

## SONG TYPES, REPERTOIRES AND SONG VARIABILITY IN A POPULATION OF CHESTNUT-SIDED WARBLERS<sup>1</sup>

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**Abstract.** To help assess the function of multiple song types in the singing of the Chestnut-sided Warbler (*Dendroica pensylvanica*), a species with two song categories, I analyzed song diversity and variability in a Massachusetts population. Individual song repertoires contained up to 12 different song types (median 6 or 7), and included both accented-ending (AE) and unaccented-ending (UE) songs. AE song types were few, and were highly stereotyped both within and between individuals. In contrast, UE songs were variable, with many different types present in the population, and with different renditions of a type showing a larger range of variation. The distinction between constrained, stereotyped AE singing and flexible, variable UE singing suggests that song forms in the two song categories are specialized for different uses. AE songs are suited to comparative assessment of singers, long-range communication, or messages in which reduced ambiguity is crucial. UE songs may be specialized for communication over short distances or during interactions in which motivations and messages change rapidly. Chestnut-sided Warblers use most of the songs in their repertoires only infrequently, and no set of song types is shared by all members of a population. Consequently, the multiple song types within each song category are probably not connected to functions in which individuals benefit by displaying repertoire size, or in which particular song types encode special messages. Repertoire function instead probably involves a communication function for switches between commonly- and uncommonly-used song types.

**Key words:** *Song; repertoire; Dendroica pensylvanica; warbler; Parulinae.*

### INTRODUCTION

Although the phenomenon of song repertoires is widespread among passerine birds, the use of multiple song forms by individuals does not seem to have a single, universal function (Harper 1991). The most commonly invoked general explanation for song repertoires is that larger repertoires increase mating success (e.g., Hiebert et al. 1989, Searcy 1992, Horn et al. 1993), but in some cases repertoire function is related not to the number of song types, but to the differences among them. In particular, the different song forms in a repertoire can be used for different communicative purposes. The song repertoires of wood-warblers (Parulinae) appear to function, at least in part, in this manner. Many paruline species have repertoires that are partitioned into two distinct groups, first category and second category songs (Spector 1992), that are used in different social and environmental circumstances (Ficken and Ficken 1962, 1965, 1967; Morse 1966, 1967; Nolan 1978; MacNally and Lemon 1985; Lemon et al. 1987; Staicer 1989, 1991; Highsmith 1989a,

1989b; Spector 1991). The two kinds of songs also differ in the degree to which they vary geographically (Kroodsma 1981, Highsmith 1989b) and in some aspects of ontogenetic development (Kroodsma 1988, Spector et al. 1989, Byers and Kroodsma 1992, Lemon et al. 1994). Most investigators have concluded that the differences between the two song categories reflect differences in function (but see Lein 1972, 1978).

The hypothesis that the two wood-warbler song categories have different functions does not, however, fully account for the variability of song form found in these species. In particular, each of the two song categories of many paruline species is itself composed of multiple song forms. The song repertoire of an individual Chestnut-sided Warbler (*Dendroica pensylvanica*), for example, is partitioned into first category (accented-ending or AE) and second category (unaccented-ending or UE) songs (Ficken and Ficken 1962, 1965), but each male uses several different song types within each category (Lein 1978).

The function of this additional level of song diversity in Chestnut-sided Warblers remains unclear, because prior studies have focused on categories or groups of song types, rather than on the presence of multiple song types within the

<sup>1</sup> Received 15 August 1994. Accepted 14 November 1994.

categories. Ficken and Ficken (1962, 1965) originally described the species' two main song categories (accented-ending and unaccented-ending), and concluded from their observations that AE songs are more attractive to females while UE songs reflect an elevated escape tendency in the singer. Kroodsma et al. (1989) also emphasized the functional differences between the AE and UE categories, and presented experimental and observational evidence that accented-ending songs "fulfill a critical intersexual function" (p. 455). Lein (1978) proposed that the two main song categories could be further subdivided into five different groups, such that the repertoire of each male contained songs from each group. He hypothesized that the five song groups formed a graded series in which the different groups were "indicative of different internal states or 'moods'" (p. 1282).

Because of their focus on song categories, these earlier studies did not analyze those aspects of song variability that must be known in order to make inferences about the role of within-category song repertoires. I here seek to provide some of the necessary information by characterizing the diversity of different song types in a population, the distribution of different song types among individuals' repertoires, and the frequency with which males use the different song types in their repertoires. To take advantage of the potential relationship between signal structure and function, I also characterize variability of song form within each category. Repertoires may play different roles within each song category, and identification of shared features of song variability and form within each category should provide clues to any such differences. An important byproduct of these analyses is compilation of a record of local song variation that can serve as baseline data for a study of cultural evolution of song form.

