

SONG-TYPE DISTRIBUTION IN A POPULATION OF KENTUCKY WARBLERS

NELLIE TSIPOURA AND EUGENE S. MORTON¹

ABSTRACT.—Male Kentucky Warblers (*Oporornis formosus*) have a single, individually distinctive song type. The songs of 29 males breeding at a single location were placed into 6 categories based upon similarity of song types. Based upon these categories, song types were randomly distributed in the breeding population; there was no tendency for neighboring males to have more similar songs than nonneighbors. Song types remained unchanged between years in three males that returned to breed. The songs in our single population were nearly as variable as a sample of songs derived from throughout the breeding range, indicating that Kentucky Warblers do not exhibit song dialects. Received 8 Jan. 1987, accepted 13 July 1987.

Like other *Oporornis* species, male Kentucky Warblers (*Oporornis formosus*) sing a single, relatively simple song type. The song consists of four to eight repetitions of identical syllables, each syllable containing several elements. Members of the genera *Seiurus*, *Geothlypis*, and *Basileuterus* also sing a single song type (Morton and Young 1986). Kentucky Warblers have the ability to change the energy distribution within their song and to raise or lower the frequencies encompassed by the song. The elements that comprise their song syllables, however, retain their shape and sequence. Thus, each male's song type, as defined spectrographically, remains the same but can be altered to match the energy distribution in songs of rivals (Morton and Young 1986). This ability may replace any advantage—as is common in species with multisong repertoires (Krebs and Kroodsma 1980)—for neighbors to copy each other's song types. With this in mind, we asked if neighboring males shared more similar song types than did nonneighbors. We also compared song-type variation in a single breeding population with a sample from throughout the breeding range. We asked if the song types that occurred in our study population represented a distinctive subset of the song types recorded from throughout the species' range. The results are discussed in relation to factors that may select for single song-type repertoires.

STUDY AREA AND METHODS

We studied warblers at the Conservation and Research Center of the National Zoological Park near Front Royal, Virginia, in 1985 and 1986. The area consists of mature and second-growth hardwoods dominated by tuliptree (*Liriodendron tulipifera*), oaks (*Quercus* spp.),

¹ National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.

and black locust (*Robinia pseudoacacia*). The breeding population at the Center consisted of 37 males in 1985 and 33 males in 1986. All males were color banded and their territories were mapped from late May through July of both years. A total sample of the songs of 29 males was tape recorded at intervals throughout the breeding seasons of the two years.

The songs of 19 additional Kentucky Warblers were obtained from the Library of Natural Sounds, Laboratory of Ornithology, Cornell University. The Cornell recordings were made in Georgia (4), Mississippi (1), Louisiana (2), Tennessee (2), West Virginia (5), Pennsylvania (1), Maryland (1), Ohio (1), and New York (2), and they encompass nearly the entire breeding range of the species.

Songs were analyzed with a Kay Elemetrics model 7800 Digital Sona-graph. Although each male's song was distinctive (see Morton and Young 1986), we could group songs into categories based upon the arrangement of elements within a song's single syllable (Table 1) (Fig. 1). This method is similar to that used by Marler and Pickert (1984) to categorize Swamp Sparrow (*Melospiza georgiana*) song syllables. Swamp Sparrow songs, like those of Kentucky Warblers, consist of the repetition of a single syllable. The criteria (Table 1) were chosen because the arrangement of elements within syllables is constant for an individual male Kentucky Warbler. Other possible components, such as the frequency range and energy distribution of an individual's song elements, were not used because they vary (see above).

We used seven categories to assess song similarity among neighboring males and to compare the Front Royal sample with songs from throughout the breeding range. For the neighbor comparison, we chose males with only a single neighbor or, where a series of territories occurred linearly along a stream valley, we compared each male with its closest neighbor. In this way, each individual was represented only once in the neighboring pair comparison.

We used a Kolmogorov-Smirnov one-sample test (Siegel 1956) to test the hypothesis that the song categories were nonrandomly distributed at the study site. Finally, the songs of three birds recorded both study years were examined for consistency between years.

RESULTS

The song of the Kentucky Warbler consists of four to eight repetitions of identical syllables composed of several elements. Each individual sang one song which was distinctive for each bird and remained unchanged throughout the breeding season (Morton and Young 1986, pers. obs.). Although all songs differed at least slightly in frequency and temporal pattern, we recognized six categories of similarly structured songs in the Front Royal population (Fig. 1). The categories were labeled A to F in order of decreasing frequency of occurrence (Table 1). The most common song category, A, was used by 13 of the 29 individuals (45%).

We recorded 19 pairs of males whose territories abutted. Numbers of neighboring pairs having the possible song-category combinations, as well as the predicted numbers for each combination, assuming random distribution, are presented in Table 2. The songs of 25 individuals were used to estimate the expected song-category distribution among neighbors. The remaining 4 birds were on isolated territories and had no immediate neighbors. The Kolmogorov-Smirnov test shows that the distribution of songs does not differ significantly from random ($P > 0.05$). Fourteen of

TABLE 1
SONG CATEGORIES AND NUMBERS OF SONGS IN EACH CATEGORY FROM THE FRONT ROYAL SITE AND THE LIBRARY OF NATURAL SOUNDS

Song category	No. of Front Royal birds in category (%)	No. of Library of Natural Sounds birds in category (%)
A. Initial low frequency chevron followed by two downslurs then a single higher upslur	13 (45)	8 (42)
B. Two cycles of connected upslurs and downslurs followed by a single higher element	6 (21)	3 (16)
C. Initial low frequency chevron followed by two cycles of connected upslurs and downslurs with a final low frequency upslur	4 (14)	5 (26)
D. Three cycles of connecting upslurs and downslurs with or without a final higher single element	3 (10)	1 (5)
E. Similar to A but with three downslurs instead of two	2 (7)	0 (0)
F. Similar to B but with a separated downslur after the two cycles of connected upslurs and downslurs	1 (3)	0 (0)
G. Two songs from the Library of Natural Sounds that did not fit into the song-type categories from Front Royal—both ended in high frequency connected up- and downslurs forming a "W" shape	0 (0)	2 (11)

the 19 neighboring pairs included one bird singing an A song (Table 2); however, only three pairs of neighboring males both used A songs. Furthermore, only 4 of the neighboring pairs of males used songs in the same category. We conclude that there is no clustering of more similar songs among neighboring males.

Songs of three individuals were recorded in both study years. All kept the same song type in both years even though they had new neighbors, with different songs, in the second year. They also occupied the same territories in both years.

Is the song-type variety in the Front Royal sample representative of Kentucky Warbler song in other areas of the breeding range? The 19 songs obtained from the Cornell Library of Natural Sounds (see METHODS for their geographical distribution) fit into 4 of the 6 song categories found at Front Royal (Table 1). Two songs, which did not "fit" into our Front Royal categories, were sufficiently similar to be placed into an additional category (G in Table 1 and Fig. 1). One G category song was obtained in Maryland and the other in Georgia. As at Front Royal, the A category was most common in the Cornell sample (8 songs, 42%). Therefore, it appears that the Kentucky Warbler songs in a single locality (e.g., Front

