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REPERTOIRE SIZE, REPERTOIRE OVERLAP, AND SINGING MODES IN THE BANDED WREN (*THRYOTHORUS PLEUROSTICTUS*)

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ABSTRACT.—We describe the song system of the Banded Wren (*Thryothorus pleurostictus*), with emphasis on within-species variation in repertoire size, song-type sharing, and singing mode, and identify some of the correlates of this variation. Unlike most of its duetting congeners, males are the primary songsters in this species. Songs are discrete, 2 to 5 s in duration, and consist of softer introductory buzzes and rattles followed by several repeated frequency-modulated whistles or note complexes and a loud terminal trill. Song types are highly distinctive. Repertoire size averaged 19.7 song types (range 15 to 24) and did not vary among three populations located within 8 km of each other in northwestern Costa Rica. Song-type sharing between neighboring males averaged 77% (range 48 to 90%) and was significantly higher among males inhabiting a continuous forest habitat area (78%) than among birds in two broken-forest/second-growth areas (62%). Populations separated by 8 km shared few song types (10%). Singing mode encompassed both the immediate variety and eventual variety patterns found in other passerines, as well as a continuous range of intermediate variety between these two extremes. We used switching rate and a modified Shannon-Wiener index of song-type diversity to quantify variation in singing modes. High-switching, high-diversity singing was associated with the dawn chorus and with soft singing in the presence of the male's mate. High-switching, low-diversity singing (alternation between two or three song types) was associated with countersinging from a distance. Low-switching, low-diversity singing (repeat mode) occurred during and after highly escalated boundary encounters. Thus, unlike most discrete-repertoire species described to date, Banded Wrens decreased their switching rate in increasingly agonistic contexts. *Received 10 April 1998, accepted 17 November 1998.*

THE SONG SYSTEMS of oscine passerines vary along three more or less independent axes: repertoire size, repertoire overlap, and mode of song-type delivery. Several decades of field research have documented the extent of this variety, but the function of variation in these three parameters is only partially understood. Comparative studies have been used with some success to examine the ecological and life-history correlates of interspecific variation in these song parameters (Kroodsma 1977, Read and Weary 1992). However, intraspecific comparisons hold more promise for unraveling the selective pressures that favor certain singing behaviors.

Repertoire size is a measure of the number of syllable types or song types in a male's song repertoire. It ranges from 1 to more than 2,000 types in different species (Catchpole and Slater 1995). Within species, average repertoire size can vary among populations. For example, Marsh Wren (*Cistothorus palustris*) repertoires range from 33 to 162 song types per male in five United States populations, with western populations having the larger repertoires (Kroodsma and Canady 1985, Kroodsma and Verner 1987). The larger repertoire size in western birds was associated with year-round residency, higher densities, and stronger competition for territories and females. Even more indicative of the precise selective factors favoring larger repertoire sizes are studies showing that males with larger repertoires have longer territory tenure, greater appeal to females, and higher offspring survival compared with males with smaller repertoires (Arcese 1989, Hasselquist et al. 1996, