-tailed Mann-Whitney U-test).

Accented Ending Type 2 (AE-2) song type.—In addition to the highly stereotyped AE-1 songs, Lein (1978) discovered that each male possesses two distinct song types with a characteristic but slightly less emphatic three-note ending. These were designated the "chee" and "see" variants based on the sound quality of the introductory notes.

The "chee" variant (Fig. 4) typically consists of several introductory notes (F), one or two high-frequency notes (G), followed by the three-note ending (H H J). Several variations were evident in the 13 recordings of this song type. In two recordings (e.g. Fig. 4b), the high-frequency note G was lacking, and occasionally four- rather than three-note endings occurred (e.g. Fig. 4f). Basically, though, the structures of the four-note types were remarkably consistent throughout the 13 recordings, and

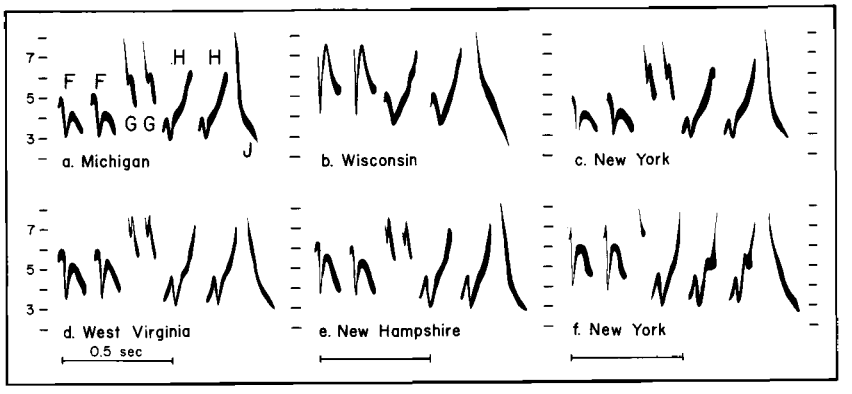

Fig. 4. Geographical variation in Accented Ending Type 2 ("chee" variant) songs of the Chestnut-sided Warbler. Notes F, G, H, and J are labelled in 4a. For display, each song was shortened by deleting several F notes from the introduction. Exact location (and source) of songs is as follows: a. Tahquamenon Park (Cornell Cut 30 = CC30); b. Clam Lake (CC33); c. Stratton (CC3); d. Cranberry Glades (CC19); e. South Lyndeboro (M. R. Lein); f. Millbrook.

songs as far distant as Michigan, New Hampshire, and West Virginia were very similar.

The "see" variant (Fig. 5) usually consists of several introductory notes (K) together with a three-note ending (L L M). All 17 recordings that I examined contained the typical three-note ending, while there was some range of structural variation in the introductory K notes. Again, though, considering the geographical range from which these samples were taken, from Wisconsin to Ontario to New Hampshire and south to West Virginia, the stereotypy of the entire song is remarkable.

Unaccented Ending songs (UE).—Lein (1978) recognized three classes of songs with Unaccented Endings: Unaccented Ending Type 2 (UE-2), Unaccented Ending Type 1 (UE-1), and Jumbled Songs (JS). In his study, each male probably had 4–6 UE-2 song types, fewer UE-1 song types (perhaps 4–5, Lein pers. comm.), and a large number of variations of Jumbled Songs. As with the Accented Ending songs, neighboring males possessed nearly identical song types (see Figs. 4–6 in Lein 1978), yet I found only portions of Lein's published New Hampshire UE songs at other localities represented in Cornell's recordings. The characteristic three-note endings of Lein's UE-2 songs (Figs. 4, 5 of Lein) did occur in typical form in one Maryland song (Cornell Cut 22) and in one Saskatchewan song (Lein pers. comm.), and similar song elements (though not at the song ending) did occur in both Minnesota and Tennessee (Cornell Cuts 35 and 42–43).

In 17 additional UE song types recorded from four neighboring males near Millbrook, I again found no entire songs similar to Lein's UE songs from New Hampshire. The adjacent males in New York, however, did share some identical song types with one another (Fig. 6). Some song components may recur throughout the range; as in the Blue-winged Warbler, though, the data reveal that the UE songs vary more between localities than do the AE songs.