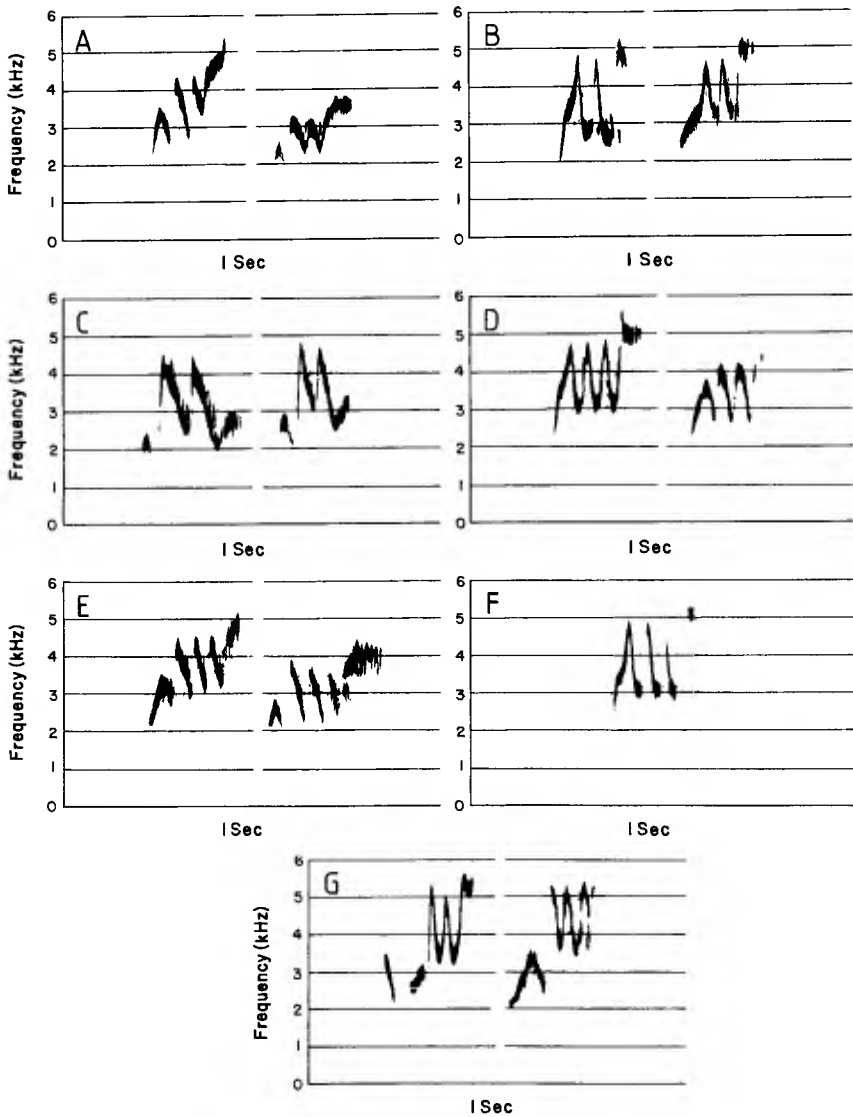


FIG. 1. Wide band spectrograms of individual syllables from Kentucky Warbler songs illustrating the 7 categories identified (see Table 1). A-F are from the Front Royal study site, G shows one from Maryland (right) and one from Georgia (left).

TABLE 2
SONG CATEGORIES OF NEIGHBORING KENTUCKY WARBLERS

Song categories of neighboring pairs ^a	No. in Front Royal population (%)	No. predicted ^b (%)
A-A	3 (16)	3.5 (18)
A-B	5 (26)	4.2 (22)
A-C	2 (11)	2.1 (11)
A-D	1 (5)	1.3 (7)
A-E	3 (16)	2.1 (11)
B-B	1 (5)	1.1 (5)
B-D	1 (5)	0.8 (4)
B-E	1 (5)	1.1 (6)
C-D	1 (5)	0.4 (2)
C-E	1 (5)	0.6 (3)

^a The songs of 25 individuals were used in estimating the expected frequency of songs among neighboring pairs.

^b Song category pairs unrepresented at the Front Royal study site are not listed.

Royal) are as diverse as a sample from throughout the breeding range. We conclude that Kentucky Warblers differ from dialect species in that song-type similarity among neighboring males is low in any one locality and perhaps generally throughout the breeding range.

DISCUSSION

Kentucky Warbler song types among neighboring birds are diverse, given the restricted number of categories into which they can, apparently, be placed. Unlike other warblers with single song types (see Morton and Young 1986), the Kentucky has no "attenuated" songs given during territorial clashes. Lein's (1981) description of the Ovenbird's (*Seiurus aurocapillus*) song is similar to our finding for the Kentucky Warbler except that the Ovenbird uses attenuated songs in border clashes with intruders. As in the Kentucky Warbler, the Ovenbird has a single song type with great variation among the songs of neighboring males (Lein 1981). Whether Ovenbird songs can be placed into higher categories of song similarity as we have attempted to do for the Kentucky Warbler is unknown. In species with dialects, songs are copied from others. In contrast, the structural variation in songs of nondialect species such as the Kentucky Warbler and Ovenbird is apparently constrained by the limits of species specificity (Falls 1963; Lemon et al. 1983). Determining what these limits are, in nondialect species where selection does not favor song similarity among neighbors (selection might be favoring individuals with song *dissimilarity* to neighbors), needs further study as song function in nondialect, single

song species may generate unique questions. For example, they may have more innate control of song element ontogeny as suggested for the contrast between song acquisition in Swamp Sparrows and Song Sparrows (*Melospiza melodia*) (Marler and Pickert 1984).

The seven categories we determined may not be relevant biologically to a discussion of Kentucky Warbler songs. The number of categories we determined is not crucial for our conclusions. We should mention, however, that only the Front Royal songs were used to set up the six initial categories. Even then, the Cornell songs, obtained from throughout the species' breeding range, fit into our categories relatively well. Moreover, if further research shows that Kentucky Warbler song variation *is* limited to seven biologically relevant categories, then perhaps this number represents the limit of song diversity needed to insure, on average, that an individual male will have a song dissimilar to those he may find as neighbors. This limit may reflect the balance between selection favoring both species specificity and individuality as found in the Kentucky Warbler. We do not suggest that birds with dissimilar songs actively "choose" each other as neighbors, only that random choice may result in neighbors having dissimilar songs if the choice is from among seven categories.

The result of song dissimilarity on vocal interactions between males is also of interest. Individuals of several species have been shown to rely on memorized songs to estimate their distance from the singer (reviewed in Morton 1986; see also Margoliash 1986 for neurophysiological evidence). Distance is estimated by comparing degradation in the perceived song with the same song type in memory (termed "ranging," Morton 1982). The species studied for their ranging ability, however, had repertoires of several to many song types with many held in common between territorial neighbors. In contrast, species such as the Kentucky Warbler, singing single, individually distinctive songs, should afford listeners inaccurate cues as to the singer's distance from them. This is due to the presumed inability of birds to use degradation in songs for distance estimation unless they have the perceived song also stored in memory (Morton 1982, 1986). A song that is not in a neighbor's memory might result in an incorrect estimation of the distance of a nonintruding rival and a response to the song as though the singer had intruded. For example, Carolina Wrens (*Thryothorus ludovicianus*) respond more vigorously to songs not in memory than to songs in memory when both are played back from outside of the males' territorial boundaries (Shy and Morton 1986). Great Tits (*Parus major*) respond vigorously to degraded songs played back within their territories only if they are unfamiliar with them (McGregor and Krebs 1984). The experimental males respond as though their territories or mates are threatened even though they are not. When

singing and foraging cannot occur at the same time (e.g., Lein 1981), valuable energy would be wasted through such responses. Thus any differences in territorial quality, particularly the food available on it over and above maintenance levels (e.g., providing energy during time used for singing and territorial defense), can be accentuated if territorial neighbors are forced to move in defense against a "sham" territorial intruder they detect through hearing song (Morton 1986).

Perhaps Kentucky Warblers, because they have but a single, distinctive song per male, have no song in memory that is precisely the same as that sung by any of their rivals. If so, following the logic of the ranging hypothesis (Morton 1986), this suggests that rivals are not able to base distance estimation on song degradation. Because of this, we predict that Kentucky Warbler songs should not be acoustically adapted to avoid degradation as, for example, was found in the Carolina Wren (Gish and Morton 1981). If degradation cannot be perceived, then singers need not develop songs resistant to degradation. On the other hand, Kentucky Warblers have the ability to modify the energy allocation and frequency in their song when responding to a particular individual rival (Morton and Young 1986). This suggests that Kentucky Warblers may have the benefit of a distinctive, unrangeable song, that disrupts listeners and provokes them into wasting energy. They may also benefit by the ability to modify the energy spectrum of their single song to match that of any rival's song. Therefore, their single song can function in the same way that multiple song repertoires may function in other species by allowing for both song matching, for threatening, and song individuality, for disrupting, in intermale competition.

An alternative hypothesis, that individuality in songs of these species confers easy "neighbor recognition" (Weeden and Falls 1959, Lein 1981), might also contribute to the restriction of song repertoire size to one and to intramale variability in song type. Further study of the contribution of specific song structures shared between neighbors, in addition to categorizing them as simply "neighbor" or "stranger," is needed (Shy and Morton 1986).

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LITERATURE CITED

- FALLS, J. B. 1963. Properties of bird song eliciting responses from territorial birds. Proc. Int. Ornithol. Congr. 13:259-271.
- GISH, S. L. AND E. S. MORTON. 1981. Structural adaptations to local habitat acoustics in Carolina Wren songs. Z. Tierpsychol. 56:74-84.
- KREBS, J. R. AND D. E. KROODSMA. 1980. Repertoires and geographic variation in bird song. Pp. 143-177 in *Advances in the study of behavior* (J. S. Rosenblatt, R. A. Hinde, C. Beer, and M.-C. Busnell, eds.). Academic Press, New York, New York.
- LEIN, M. R. 1981. Display behavior of Ovenbirds (*Seiurus aurocapillus*) II. Song variation and singing behavior. Wilson Bull. 93:21-41.
- LEMON, R. E., J. STRUGER, AND M. J. LECHOWICZ. 1983. Song features as species discriminants in American warblers (Parulidae). Condor 85:308-322.
- MARGOLIASH, D. 1986. Preference for autogenous song by auditory neurons in a song system nucleus of the White-crowned Sparrow. J. Neurosci. 6:1643-1661.
- MARLER, P. AND R. PICKERT, 1984. Species-universal microstructure in the learned song of the Swamp Sparrow (*Melospiza georgiana*). Anim. Behav. 32:673-689.
- MCGREGOR, P. K. AND J. R. KREBS. 1984. Sound degradation as a distance cue in Great Tit (*Parus major*) song. Behav. Ecol. Sociobiol. 16:49-56.
- MORTON, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules. Pp. 182-212 in *Acoustic communication in birds, vol. 1* (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York, New York.
- . 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99:65-86.
- AND K. YOUNG. 1986. A previously undescribed method of song matching in a species with a single song "type", the Kentucky Warbler *Oporornis formosus*. Ethology 73:334-342.
- SHY, E. AND E. S. MORTON. 1986. The role of distance, familiarity, and time of day in Carolina Wrens responses to conspecific songs. Behav. Ecol. Sociobiol. 19:393-400.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York.
- WEEDEN, J. S. AND R. B. FALLS. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343-351.

**CENTENNIAL MEETING IN PHILADELPHIA, PENNSYLVANIA,
8-12 JUNE, 1988**

The Wilson Ornithological Society will hold its Centennial Meeting at Rosemont College in suburban Philadelphia, Pennsylvania, from 8 to 12 June 1988. Frank B. Gill is chair of the Committee on Arrangements. Jerome A. Jackson chairs the Centennial Committee, and Richard C. Banks is the chair of the Scientific Program Committee. Highlights of Centennial Day, Friday, June 10, include festivities scheduled at the Academy of Natural Sciences of Philadelphia. Featured are a symposium on Paridae with presentations by international researchers, historical talks, an exhibit, and a gala reception. Wilson Society memorabilia assembled by the Centennial Committee will be on display at Rosemont College throughout the meetings. Registration forms for the meeting should be returned to the Academy of Natural Sciences of Philadelphia by 1 May 1988. Further information can be obtained by contacting Dawn F. Coughlan, Academy of Natural Sciences of Philadelphia, 19th Street and The Parkway, Philadelphia, PA 19103. Plan now to attend this historic event.