## METHODS

My study site was located in the Savoy State Forest, Town of Florida, Berkshire County, Massachusetts. Most recording took place along two more or less parallel power line rights-of-way that traversed heavily forested, rolling hills. These power line "cuts" averaged about 30 m in width, and effectively formed corridors of low shrubby habitat, suitable for Chestnut-sided Warbler breeding territories, within the surrounding deciduous forest. Vegetation in the cuts consisted

largely of meadowsweet (*Spiraea alba*), steeplebush (*Spiraea tomentosa*), brambles (*Rubus* sp.), northern arrowwood (*Viburnum recognitum*), and other shrubs, with some areas dominated by ferns and other herbaceous growth. Saplings of tree species from the surrounding forest (e.g., *Betula*, *Prunus* and *Acer* sp.) were interspersed. Birds were sampled along a 0.9 km long section of the southernmost of the two cuts (hereafter referred to as cut 1) and along a 1.4 km section of the northern cut (cut 2). The two cuts were separated by about 500 m.

During the breeding seasons of 1988, 1989, and 1990, I recorded the songs of male Chestnut-sided Warblers on cassette tapes (with a Sony TCM-5000 or Marantz PMD recorder and a Sennheiser ME88 microphone) or on open reel tapes (with a Nagra IV-S recorder and Sennheiser MKH106 microphone mounted on a 60 cm parabolic reflector). The recording period began each year in early to mid-May with the arrival of returning migrants and continued until mid-July, by which time singing had declined to very low levels. Recordings were made six days per week until roughly the end of June, and on three days per week thereafter. On all days, recording sessions began before sunrise and included the first songs of the day in the sampled area.

I began each sampling day by stationing myself, before the onset of singing, on the territory of a resident male. When singing began, I usually recorded the resident bird for 5–20 min. I then walked along the cut, stopping to record a sample of similar length from each singing bird that I encountered. This sampling pattern was continued, walking back and forth within that day's designated sampling area, for 5 to 7 hr each day. On occasion, samples of up to 40 min in length were taken.

For sampling and analysis purposes, individual males were designated as primary, secondary, or peripheral. Primary males were sampled on at least one of every three sampling days. Sampling on most days was thus restricted to a primary area in cut 1, and the males in this area were sampled two or three times on each sampling day. (Recordings of a particular bird were operationally designated as a new sample if more than 30 min had elapsed since the last recorded song from that bird.) I systematically varied my starting point in this area, so that each primary male's total sample would include songs recorded in all portions of the sampling day.

TABLE 1. Summary of sampling intensity during a study of Chestnut-sided Warbler singing in western Massachusetts from 1988–1990. For each year, the number of individual Chestnut-sided Warblers whose songs were recorded, the number of songs recorded, and the number of discrete sampling periods are shown. Each male was designated as primary, secondary, or peripheral, according to how frequently he was sampled.

	<i>n</i> Males	Number of songs				Number of samples			
		Minimum	Median	Maximum	Total	Minimum	Median	Maximum	Total
Year 1 primary	14	688	1,326	3,360	22,857	25	47	107	828
Year 1 secondary	20	57	103	328	2,300	6	9	18	228
Year 1 peripheral	13	10	42	64	655	1	2	3	28
Year 1 total	47				25,812				1,084
Year 2 primary	18	454	710	1,971	15,518	16	33	68	624
Year 2 secondary	24	49	11	364	2,906	6	8	17	198
Year 2 peripheral	11	5	33	58	477	1	1	3	16
Year 2 total	53				18,901				838
Year 3 primary	14	373	1,092	2,381	15,181	16	35	74	558
Year 3 secondary	13	31	64	620	1,612	6	7	20	91
Year 3 peripheral	15	8	45	188	829	1	2	4	37
Year 3 total	42				17,622				670

Secondary males were sampled about once a week. Once or twice each week, I sampled songs in the secondary area of cut 1 or in cut 2. Each secondary sampling day began at a different territory. Secondary males were typically sampled only once or twice during a sampling day.

Peripheral males were sampled only once or twice. Birds in this category included those that arrived early in the breeding season but were unable to establish a territory in the study site, late-season “invaders” who attempted unsuccessfully to evict residents from their territories, and birds that were recorded on the periphery of the study area (i.e., in the surrounding woods) and whose status was therefore unknown.

All primary and most secondary males were marked for individual identity with colored leg bands and aluminum U.S. Fish and Wildlife Service bands. Peripheral birds, except early arrivals, were unmarked. Sample size varied among birds within each category (Table 1) due to the ad hoc nature of the sampling regime and variability among birds in arrival date and amount of time spent singing.

All recorded songs (over 62,000 songs from 120 different individual birds) were analyzed with a Kay Model 5500 real-time spectrum analyzer. The analyzer was set to display simultaneously narrow-band (256 point FFT, equivalent to 117 Hz bandwidth) and wide-band (100 point FFT, equivalent to 300 Hz bandwidth) sonagrams. The first analyzed occurrence of each song type of each individual was printed as hard copy. All

subsequent songs were compared to the printed sonagrams, and the song type was noted (at this time songs of a given bird were compared only to prints of songs sung by that individual). As analysis proceeded, multiple renditions of each song type of each subject were printed as hard copy, so that a “portfolio” consisting of three or four printed renditions of each identified song type was developed for each primary and secondary bird in each year.

After all recordings were analyzed, all printed sonagrams were photocopied so that identifying labels could be replaced with coded ones. The copies were pooled into a collection of all songs from all years, and I sorted the pooled collection into groups of the same song type. Songs were assigned to the same type if the form and sequence of individual song elements were the same. Assignment to song type was not affected by the number of repetitions of initial introductory elements or by whether or not the termination sequence was complete (see RESULTS below for definitions of introductory and termination elements).

A naive observer, working with a somewhat reduced song set consisting of only one or two renditions of each song type in each male’s repertoire, also sorted the sonagrams into song types. The results of this second classification were similar to my original one. Only 33 of 660 songs were classified differently by the naive observer, and all differences were due to his splitting some of my types into two types. I regarded this high

level of agreement as a reasonable confirmation of my initial assignment of songs to song types, and gave each type a unique identifying number.

To assess the degree to which the AE and UE song categories and the different song types within each category were acoustically distinct, I examined song forms at a level finer than that of the whole song. In particular, I classified the individual song elements (defined operationally as discrete sounds represented by continuous traces on a spectrograph) that compose songs. These elements were cut from sonagrams and then sorted, again by visual inspection, into groups of similar elements. Although my classification of song elements was not verified by a naive observer, I was "blind" with respect to the source of the elements, and believe that I maintained a level of internal consistency that was adequate for the comparisons of relative variability that I made in this phase of the study. My classification scheme recognized two levels of similarity among song elements (Fig. 1). Elements of the same basic form or shape were assigned to the same element type and given a numeric designation. To help assess the degree of variability within each element type, I also identified different variants of a type. Within a type, elements that were closely matched in terms of frequency range, elapsed time, and fine structure were judged to be of the same variant, and given an alphabetic designation. Each element thus had an identifier of the form  $Xa$  (where  $X$  is a number and  $a$  is a letter) that showed its type and also its membership in a particular subset (variant) of especially similar members of that type.

## RESULTS

### SONG DIVERSITY AND VARIABILITY

*Number of different types.* UE songs were far more diverse and less standardized than AE songs. I identified 145 different UE song types in the sample, of which only 29 were recorded in more than one year. Although the number of different UE song types in the population was large, many types did share features in common. In particular, two different sequences of terminating elements occurred in a number of different UE song types (Fig. 2). Although these shared termination sequences (here designated sequence 1 and sequence 2) were widespread among UE songs, some UE song types lacked either termination sequence.

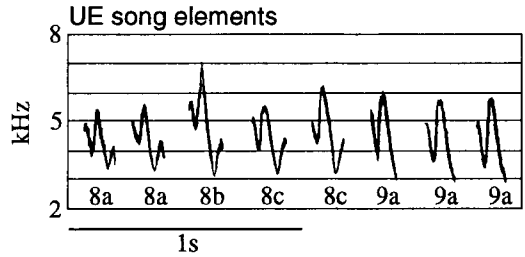


FIGURE 1. Examples of song element types 8 and 9, extracted from unaccented-ending Chestnut-sided Warbler songs to illustrate a two-level classification scheme for song elements. Each element shown was sung by a different bird at a study site in western Massachusetts between 1988 and 1990.

In contrast to the diversity and variability of UE song types, all 33,037 AE songs in the recorded sample fell into five, stereotyped song types in both my classification and that of the naive observer (Fig. 3). I subsequently re-classified one type (type AE-1a; songs D, E, and F in Fig. 3) as a stereotyped variant of type AE-1 (A, B, and C in Fig. 3). This re-classification was based on the apparent similarity of types AE-1 and AE-1a, which differed only in the absence of element type i2 from song type AE-1a. Behavioral observations also supported the re-classification. None of the several hundred Chestnut-sided Warblers that I have observed and recorded has sung both AE-1 and AE-1a songs. Every other possible combination of AE types occurred commonly in Chestnut-sided Warbler repertoires, so the absence of AE-1/1a combinations in the repertoires of individual males suggests that the two function as variants of a single type.

*Number and sequence of elements.* The sequence of elements in both AE and UE song types generally remained the same from rendition to rendition by a given bird. The two song categories differed, however, in the consistency with which the number of elements was maintained among different renditions. Within each of the AE types in a bird's repertoire, the number of repetitions of each element was consistent. Even among individuals across the study population as a whole, deviations from the song forms shown in Figure 3 were extremely rare, with the exception that the number of repetitions of elements in the introductory sequences was somewhat variable (range, 2–5 repetitions). Termination sequences were basically fixed across the sample. AE-1 terminations, for example, almost always

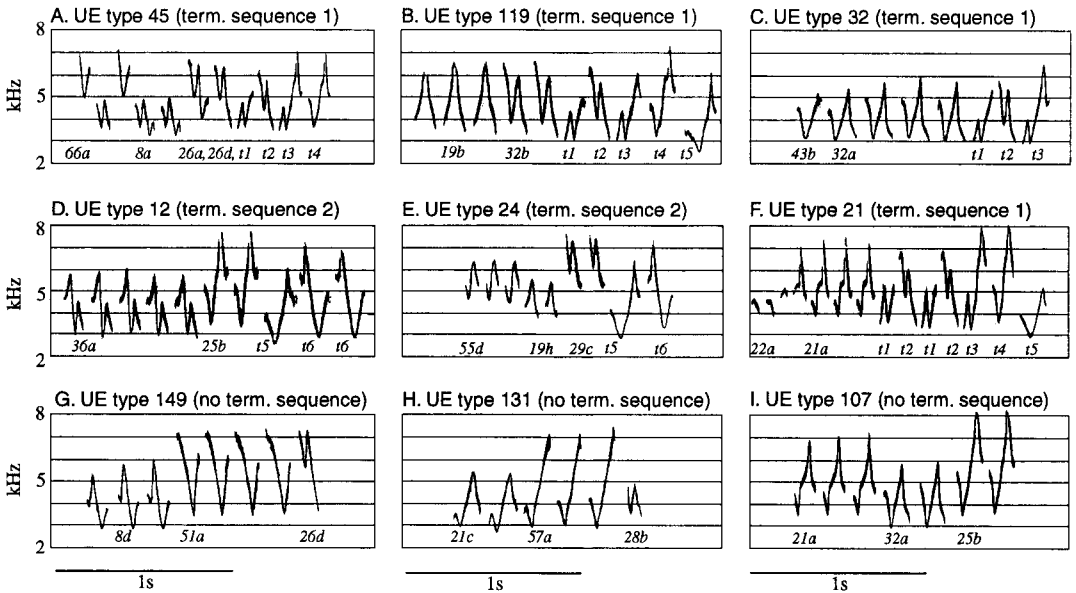


FIGURE 2. Examples of unaccented-ending (UE) songs, showing characteristics of the types found in the study population. Many song types (A, B, C, F) share a standardized termination sequence (elements labeled t1 through t5), and other types (D, E) share a different, shorter ending (elements t5 and t6). Some songs (G, H, I) lack either standard termination sequence. Note that the same introductory element variant can appear in different song types (e.g., element 32a in C and I). Each illustrated type was sung by a different bird.

consisted of two repetitions of at1, followed by one at2 and one at3, and terminations of the other AE types were similarly invariant. In contrast, the number of both introductory and termination elements within a UE type was variable, both within and between individuals. For example, the termination sequences of UE songs were very commonly shortened (Figs. 2A, C) or lengthened by extra repetitions of some elements (Fig. 2F).

*Stereotypy of individual elements.* AE and UE songs also diverged in the degree to which the form of individual elements was stereotyped, and in the flexibility with which element types were used to form songs. AE song elements were stereotyped (Fig. 3). Only 16 different element types were identified, and variability within each type was sufficiently small that no elements were classified as variants. AE song element types were also generally unique to the song type from which they were drawn. Element types i1, i2, at1, and at2 occurred only in AE-1 (or 1a) songs; i3 and at4 only in AE-2 songs; i4 and at5 only in AE-3 songs; and i5 and at6 only in AE-4 songs. The lone exception to the exclusive connection between particular element types and song types was the element at3, which was the final element

in all AE types. This rapid, downward frequency sweep of 4–4.5 kHz was unlike any other song element in the recorded sample.

Unlike AE song elements, almost all UE element types were variable enough that multiple variants were identified. Also unlike AE elements, UE element types were not tied to particular song types. A given UE introductory element type or variant could be a component of a number of different song types (Figs. 2C, I). Similarly, different UE song types shared the same terminating sequence; a termination sequence was not characteristic of a particular song type as was the case with AE songs.

#### SONG REPERTOIRES

More than one song type was recorded from every primary and secondary male in each year (Table 2). Song type repertoires ranged from 2 to 12 types (median 6 or 7 for primary males, 4 for secondary). The somewhat larger repertoires recorded from primary birds suggest that samples sizes for secondary birds were not sufficient to obtain full repertoires, but the relationship between sampling intensity and recorded repertoire sized was not a simple one.

The sizes of recorded repertoires of AE song

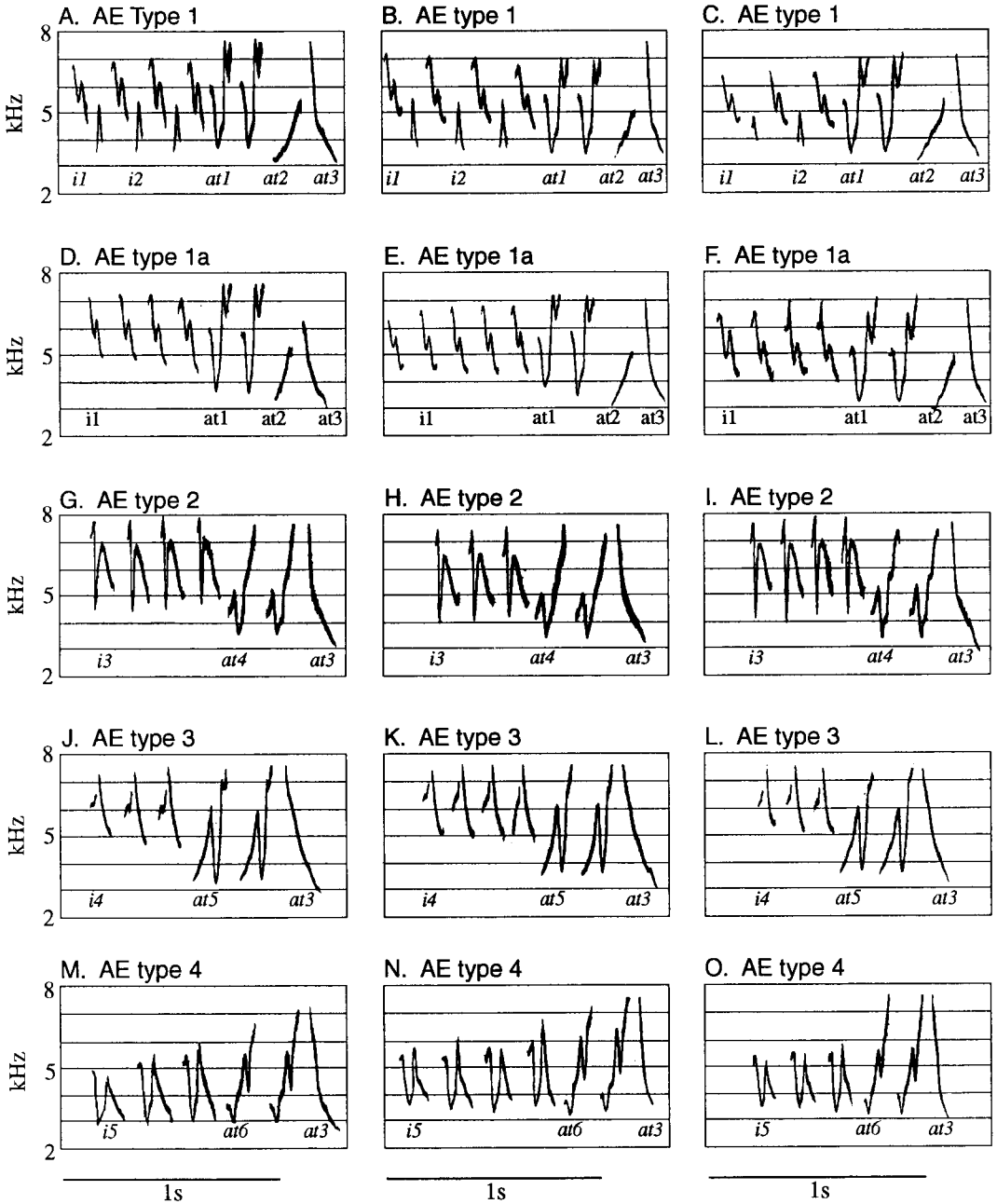


FIGURE 3. Examples of accented-ending songs (AE), selected to show the range of inter-individual variation within a type. Only the five forms shown were found among males in this study. Each illustrated song was sung by a different bird.

types did not appear to differ between primary and secondary males (Table 2), which suggests that estimation of the AE repertoires of secondary birds was not affected by the less intensive

sampling of those individuals. Further, no strong correlation was found between observed AE repertoire sizes and either number of recorded songs or the number of samples recorded from an in-

TABLE 2. Measured song type repertoires of 80 males. Twenty individuals were recorded in more than one year, and three of those birds were recorded in all three years of the study. Note that accented-ending (AE) repertoires were drawn from only four available song types, but that 145 different unaccented-ending (UE) types were available.

	n Males	AE repertoire			UE repertoire			Total repertoire		
		Minimum	Median	Maximum	Minimum	Median	Maximum	Minimum	Median	Maximum
Year 1 primary	14	1	1	4	2	5	7	3	7	10
Year 1 secondary	20	1	1	3	1	3	7	2	4	8
Year 2 primary	18	1	2	4	2	5	7	3	6	9
Year 2 secondary	24	1	2	4	1	2	6	2	4	8
Year 3 primary	14	1	2	3	1	4	10	2	6	12
Year 3 secondary	13	1	2	3	1	2	5	2	4	8

dividual (Table 3). It seems likely that sampling of both primary and secondary males yielded good estimates of AE repertoire size.

In contrast, observed UE song type repertoires were more influenced by sampling intensity. Although smaller sample sizes did not preclude large observed UE repertoires (maximum values of UE repertoire size were similar for primary and secondary males in two of three years), the typical secondary male clearly had a smaller recorded UE repertoire (Table 2). This difference is reflected in the moderately strong correlation between UE repertoire size and number of recorded songs and samples (Table 3). A larger sample size was apparently necessary for good estimation of UE repertoire sizes than for AE repertoires, and the UE repertoires of some secondary males in this study were probably underestimated.

Individual males did not sing all of the songs in their repertoires with the same frequency, because each bird tended to favor particular songs. Typically, one UE type and one AE type accounted for the bulk of an individual's singing. For example, in year 1 of the study, a single AE type accounted for 70% or more of AE singing for 31 of 34 primary and secondary males and,

for the other three birds, two AE types accounted for 70% or more of AE songs. Similarly, 23 of 31 birds that year used a single UE type for 70% or more of UE singing, seven birds used two types and one bird used three types to account for more than 70% of UE songs. Similar results were found in the other years of the study.