Discussion

The functions of these different song types must be clarified before the biological significance of differences in geographical variation can be understood. Members of

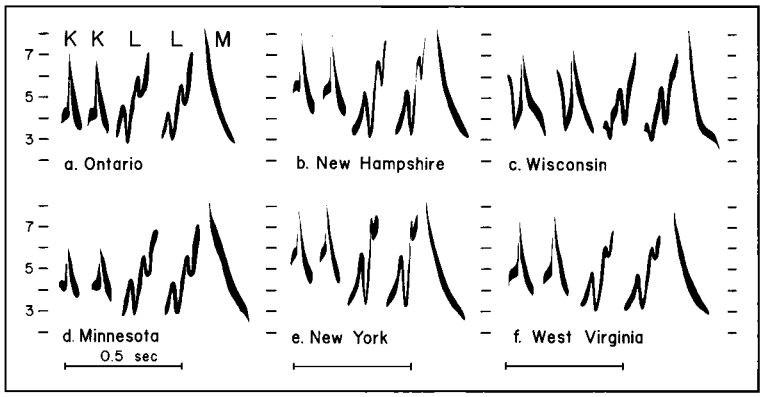

Fig. 5. Geographical variation in Accented Ending Type 2 ("see" variant) songs of the Chestnut-sided Warbler. Notes K, L, and M are labelled in 5a. Again, several K notes were deleted to abbreviate the displays. Exact location (and source) of songs is as follows: a. Kirkland Lake (Cornell Cut 39 = CC39); b. South Lyndeboro (M. R. Lein); c. Clam Lake (CC32); d. Ely (CC34); e. Millbrook; and f. Cranberry Glades (CC17).

several warbler genera, including *Dendroica, Vermivora, Parula, Mniotilta,* and *Setophaga,* sing at least two different song types, which appear to be used in different circumstances, but the functional interpretation of these song types is uncertain (e.g. see debate in Lein 1972, 1978). One item, however, is clear: during intraspecific territorial clashes with other males (i.e. when motivation appears highly agonistic), the song type selected by males is highly predictable. In the Chestnut-sided Warbler, Yellow Warbler (*Dendroica petechia*), and American Redstart (*Setophaga ruticilla*), the song types selected are the "unaccented songs" (Ficken and Ficken 1962, 1965; Morse 1966; Lein 1978) In the Blue-winged Warbler, males sing Type II songs (Ficken and Ficken 1967). Prairie Warblers (*Dendroica discolor*) sing "type B" songs (Nolan 1978), while Blackburnian (*Dendroica fusca*) and Black-throated Green (*Dendroica virens*) warblers sing their "type A" songs (Morse 1967, 1970). Furthermore, in the latter species, isolated territorial males that do not encounter neighboring males rarely used their "type A" songs (Morse 1970). Other warbler species are less well studied, but this same pattern undoubtedly exists for many of them as well [e.g. Yellow-rumped Warbler (*Dendroica coronata*) and Black-and-white Warbler (*Mniotilta varia*); Lein, pers. comm.].

One other fact appears consistent among the warbler species: when males first arrive on territory and are unmated in the early spring, they consistently sing their "other" song type (Accented, Type I, etc.), and the usage of this "other" song type often drops dramatically when nesting begins. Thus, unmated Chestnut-sided Warblers sang an average of 247 songs/h during a typical morning, and 225 (91%) had the "Accented Ending"; during courtship, singing dropped to 207 songs/h, but only 141 (68%) were Accented. During this same period, one particular Accented Ending song, the AE-2, dropped even more dramatically, from 152 to 45 songs/h (61 to 21% of the total song output; Lein 1978). In the Yellow Warbler, unmated males in populations of low density spent 96% of their singing time using accented songs, while this dropped to 47% during pair formation, nest building, and egg laying; percentages for males in dense populations dropped similarly, from 44 to 14% (Morse

