ACOUSTICAL FEATURES OF SONG CATEGORIES OF THE ADELAIDE'S WARBLER (*DENDROICA ADELAIDAE*)

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ABSTRACT.—I identified acoustical features that distinguish the two song categories, A and B, of the Adelaide's Warbler (*Dendroica adelaidae*). Like many other wood-warbler species, male Adelaide's Warblers have functionally structured song repertoires such that A and B song categories are distinguished by common usage among males. The particular song types used in a given category, however, vary greatly among individual males. Therefore, I focused my analysis on acoustical features other than song types. Song categories were distinguished by three major features: (1) the sound energy within a given B song was concentrated into a narrower frequency band, which was shifted about 600 Hz lower than for A songs; (2) the structure of B songs tended to be more complex, as they contained more note types and greater contrast between successive types than did A songs (discriminant function analysis using structural and frequency data correctly classified 85% of songs to category); and (3) the singing behavior associated with B-song sequences was more complex, due to inclusion of a larger number of song types, more frequent switching or alternating between them, and a more rapid rate of song delivery. Overall, the B category appears to represent a more complex and lower frequency signal than the A category. Differences between the two song categories, which parallel data available for other paruline species, should reduce signal ambiguity and are consistent with several nonmutually exclusive functional interpretations: The B-song category, used in intrasexual interactions, might represent a more aggressive signal or might be specialized for carrying motivational information. Females might find the higher-frequency A-song category more appeasing or stimulating. Song categories A and B also might be specialized for traveling different distances, at different times of day, or through different microhabitats. *Received 5 December 1994, accepted 16 February 1995.*

ACOUSTIC SIGNALS within a bird's vocal repertoire typically differ in structure, mode of presentation, and situation of use such that different functions often can be ascribed to each signal (e.g. Smith 1966). Different song types within an individual's repertoire, however, may represent redundant signals, at least in some species (e.g. Smith and Reid 1979). Well-studied species in which males use different song types in similar situations (i.e. song types are functionally redundant) include the Great Tit (*Parus major*), Red-winged Blackbird (*Agelaius phoeniceus*), and Song Sparrow (*Melospiza melodia*). Nonetheless, males of these species are attentive to variation in song structure (Falls et al. 1982, Stoddard et al. 1988) and the order of presentation of song types (Kramer et al. 1985, Searcy and Yasukawa 1990). These features cor-

respond to two signaling repertoires; i.e. songs represent units of the signal, and singing behavior reflects rules that describe the sequential organization of units (Smith 1991).

Among other species, males use different song types or, more generally, different song categories (particular groups of song types) in different situations, suggesting song categories represent signals that serve different functions (see Nelson and Croner 1991, Spector 1992). Evidence for functional differences between song categories includes their association with different social circumstances (e.g. attracting females vs. repelling other males) or environmental contexts (e.g. dawn vs. daytime), as well as differential response by males or females to playbacks of different song categories (e.g. Järvi et al. 1980, Catchpole et al. 1986, Nelson and Croner 1991). Few studies have presented quantitative analyses of the acoustical differences between song categories (e.g. Cosens and Falls 1984, Staicer 1989, Nelson and Croner 1991, Byers 1995). Such data are requisite for explor-

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ing the perception of song categories and the relationship between their structure and function.

The wood-warbler subfamily (Emberizidae: Parulinae) includes a large group of species (especially the closely related genera *Vermivora, Parula, Dendroica, Mniotilta,* and *Setophaga*) that appear to have functionally structured repertoires consisting of two song categories, A and B (i.e. the first and second categories of Spector [1992]). Category A predominates early in the season and during intersexual interactions, whereas category B is more common later in the season, at dawn, during nesting, and in intrasexual interactions (e.g. Ficken and Ficken 1962, Nolan 1978, Highsmith 1989, Kroodsma et al. 1989, Staicer 1989, Spector 1992). Males learn their two song categories in different ways (e.g. Byers and Kroodsma 1992, Lemon et al. 1994) and shift their usage of the categories when mating status is manipulated (e.g. Kroodsma et al. 1989, Spector et al. 1991, Staicer 1996). Accumulated evidence thus suggests that song categories A and B carry different information (e.g. Lein 1978), serve different purposes (e.g. Lemon et al. 1987, Kroodsma et al. 1989, Spector 1991), and have been shaped by different selection pressures (e.g. Kroodsma 1981, Staicer 1989). Further work is needed, however, to determine how song categories differ in acoustical structure within and among species.

In this paper, I compare the acoustical features of song categories of the Adelaide's Warbler (*Dendroica adelaidae*), a tropical resident species confined to four Caribbean islands (Bond 1930). Males use their song categories in contexts similar to those observed for other wood-warblers, but exhibit two unusual characteristics (Staicer 1991, 1996) seen to a lesser degree in their presumed closest relative, the Grace's Warbler (*D. graciae*; Webster 1961, Staicer 1989). First, male Adelaide's Warblers use song types (as identified using sonagrams) in largely individual-specific ways (i.e. two males can use the same song type in different categories; this is also the case for American Redstarts [*Setophaga ruticilla*]; Staicer unpubl. data). Second, song types have limited microgeographic ranges (i.e. few song types are shared by males >500 m apart). Dispersing males thus encounter unfamiliar songs but must somehow recognize A and B song categories, learn suitable exemplars, and use them in appropriate contexts. Therefore, features that distinguish song categories

should have important implications for song learning and vocal communication among Adelaide's Warblers. In my analysis, I examine details of both songs and singing behavior because both might contribute to the distinctiveness as well as any functional differences between the two song categories.

METHODS

Study area and subjects.—My study area was located in the Cabo Rojo National Wildlife Refuge in southwestern Puerto Rico (17°59'N, 67°10'W). The second-growth, deciduous-dry vegetation comprised a low, open canopy of trees (≤6 m) with an understory of grasses and shrubs (1–2 m). The subjects, male Adelaide's Warblers whose territories were <1.5 km apart, were recorded between 1984 and 1988; most were present for two or more of these years. All subjects organized their song repertoire (23 song types on average) into two groups, use of which matched the suite of temporal and contextual patterns of song use observed for temperate warblers. Through intensive and extensive observations of each male, I determined which song types he used in the context-defined categories A and B. Category B was the group of song types a male sang in his dawn bout during the breeding season, and category A was the group of song types he switched to singing after sunrise. Occurrence of additional bouts of B song types later in the day depended on time of year and the male's breeding status. Song types in a male's B category tended to outnumber those in his A category. All song types typically were shared by neighbors, who countersang by matching song types, suggesting meaningful perceptual units (Staicer 1991).

SONG FEATURES

Recording and selection of samples.—My data set allowed a comparison of song categories such that samples were independent in terms of male and song type identity, two factors that might influence song structure. Songs were obtained by sampling without replacement. I randomly selected, from each of 20 males, one A song and one B song such that song types were sampled without duplication. These 40 song types were common and encompassed typical variation within and among birds. Statistical significance was tested using two-tailed Wilcoxon signed-ranks tests, A and B songs paired within males ($n = 20$). Unless otherwise noted, statistical analyses were performed with SYSTAT for the Macintosh (Wilkinson 1987).

The pair of A and B songs from each individual came from high-quality recordings made with identical recording equipment (a particular microphone and tape recorder) and the same brand of magnetic
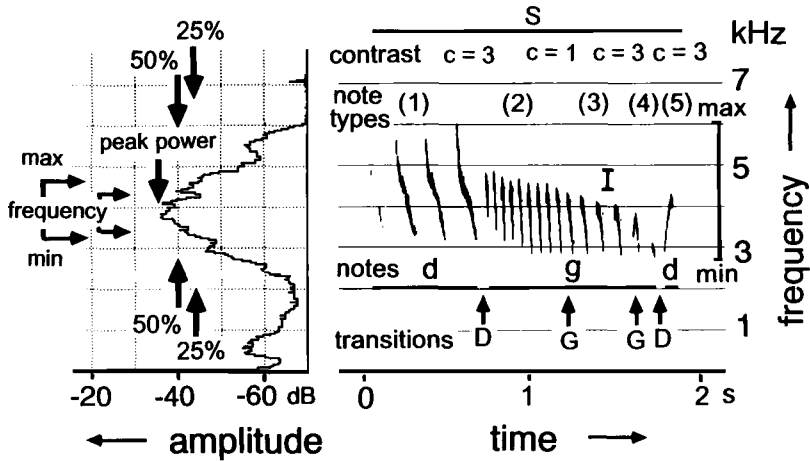
FIG. 1. Methods for quantifying shape of power spectra and complexity of songs. Averaged power spectrum (amplitude vs. frequency display, with amplitudes summed across frequencies; left) and sonagram (time vs. frequency display; right) of same Adelaide's Warbler song. On the power spectrum (left), peak power was maximum amplitude of this averaged power spectrum, whereas amplitudes of 50% and 25% of peak power had, respectively, 3 dB and 6 dB less sound energy than did peak power. Minimum and maximum frequencies (horizontal arrows) for amplitudes of 50% and 25% of peak power were lowest and highest frequencies at which screen cursors for each of these amplitudes (vertical arrows) intersected curve of the averaged power spectrum. The sonagram (right) illustrates that songs consisted of several notes of one or more types. A transition occurred when shapes of successive notes within song changed sufficiently to consider them different types. Notes and transitions could be either graded or discrete. Within series of graded notes (g), note shape changed gradually from one form to another, whereas within series of discrete notes (d), note shape remained relatively constant. A graded transition (G) occurred when note shape changed in graded manner from one type to another, whereas discrete transition (D) was abrupt switch between note types. Qualitative degree of difference between successive note types, note contrast (C), was assigned value of 1, 2, or 3 for low, moderate, or high. Song in this example has 20 notes of five types (1–5); 15 notes are graded in one long graded transition encompassing three note types (2–4), and 5 notes are discrete, with discrete transitions between the first two (1–2) and last two note types (4–5). Contrast is high (C = 3) between note types 1–2, 3–4, and 4–5, but low (C = 1) between note types 2 and 3; average note contrast is (3 + 1 + 3 + 3)/4 = 2.5. Temporal measures included song duration (S) and internote-interval duration (I).

tape, at 19 cm/s. I used either a Uher 4000 Report IC monaural or 4200 stereo reel-to-reel tape recorder, and either a 45-cm Dan Gibson parabolic microphone or a Sennheiser MKH-816 shotgun microphone. I chose the pair of songs from recordings as close in time to one another as possible, usually within minutes to a few hours, and used only recordings with a strong, but not overloaded, song signal and low background noise. The distance from the bird was similar during recording of A and B songs, typically 7 to 12 m. For sound analysis I used a Kay Elemetrics DSP model 5500 Signal Analysis Workstation. I measured frequency and amplitude features by using cursors on the video display (see below), and measured temporal and complexity features on printed sonagrams (where the point transform size simulated a wideband, 234-Hz analog filter).

Frequency measures.—The power spectrum (a frequency vs. amplitude display; Fig. 1) is a useful tool for describing the overall distribution of sound energy among frequencies within a song. I set the record level such that song amplitude peaked at approximately −40 dB and then invoked the "power between cursors" command on the Kay Workstation. This produced an averaged power spectrum, which summed energy, to the nearest decibel, across the entire song at 20-Hz intervals.

Using the screen cursors, I quantified several features of the power spectrum curve (Fig. 1). I chose the levels 50% and 25% of peak power as natural curve-shape descriptors that would allow comparison of the overall distribution of sound energy within A and B songs. The 50% level represents a halving of the peak power or maximum amplitude of the song, and the 25% level a further halving of the peak power. From these data I calculated the following variables: frequency range (maximum − minimum), midpoint frequency (minimum + [range/2]), and the proportion of the entire frequency range of the song encompassed by each level. I measured minimum and maximum frequencies of entire songs using screen cursors on the sonagraphic display (where the point-trans-

form size simulated a narrow-band, 59-Hz analog filter). I then calculated frequency range and midpoint frequency as previously described. Frequency data were compared for A and B songs using a univariate paired-comparison test (Wilcoxon signed-ranks, data paired within males) and also a multivariate F-test, comparing the group of A songs to the group of B songs.

Complexity measures.—Complexity was defined as the amount of change in note structure (i.e. sound-encoded information) from beginning to end of the song. This analysis assumed that the relative degree of complexity visible in sonagram patterns would be proportional to the relative degree of complexity audible to birds listening to the songs. "Blind" judges assisted my evaluations of song complexity. All judges were familiar with sonagrams but were blind to song category, hypotheses of interest, and directions of expected differences. The judges provided data for two analyses, one qualitative and one quantitative, by examining good-quality photocopies of sonagrams (where the point-transform size simulated a wide-band, 234-Hz analog filter).

For the qualitative analysis, I photocopied the pair of A and B songs for each male onto a single page (n = 20), randomizing which song was placed at the top and bottom. Looking at each page, five judges independently determined which song of the pair was more complex. With these data I calculated a sign test (Sokal and Rohlf 1981) to compare the apparent complexity of A and B songs. For the quantitative analysis, I photocopied sonagrams for each of the 40 songs onto separate sheets of paper and presented these in random order to three judges (two were persons used in first analysis). The judges provided values for several indices of song complexity that I developed (described in Fig. 1). I explained these indices to the judges by presenting hypothetical examples (drawings of sonagrams that conceptualized a range of patterns) and values for the indices as I would have measured them. Each judge, however, independently determined any "rules" that she or he used to make the measurements. Indeed, values of a given index for the same song varied considerably among the judges. Average scores of the three judges were used when comparing complexity measures for A and B songs.

In addition, I used printed sonagrams (where the point-transform size simulated a narrow-band, 59-Hz analog filter) to quantify several temporal features that might differ among songs (Fig. 1). I measured the duration of songs, and within songs the duration of silent periods between notes (internote intervals). I also counted the number of notes and calculated the average note rate within songs (number of notes per s).

Multivariate classification.—The frequency and complexity variables were combined for a discriminant function analysis to determine whether information contained within these variables could be used to correctly classify songs to category. The SYSTAT procedure (Wilkinson 1987) used dependent-variable canonical coefficients to produce the discriminant scores and Fisher discriminant functions to classify the raw data; a jackknifed procedure was not used to test the efficacy of the discriminant function.

SINGING BEHAVIORS

Sampling rationale.—To determine whether different singing behaviors were associated with the A and B song categories, I compared sample sequences containing 20 consecutive songs. In selecting sequences, I attempted to minimize sources of variation that might confound differences in singing behavior. To avoid effects of season and pairing status, I included only data from paired males during the breeding season. To avoid confounding time of day effects, I selected samples recorded at a time of day that A and B songs typically occur (see below). I compared data within males (as in the preceding analyses) to avoid individual effects and compared sequences of a given male from the same day to avoid day effects.

Selection of sequences.—I used the following criteria to select typical samples of A and B song sequences. I obtained dawn B sequences from the middle of the dawn bout, approximately 20 min before sunrise, and morning B sequences beginning at least 1 h after sunrise (range of times 0749–0930 AST). These samples should encompass the range of probable characteristics of B sequences, because the singing behavior associated with category B is likely to be most different at these times (e.g. Staicer 1989, Staicer et al. 1996). I selected A sequences beginning well after the dawn bout had ended and usually more than 20 min after sunrise (range: 0603–0823 AST), when A singing was most frequent. After changing behaviors or locations, some males had long pauses between songs (i.e. duration >5 times median pause in sequence). I avoided sequences containing such pauses, and also those in which males switched song categories, because these sequences may have been confounded by other factors.

Within each category, observations were independent because each data point (representing an entire song sequence) was from a different male on a different day. For 18 males I had long recordings of B songs at dawn and extensive recordings of A songs during the 3-h period following sunrise (hereafter called morning), both on the same day in the middle of the breeding season. For nine males I also had recordings of B songs during morning on the same days (the other nine did not use B songs during morning periods on these days). My data set thus contained 18 dawn B sequences, 18 daytime A sequences, and 9 daytime B sequences from a total of 18 males. All samples contained 20 consecutive songs except one

sequence of morning B songs (15 songs) and five sequences of A songs (15, 12, 12, 8, and 8 songs).

Singing-behavior measures. —For each sequence I counted the numbers of songs, song types, and song transitions (i.e. when following song differed from preceding song by one or more phrases). I also measured the total time elapsed between the beginnings of the first and last songs, and used this value in calculating rates. I then calculated the following singing-behavior variables: song rate (no. songs per min), type rate (no. song types per min), transition rate (no. song transitions per min), type index (no. song types per song in the sequence), and transition index (no. song transitions per song in the sequence). Sequences were compared by Wilcoxon signed-ranks tests (data paired within males) and Mann Whitney *U*-tests (grouped data).

RESULTS

Frequency characteristics. —Frequencies emphasized in A songs tended to be higher than those in B songs (Table 1). Song categories differed significantly for the frequency maxima, midpoints, and ranges that corresponded to the portion of the song with amplitudes 50% or more of peak power and 25% or more of peak power. Also, the frequency range of B songs that contained amplitudes 25% or more of peak power made up a smaller proportion of the frequency range of the entire song. In contrast, frequency measures for entire songs did not differ significantly between categories. Thus, although A and B songs overlapped in frequency, B songs had a larger proportion of their sound

TABLE 1. Summary of frequency characteristics of A and B songs for Adelaide's Warblers at the Cabo Rojo National Wildlife Refuge, Puerto Rico. Medians (kHz) for 20 songs per category, one A and B song per male ($n = 20$), and representing 40 different song types.

Frequency characteristic	A	P^a	B
Entire song			
Minimum frequency	2.40	ns	2.26
Maximum frequency	7.76	ns	7.60
Frequency range	5.40	ns	5.16
Midpoint frequency	5.02	ns	4.91
Frequency of peak power	4.82	ns	4.18
Portion at 50% or more of peak power			
Minimum frequency	3.82	ns	3.44
Maximum frequency	5.50	**	4.66
Midpoint frequency	4.69	*	4.09
Frequency range	1.59	*	1.30
Proportion of entire song's range	0.30	ns	0.23
Portion at 25% or more of peak power			
Minimum frequency	3.23	ns	3.20
Maximum frequency	5.88	***	5.18
Midpoint frequency	4.64	**	4.29
Frequency range	2.61	***	1.90
Proportion of entire song's range	0.47	**	0.37

[a] Two-tailed Wilcoxon signed-ranks tests, with A and B songs paired within males; ns, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

energy focused into a narrower range of lower frequencies (see Fig. 2).

Multivariate intergroup comparisons gave results similar to univariate tests. A multivariate *F*-test, which included the minimum frequency, maximum frequency, frequency range, and proportion of entire song's range that corre-
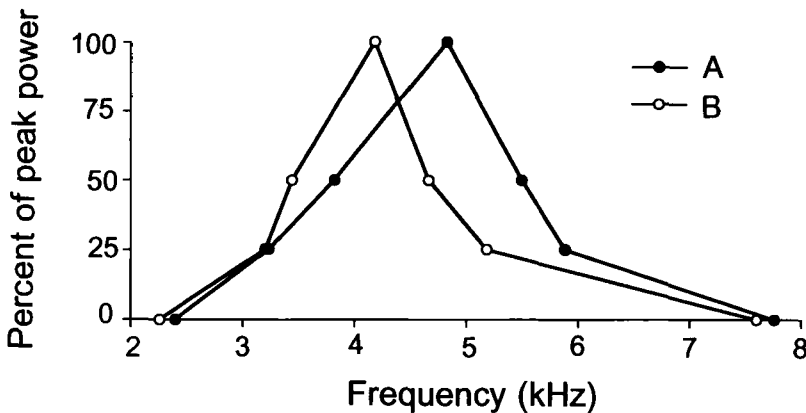

FIG. 2. Comparison of shapes of averaged power spectra for A and B songs. Points correspond to median values ($n = 20$ males per point) for frequency that contained the highest amplitude in the power spectrum (100% of peak power), for the lowest and highest frequencies that contained amplitudes 3 dB below peak amplitude (50% of peak power) and 6 dB below peak amplitude (25% of peak power), and for the minimum and maximum frequencies of the entire song (defined as 0% of peak power).

TABLE 2. Summary of complexity characteristics of A and B songs of Adelaide's Warblers. Medians for 20 songs per category, with one A and one B song per male ($n = 20$).

Characteristic	A	P[a]	B
Song duration (s)	2.07	ns	1.92
Note rate (notes/s)	11.83	ns	11.74
Average internote interval (milliseconds)	48.72	ns	47.90
Proportion of notes graded	0.46	ns	0.43
Proportion of transitions graded	0.27	ns	0.24
Different note types	3.00	*	3.67
Average contrast between note types	2.00	*	2.19

[a] Two-tailed Wilcoxon signed-ranks tests, with A and B songs paired within males; ns, $P > 0.05$; *, $P < 0.05$.

sponded to the song portions 50% or more and 25% or more of peak power, revealed a significant difference between song categories ($F = 2.29$, $P = 0.04$). When I included only the frequency at peak amplitude, minimum frequency, maximum frequency, and frequency range for the entire song, however, I found no difference ($F = 1.41$, $P = 0.25$). Thus, the patterns of sound energy distribution among frequencies differed for A and B songs, even though their overall frequency ranges overlapped considerably (see also Fig. 2).

Song complexity.—In the first complexity analysis, which was subjective, the consensus among judges was that song categories differed in complexity, as determined by the judges' own criteria (i.e. their conceptual notions of structural variety). Of the 20 pairwise comparisons, a majority of the judges (≥ 3 of 5) considered the B song more complex in 13 cases and the A song more complex in only three cases. In the remaining four cases, two or more judges found the pair of songs equally complex, reducing n for the sign test. Overall, however, B songs were judged significantly more complex than A songs ($z = 2.5$, $n = 16$, $P < 0.02$). When I judged the 20 pairs of songs, I concurred with all decisions for which three or more judges had agreed.

The second analysis, which was more objective, revealed a quantitative basis for the subjectively greater complexity of B songs perceived by the judges in the previous analysis. The number of different note types and the average contrast between note types were significantly higher in B songs than in A songs (Table 2); these features were not correlated with one

another. Median values for other measures were slightly higher for A songs than B songs, but these differences were not significant (Table 2).

Divergent features.—Significant findings are highlighted in a visual comparison of power spectra and sonagrams from several males (Fig. 3). A songs often consisted of graded series of notes in which their "shape" changed gradually through the song. In contrast, B songs more often had several distinct note types, the shape of which changed rather abruptly through the song, creating a more complex signal. In addition, the sound energy of A songs was spread over a broader frequency range than in B songs, which tended to emphasize lower frequencies.

Emphasis of a narrow-frequency band within a given note was more common among B songs than A songs. In sonagrams, an emphasized frequency appears as a thicker, blacker portion of the note, a feature evident in the B songs in Figure 3. By obtaining power spectra for single notes, I verified that these thickened portions contained more sound energy. The frequency band representing 25% or more of peak power corresponded closely to the emphasized frequencies of notes apparent on sonagrams. Exceptions were songs that ended with a high-frequency trill, a feature found in both A and B songs. Presence of these trills did not shift the band towards higher frequencies because of low amplitude and brief duration.

Classification of songs.—I used a discriminant function analysis to determine whether information contained within frequency and structural variables was sufficient to place songs in the correct category. The mathematical classification function derived from the combined set of variables correctly classified 34 of 40 (85%) songs. Thirty-two songs (80%) were correctly classified using the five most significant and independent variables (based on univariate F-tests and Spearman rank correlation coefficients): (1) maximum frequency at 25% of peak power; (2) frequency range of song at 25% or more of peak power; (3) ratio of this range to entire song's frequency range; (4) number of note types; and (5) average note contrast. Thus, songs typically contained sufficient information to enable category identification.

Singing behaviors.—Sequences of A and B songs were characterized by markedly different singing behaviors (Table 3). Over a given time interval, males sang more songs (i.e. higher song
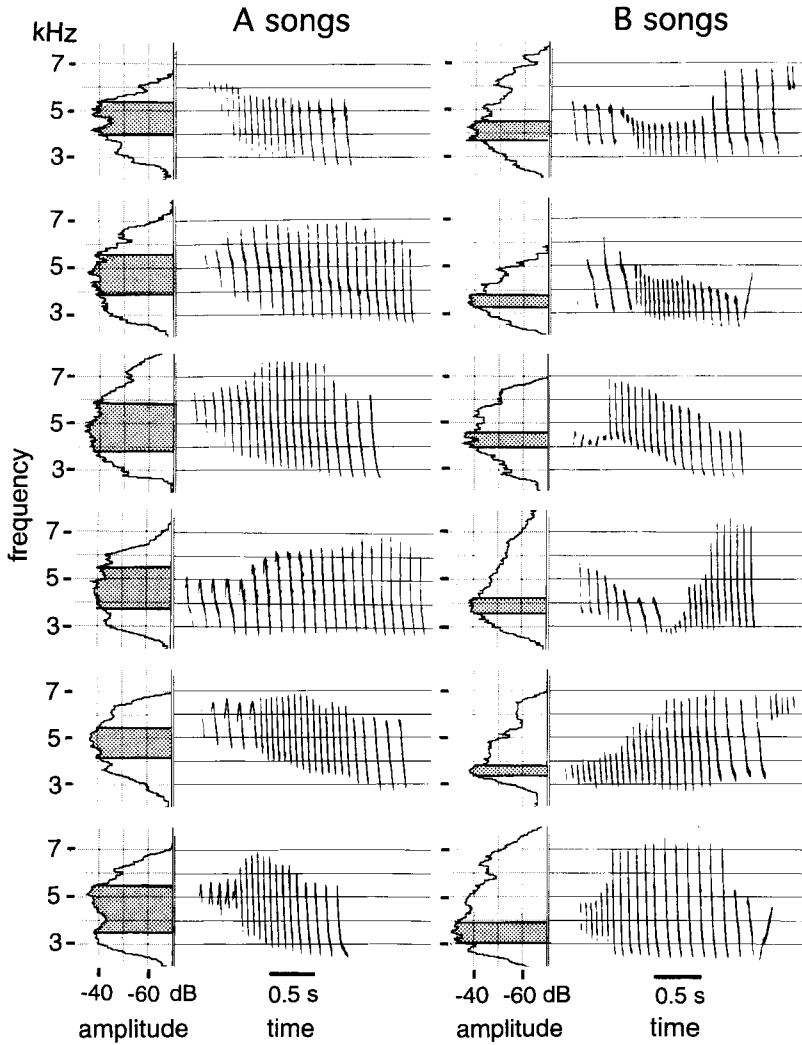
FIG. 3. Divergent features of A and B songs of Adelaide's Warblers. One A song (left column) and one B song (right column) from each of six males illustrate the variety of common song types used in the A and B categories. Each row displays the pair of songs analyzed from a different male. Shown for each song are an averaged power spectrum (left side of column), where amplitude increases to the left, and a sonagram (right side of column), where time increases to the right. Stippled areas of power spectra correspond to the frequency bands delimited by minimum and maximum frequencies that contained 25% of peak amplitude and indicate which frequencies were emphasized in each song. Note the tendency for B songs to emphasize a narrower and lower range of frequencies and to have a more complex structure, with more note types and greater contrast between them, as compared with A songs.

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TABLE 3. Median values (and ranges) for singing behavior variables calculated for sequences of consecutive Adelaide's Warbler songs of category A and B.[a]

Variable	Type of sequence		
	Morning A	Morning B	Dawn B
Song rate	1.14 (0.59–1.64)	3.33 (1.45–7.02)	9.81 (5.36–13.99)
Type rate	0.07 (0.04–0.41)	0.56 (0.14–1.50)	3.34 (1.79–6.08)
Transition rate	0.00 (0.00–1.44)	2.38 (0.00–4.56)	8.51 (4.29–12.84)
Type index	0.08 (0.05–0.25)	0.15 (0.07–0.40)	0.40 (0.20–0.45)
Transition index	0.00 (0.00–0.88)	0.55 (0.00–0.90)	0.93 (0.08–0.95)

[a] All comparisons significant in two-tailed Wilcoxon signed-ranks tests, with data paired within individuals: $P < 0.001$ for morning A versus dawn B sequences; $P \leq 0.012$ for morning A versus morning B sequences; $P \leq 0.01$ for B sequences at dawn versus B sequences in morning. Samples were sequences of consecutive songs, usually 20. Each median value was obtained from samples of 9 or 18 males ($n = 18$ males for dawn B and morning A; $n = 9$ of the same 18 males for morning B; all samples from a given male were recorded on the same day).

rate), more song types (i.e. higher type rate), and switched song types more frequently (i.e. higher transition rate) in sequences of B songs. For a given number of consecutive songs, males sang more song types (i.e. higher type index) and switched song types more often (i.e. higher transition index) in B sequences. Although B songs showed significant time of day effects (i.e. higher values at dawn than during morning), both dawn and morning B sequences were significantly higher than A sequences for all measured variables. All tests were statistically significant ($Ps \leq 0.012$); the three data sets overlapped only slightly (Table 3). Mann-Whitney U-tests (comparing two data sets per analysis) gave similar results. I concluded that distinct singing behaviors were associated with the two song categories.

DISCUSSION

DISTINCTIVE FEATURES

The A and B song categories of male Adelaide's Warblers are structurally distinct in the two measured components of their signaling (Smith 1991); viz. songs (units) and singing behavior (rules that govern sequential delivery of units). Compared with songs used in category A, those used in category B are more complex, and they generally contain more note types and greater contrast between successive note types. The frequency range of A and B songs overlaps substantially, yet B songs tend to emphasize lower frequencies such that the sound energy contained in the song is concentrated within a narrower range of frequencies. On average, the

peak amplitudes in B songs occurred at frequencies 600 Hz lower than in A songs. This difference, which should be detectable by the birds, is likely to be meaningful. Males of at least one species of paruline warbler perceive and respond to a smaller, 200-Hz shift in frequency (Morton and Young 1986). Compared with the singing behavior associated with A-song sequences, that for B-song sequences is more complex, with more alternation between a larger variety of song types and variations. Also, B sequences are characterized by a more rapid rate of song delivery.

Similar features have been reported to distinguish song categories for other species. For example, differences in the number of note types contribute to differences in song complexity in Field Sparrows (*Spizella pusilla*; Nelson and Croner 1991) and Grace's Warblers (whose B songs have more note types than A songs; Staicer 1989). In Yellow Warblers (*Dendroica petechia*; Spector 1991), category A songs have higher frequencies and exhibit a greater amplitude crescendo over the first two syllables than do category B songs. Male American Redstarts (Lemon et al. 1985), Grace's Warblers (Staicer 1989), and Yellow Warblers (Spector 1991) have more B songs in their repertoire and sing these in a more versatile manner, alternating B song types; males repeat monotonously their fewer A song types. Among these and other species, males deliver B songs at more rapid rates (see also Highsmith 1989).

Adelaide's Warblers have available several potentially useful cues, including song structure and singing behavior, for identifying song categories. Use of singing behavior would require more time and effort than use of single

songs because listeners would need to remember and compare songs within a sequence, or at least detect switches and their rate. In my study, frequency and complexity data for individual songs showed more overlap between categories than did song sequence data. Furthermore, a discriminant function analysis using structural features (frequency and complexity measures) classified only 85% of the songs to the correct category. Thus, at least based on the samples and measures I used, singing behavior seems to provide more reliable information regarding song category than does song structure. Note, however, that cases in which singing behavior is likely to provide ambiguous information, such as when males switch from one category to another, were excluded from my samples (e.g. the transition between the dawn bout of B songs and switch to A songs was sometimes gradual; Staicer 1991).

Considerable variation exists among wood-warblers in whether a particular song category is reflected in the structure of a single song (i.e. its song type). Early studies, which relied mainly on aural discrimination, equated song categories with song types (e.g. Ficken and Ficken 1962). Song types reliably distinguish song categories for some *Vermivora* species in which males have only two song types and share these with conspecific males (Kroodsma 1981, Highsmith 1989). Similarly, male Chestnut-sided Warblers (*D. pensylvanica*) share song types in their A category across the species' geographic range, even though individuals use several song types per category (Kroodsma 1981). In contrast, males of three other well-studied species that have large repertoires, i.e. American Redstart (Lemon et al. 1985), Grace's Warbler (Staicer 1989), and Yellow Warbler (Spector 1991), show much less conformity in A-song structure both within and among populations (see below). Interestingly, the A songs of species in both groups are more stereotyped within and among individuals than their B songs (Staicer 1989, Byers 1995).

Individual-specific song type use is common in some paruline species. For example, male American Redstarts (Lemon et al. 1985), Grace's Warblers (Staicer 1989), Yellow Warblers (Spector 1991), and Adelaide's Warblers (Staicer 1991) may use in their A category the same song type that a neighbor uses in its B category. These observations suggest that song types provide somewhat ambiguous information about song categories, although whether B songs might be lower in frequency than A songs of the same type remains to be studied. Interestingly, distinct singing behaviors are associated with the A and B song categories for these four species. How do birds identify song categories, and how do males learn to use songs appropriate for each category? Laboratory experiments have revealed that male wood-warblers can use other cues, such as time of day and singing behavior, to guide their learning process (Kroodsma 1988, Spector et al. 1989).

A potentially important factor to consider in studies of song structure is whether the singer has the ability to alter reversibly the frequency characteristics of his songs. Such a phenomenon occurs in males of at least one wood-warbler species with a single-song repertoire, the Kentucky Warbler (*Oporornis formosus*; Morton and Young 1986), as well as in the Black-capped Chickadee (*Parus atricapillus*; Horn et al. 1992). To date, no similar experimental data are available for species with song categories. The proposed functions of frequency shifting include increasing the information content of small repertoires, and enabling frequency-based (rather than song-type-based) matched countersinging (Morton and Young 1986, Horn et al. 1992). Thus, frequency shifting is less likely to occur in species with repertoires, because different song types or categories could serve these functions.

FUNCTIONAL SIGNIFICANCE OF STRUCTURAL DIFFERENCES

Below, I explore several possible links between the structure of the two signals, song categories A and B, and their proposed functions. Accumulated observational and experimental evidence suggests that A songs have a relatively more important intersexual function, whereas B songs have a relatively more important intrasexual function (Ficken and Ficken 1962; Nolan 1978; Lemon et al. 1987; Highsmith 1989; Kroodsma et al. 1989; Staicer 1989, 1996; Spector 1991, 1992; but see Lein 1978). For example, A songs are associated with mate attraction and interactions between mates, whereas B songs are associated with close-range aggressive interactions between males. Furthermore, males learn songs they use in the two categories

in different ways. Social interaction is necessary for the development of B songs (Byers and Kroodsma 1992), and these tend to be learned later than A songs, from territorial neighbors (Lemon et al. 1994). Thus, one might expect A songs to be more effective at attracting females and B songs to be more effective at repelling males. Even within this conceptual framework, structural differences between song categories might have multiple functions. Accordingly, the functional explanations discussed below need not be mutually exclusive.

Consistent with the posited intrasexual function of B songs is the importance of encoding motivational information during vocal interactions among males (Becker 1982). For Adelaide's Warblers, singing behavior A varies relatively little and mainly in relation to females, whereas singing behavior B varies seasonally, diurnally, and within a given dawn bout (Staicer 1991). Variability within the B category represents a continuum between the most intense and versatile singing (e.g. in middle of dawn song bout) to the least intense and versatile singing (e.g. song bouts later in morning). Similar patterns in variability have been reported for the B songs of some temperate warblers (Spector 1989, Staicer 1989, Staicer et al. 1996). Thus, the complex and variable features of B-song sequences in Adelaide's Warblers and several other species suggest a graded signal with the potential for carrying much information that could function in the assessment of relative competitive abilities among males (Lemon et al. 1987).

Features that distinguish song categories might be related to sexual differences in the perception of song. In a tropical tree frog, females preferentially approach the higher frequency portions of male calls because female ears are tuned to higher frequencies than are male ears (Narins and Capranica 1980). Although such a simple mechanism is unlikely to explain structural differences between the song categories of birds, evidence is accumulating that among birds, females and males are attentive to different features of songs. Females have been shown to respond differently than males to songs of altered structure and sequential organization (Searcy et al. 1981) and to be more discriminating in response to song than are males (Searcy and Brenowitz 1988). Sexual differences in response to song might be based on features that are degraded to a lesser extent when

traveling over typical communication distances or passing through typical microhabitats, which often tend to differ for male and female listeners (Dabelsteen and Pedersen 1993).

According to motivation-structural rules, appeasing vocalizations tend to incorporate higher frequencies, whereas aggressive vocalizations tend to incorporate lower frequencies (Morton 1977). Application of these rules to wood-warbler song categories predicts that A songs should be higher in frequency than B songs. Available data are consistent with this interpretation. The higher-frequency A songs are used preferentially when males interact with females, a situation when appeasing songs might be expected, and the lower-frequency B songs are largely confined to interactions among males, a situation when aggressive songs might be expected. Overall, the two song categories of wood-warblers differ less in frequency than do the different "calls" in the repertoire of most birds, because the forms of songs generally are constrained by the requirements of long-distance propagation whereas calls, which are used in closer-range communication, are not similarly constrained (Morton 1977).

Differences in song structure also might reflect specialization for transmission over different distances (Wiley and Richards 1978, Cosens and Falls 1984). Among wood-warblers, males sing B songs most intensely at dawn, when higher humidity and reduced wind turbulence are expected to enhance sound transmission (Henwood and Fabrick 1979). Furthermore, when singing B songs either at dawn or during daytime, male Adelaide's Warblers tend to be closer together, and they appear to direct their songs more towards particular neighbors than when singing A songs. In contrast, males deliver A songs throughout the day, at a relatively constant (albeit slow) rate, and tend to be farther from neighbors when countersinging with A songs. At least some of the time, A songs are directed towards females. Unpaired males sing mostly A songs and presumably would benefit by projecting A songs as far as possible. Based on these behavioral observations, if song categories typically differ in transmission distance, I predict that A songs should travel farther than B songs. If, on the other hand, B songs were given from higher, more exposed perches (not the case in Adelaide's Warblers), B songs could travel farther than A songs.

Sound-transmission studies emphasize a trend

for higher frequencies to attenuate more rapidly over a given distance (Morton 1975, Linskens et al. 1976, Marten and Marler 1977, Marten et al. 1977). Thus, lower-frequency B songs would be expected to travel farther than A songs. A close examination of data from habitats similar to my study area (i.e. open forest, scrub, edge), however, cautions against such a prediction. Excess-attenuation data (the amount of sound energy lost in excess of 6 dB per doubling of distance traveled) from these studies are extremely variable over the range of frequencies emphasized in Adelaide's Warbler songs (3.5–5.0 kHz) and are thus inconsistent with the idea that attenuation increases with frequency over this particular range. Sound-transmission data for my study site are needed in order to determine whether frequency differences between A and B songs affect their propagation in any consistent way.

Alternatively, song structure might not be related to the function of song categories in any adaptive way. Nonetheless, differences that arise between the songs or singing behaviors that characterize the A and B categories still could be reinforced because features that contribute to the distinctiveness of the song categories would reduce the ambiguity of signals and thereby increase their effectiveness. If the structural differences between A and B songs were nonadaptive, then one might expect the A and B songs of different species of wood-warblers to have diverged in numerous ways that are unrelated to ecological or social differences among species. This question cannot be addressed until quantitative data are available for more species. Also needed are studies designed to test the various functional explanations that have been proposed herein to link the structure and function of song categories.

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