An obvious consequence of each bird's tendency to favor particular types is that the other types in a male's repertoire were sung infrequently or rarely (although song types used rarely by a particular individual were not necessarily rare in the population as a whole). For example, among 5,545 songs recorded from Bird 6 in 103 samples taken on 55 different dates over a two-year period, song type 14 was recorded only 14 times, all in a single run of songs, preceded and followed by long runs of this individual's most common UE song type. (Despite its rarity, the form of song type 14 was fixed, with each rendition in this sequence from Bird 6 substantially like the others.) The existence of such extremely rare songs in the repertoires of at least some individuals means that an observer could never be completely certain that all songs in a bird's repertoire had been recorded. In any given bout of singing, a bird was likely to use only a portion of his

TABLE 3. Pearson correlation coefficients and Bonferroni-adjusted significance levels (in parentheses) for correlations between repertoire size and sampling intensity, showing that measured UE repertoire sizes were dependent on sample size, but measured AE repertoire sizes were not. Primary and secondary males were included in this analysis.

	Number of songs recorded				Number of samples			
	Year 1	Year 2	Year 3	Pooled 3 yr	Year 1	Year 2	Year 3	Pooled 3 yr
AE repertoire size	0.261 (0.71)	0.111 (0.68)	0.253 (0.61)	0.27 (0.03)	0.261 (0.84)	0.036 (0.75)	0.166 (0.89)	0.25 (0.08)
UE repertoire size	0.559 (0.007)	0.646 (0.001)	0.620 (0.008)	0.60 (0.0001)	0.593 (0.003)	0.640 (0.001)	0.652 (0.004)	0.64 (0.0001)

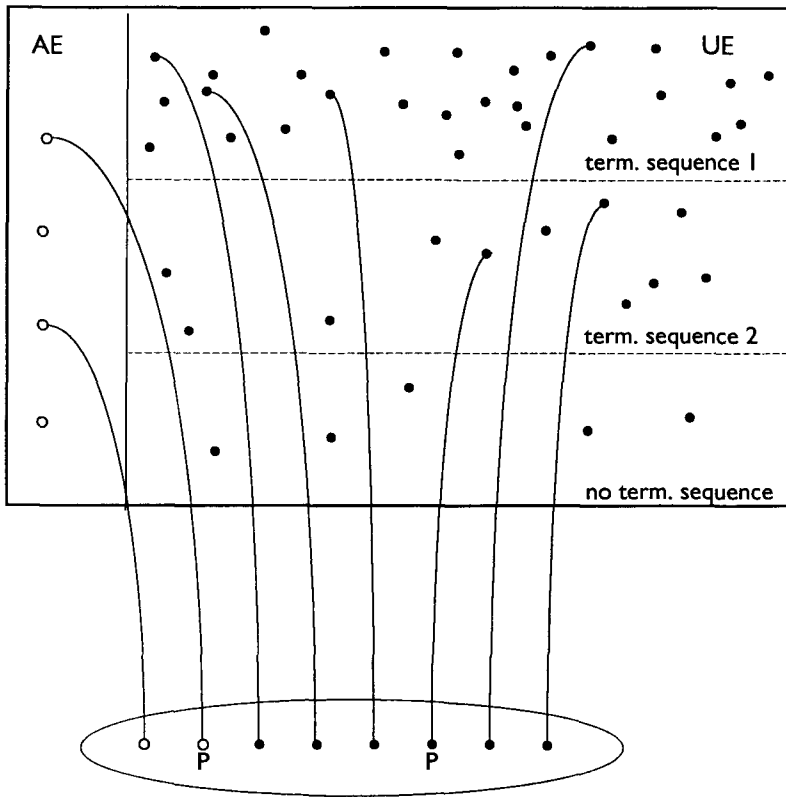


FIGURE 4. Schematic representation of the construction of Chestnut-sided Warbler song repertoires. Box at top represents the pool of local song types from which individual repertoires may be drawn. Open circles represent the few available AE types, filled circles the many available UE types, which fall into three broad groups based on the presence or absence of shared termination sequences (songs with termination sequence 1 are by far the most common). Individual repertoires, represented by the oval at the diagram's bottom, typically consist of one or two AE song types and four to seven UE song types. Each individual uses a few types (typically one AE type and one UE type) as his predominant songs (indicated by a "p" in the diagram).

repertoire, and UE song types in particular often remained "hidden" for long stretches.

Chestnut-sided Warbler song repertoires can be pictured as samples assembled from two distinct pools of available song types (Fig. 4). Individuals drew one or more AE types from a very small pool of stereotyped forms, and drew several UE types from a much larger pool of much more variable song forms (that nonetheless had some stereotyped aspects, such as termination sequences, in common). Not all UE types in the pool were equally likely to be included in repertoires; a few types were widespread among birds, but many other types were sung by only a single individual (Table 4). Most UE types in the pool contained termination sequence 1. Only a small proportion of types contained termination sequence 2 (9 types in year 1, 7 in year 2, and 3

in year 3), and songs lacking either shared termination sequence were even rarer (none recorded in year 1, 1 type in year 2, 2 in year 3). Consequently, most individuals' recorded UE repertoires consisted entirely of songs that ended with termination sequence 1.

## DISCUSSION

### COEXISTENCE OF VARIABLE AND STEREOTYPED SIGNALS

Both AE and UE songs vary within individuals, but the range of variation in UE songs seems especially well-suited to encode messages in within-category variability. UE song form is comparatively unrestricted and free to vary. Songs are constructed from a large pool of elements, element types are freely reused and recombined



TABLE 4. Counts of unaccented-ending song types, grouped by the number of different individuals that shared them in each year of the study, showing that about half the types in a given year were unique to a single individual, and that relatively few types were used by more than two individuals. Numbers in parentheses indicate the number of song types in each group that were sung by primary males.

Number of males sharing a type:	Number of UE song types		
	Year 1 (42 males, 14 primary)	Year 2 (49 males, 18 primary)	Year 3 (40 males, 14 primary)
1	36 (8)	34 (14)	30 (17)
2	12 (8)	11 (6)	9 (6)
3	3 (2)	6 (4)	3 (2)
4		5 (3)	2 (2)
5	2 (3)		1 (1)
6		1 (1)	
7		1 (1)	1 (1)
8			
9	1 (1)	2 (2)	
10		1 (1)	
11			
12	1 (1)	1 (1)	
13	1 (1)		
14		1 (1)	
15			1 (1)
16			1 (1)
Total number UE types	56	63	63

in different song types, and innovation of new types is apparently common (as suggested by the high proportion of UE types that are locally unique to one individual). Even the stereotyped UE song endings are not used in all song types, and vary among renditions to a much larger degree than do AE song endings.

In contrast to the flexibility and variability of UE songs, AE song form is limited to a few types that are rigidly standardized throughout the population. Each of the available types is unique, distinctive, and stereotyped, so that a human observer can assign an AE song to its type on the basis of even an element or two of its sonagram. The stereotypy of AE songs seems to be enforced by some unknown behavioral rules, one of which seems to be that the similar AE-1 and AE-1a forms cannot be included in the same repertoire. That the birds are able to adhere to these rules suggests that they, too, perceive sharp distinctions among AE forms. In general, the strong divergence in mode of expression between AE and UE repertoires strongly suggests Chestnut-sided Warblers perceive and respond to the two classes of songs in distinct ways.

Despite their individual distinctiveness, the various AE song types all have one stereotyped element (at3) in common. This element is always the final one in an AE song, so listeners could presumably determine a song's type before at3 was uttered. The presence of at3 in a song type thus serves to include the type in the AE category without compromising the distinctiveness of the type. Another intriguing possible role for element at3 is in the mechanism for maintaining the stereotypy of AE songs across generations. During song development, Chestnut-sided Warblers seem to have a predisposition to imitate AE, rather than UE songs (Byers and Kroodsma 1992). This preferential attention to AE songs in the acoustic environment of young birds must be triggered by some aspect of the AE signal. Element at3, as a reliable common denominator among AE songs, seems a likely candidate for such a cue.

The contrast between constrained, ritualized AE singing and flexible, variable UE singing is dramatic, and is probably connected to differences in the communicative function of the two signal categories. Stereotyped signals can serve to reduce ambiguity ("a signal that is constant in form cannot be mistaken," Morris 1957, p. 1), to enable accurate comparative assessment of differences between singers ("small differences between displays can only be perceived against a standard mode of display," Zahavi 1980, p. 80), or to reduce the chance of errors in signal detection (Wiley 1983). Variable signals may be more suitable for graded messages and/or close-range signaling (Green and Marler 1979).

#### FUNCTION OF MULTIPLE SONG FORMS

Wood-warbler species with two-category song systems seem to fall into two general groups in terms of how song repertoires are organized (Spector 1992). In one group, which includes the Yellow Warbler (*Dendroica petechia*), American Redstart (*Setophaga ruticilla*), and Grace's Warbler, (*Dendroica graciae*), the two song categories are distinguished by mode of delivery. First category singing is characterized by consecutive repetitions of a single song type, and bouts of second category songs are characterized by frequent switching among multiple song types. Song category is thus "performance-encoded," in the sense that an individual song cannot be assigned to a category without additional information on how song types are sequenced.

Chestnut-sided Warblers, along with Prairie Warblers (*Dendroica discolor*), Blue-winged Warblers (*Vermivora pinus*), Golden-winged Warblers (*Vermivora chrysoptera*), and Black-throated Green Warblers (*Dendroica virens*), are in the second group. In these species, each song category is associated with a particular kind of song form. Song category is "form-encoded," and any given song can be assigned to a category on the basis of the song's structure alone.

As members of the form-encoded group, Chestnut-sided Warblers do not require large repertoires to encode song category. Nonetheless, Chestnut-sided Warbler repertoires are large relative to those of other form-encoding species, and similar in size to those more typically found in the performance-encoded group. Unlike performance-encoding species, however, Chestnut-sided Warblers do not generally reveal their entire repertoires in a given bout of singing. Switching between song types is a relatively uncommon phenomenon (e.g., 511 song type switches among 25,812 songs analyzed for year 1 of this study), and a few song types ordinarily account for most of a male's singing, regardless of his repertoire size. To a short-term listener, Chestnut-sided Warbler repertoires would seem small, similar to the two- or three-song repertoires of a Blue-winged Warbler or a Prairie Warbler.

The tendency of Chestnut-sided Warblers to hide portions of their song repertoires suggests that many of the proposed functions of song repertoires do not apply to this species. For example, it seems unlikely that repertoire size serves to advertise male quality. Any influence of male song repertoire size on female mate choice or on territorial contests among males would be possible only if repertoires were performed in a manner such that timely assessment by rivals or potential mates were possible. Similarly, the hypothesized antihabituation function of repertoires (i.e., repertoires of contrasting songs serve to prevent listener habituation and consequent failure to respond, Hartshorne 1973, Kroodsma 1978) seems to depend on a performance mode that exposes the songs in a repertoire within a relatively short period.

If functions related to the sheer number of different types are unlikely, why do Chestnut-sided Warbler males have so many song types? Lein (1978) hypothesized that repertoires are partitioned into five (or more) functional categories that are arranged in a motivational con-

TABLE 5. Distribution of accented-ending song types among males.

	Number of males singing type		
	Year 1 (34 males)	Year 2 (42 males)	Year 3 (27 males)
AE-1	10 (29%)	18 (43%)	6 (22%)
AE-1a	9 (26%)	9 (21%)	6 (22%)
AE-2	25 (74%)	24 (57%)	14 (52%)
AE-3	6 (18%)	9 (21%)	6 (22%)
AE-4	9 (26%)	14 (33%)	13 (48%)

tinuum reflecting increasing levels of agitation and aggression. It appears, however, that the pattern of repertoire organization proposed by Lein is not universal among Chestnut-sided Warbler populations. Although Lein reported that each male at his New Hampshire study site sang at least one song type from each of the five proposed song categories, such was not the case at my Massachusetts study site.

The repertoires of most birds in my study area lacked songs from at least one of Lein's song groups. For example, one of Lein's groups consisted of type AE-1, but in all three years of my study the repertoires of at least 35% of males at my study site lacked AE-1 songs (Table 5). Similarly, UE songs lacking either of the shared termination sequences (equivalent to Lein's group UE-1) were uncommon at my study site, and absent from the repertoires of the majority of individuals in all three years. At my site, the only repertoire features shared by all birds were the inclusion of both AE and UE song types, and the tendency to divide the repertoire into predominant and uncommonly-sung types. The only viable possibilities for universally shared signal features are thus the two main song categories (AE and UE), and variation within them (e.g., in song duration, amplitude, type-switching).

I am puzzled by the discrepancy between Lein's observations and my own. Lein's description of five song groups that were shared by all birds in a population is at odds with my finding that only a few individuals' repertoires contained songs from all five of those groups. This difference might be attributable to the differences in time (1970–1972 versus 1988–1990) or location (New Hampshire versus Massachusetts) between the two studies. It is, however, difficult to conceive of a mechanism by which these factors could lead to such large differences in singing behavior. Another possibility is that, despite the very large

number of songs that I recorded, my sampling missed many songs that were actually in repertoires. Conversely, Lein's findings may have been an artifact of the comparatively small number of different individuals that he observed. In any case, the seeming absence of universally shared song categories other than AE and UE means that Chestnut-sided Warbler singing probably does not consist of a series of graded signal classes.

If Chestnut-sided Warbler repertoires are not organized such that an individual's multiple song types reflect multiple species-universal categories, and are not used such that antihabituation effects or assessment based on repertoire size is possible, what possible functions remain? One possibility is that type-switching or acoustic contrast achieved by use of rare song types encodes infrequently-needed messages that are not encoded by the more common (at least in UE singing) within-type variability. Use of the "hidden" portion of UE repertoires may be reserved for infrequent but key interactions, perhaps involving high-stakes contests.

It is unclear if AE songs could be used in this manner. An ability to encode messages in type-switches would seem especially useful in AE singing, because AE songs show so little within-type variability. A function for AE type-switching would also help explain the existence of several different AE types, even though the advantages gained from signal stereotypy would presumably be maximized if the signal took only a single form. Nonetheless, the repertoires of many Chestnut-sided Warblers include only a single AE type, so a message-encoding function for AE type-switching would require that any such message be extremely rare or limited to certain individuals. A message-encoding function for within-category song repertoires thus seems less plausible for AE than for UE songs. In any case, confirmation of Chestnut-sided Warbler repertoire function must await further exploration and experimentation based on the descriptive data summarized here.

#### ACKNOWLEDGMENTS

I thank Donald Kroodsma and two anonymous reviewers for advice and critical review of the manuscript, and David Spector for thoughtful discussion and help with the analyses. The Western Massachusetts Electric Company and the state of Massachusetts generously granted access to the study site. This research was supported by the National Science Foundation

(Graduate Fellowship and BNS-8812084, BNS-9111666 to D. Kroodsma).

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