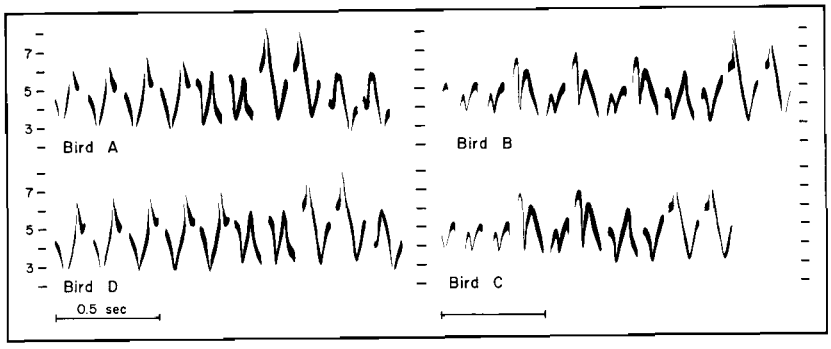

Fig. 6. Unaccented songs of four Chestnut-sided Warbler males at the Rockefeller University Field Research Center, Millbrook, New York. Neighboring males have similar songs: songs of Birds A and D match, as do the songs of Birds B and C.

1966). In dense populations of the Black-throated Green Warbler, the usage of the "other" song type (here "B") "dropped precipitiously" after "apparent pairing" (Morse 1970). In the Prairie Warbler, usage of the "other" song types ("A" here) dropped from 97% to 65% when nest building began (Nolan 1978). Observations for the Blue-winged Warbler, American Redstart, and several other species appear similar (Ficken and Ficken 1962, 1967).

Lein (1978) argued that all song types in the Chestnut-sided Warbler served primarily in territorial advertisement and defense and that any role that songs played in "initial attraction of the female" or coordination of male and female activities was merely "supplemental." Close proximity to the female appeared to inhibit singing, and the major song types could be arranged in a series according to their use in a variety of situations regarding territorial functions (e.g. dawn or dusk singing, central or peripheral position on territory, proximity to other males, switching between song types, and probability of agonistic encounters). Lein did observe a three-fold decline in usage of AE-2 songs during pair formation, but believed ". . . this change is related to territorial establishment rather than to pair formation . . . ." Nolan (1978), however, discovered that male Prairie Warblers revert to their early season song types if they lose a mate during mid-season; in addition, unmated males fighting at a territorial boundary but in the presence of an unattached female never (10 out of 10 cases) sang the usual song for male/male encounters, but rather sang the "A" (= mate attraction?) songs. There are some striking differences in the overall singing behaviors of Prairie and Chestnut-sided warblers, but Nolan's observations suggest that Lein's data for the Chestnut-sided Warbler should be supplemented with further observational or perhaps experimental evidence.

The proportions of the different song types used by a territorial male appear to indicate whether or not he is paired, and it would be surprising if potential mates did not use such information. Furthermore, although Morse (e.g. 1970) and Lein (1978) debate whether certain song types are used "chiefly in the presence of conspecific females," the mate actually need only be within earshot in order for the songs to function intersexually.

If these different song types do function primarily inter- or intrasexually, then the significance of the differences in geographical variation between the Accented and Unaccented songs of the Chestnut-sided Warbler and the Type I and Type II songs

of the Blue-winged Warbler could be related to mate selection and territorial defense, respectively. Those songs used in the center of the territory, most frequently by unmated males and possibly intersexually, are remarkably stereotyped from male to male over the geographical range of the species. Given the species distinctiveness of these song types in the Chestnut-sided Warblers [as well as in Yellow Warblers (Morse 1966)] and both Blue-winged and Golden-winged (*Vermivora chrysoptera*) warblers (Gill and Murray 1972), the AE songs could serve as classical ethological isolating mechanisms. On the other hand, those songs used primarily intrasexually on the territorial boundary change more from one population to the next. The fact that only those songs used in the more intense male/male interactions seem to vary significantly from population to population suggests that local "dialects" in these warblers and perhaps other songbirds may be a consequence of intra- rather than intersexual selection. Use of these locally distinctive song types by male songbirds often takes the form of countersinging with matching song types [for most extreme examples, see Verner 1975, Kroodsma 1979; Chestnut-sided Warblers may not countersing with like songs, though (Lein, pers. comm.)]. Vocal learning, together with limited dispersal from the site of learning, insures that interacting males will possess like vocal signals. Females, on the other hand, tend to be more mobile (Dhondt and Huble 1968, Greenwood 1980), and greater stereotypy in vocal signals used in mate selection might be predicted. Unfortunately, nothing is known of dispersal of the sexes in any of these warbler species.

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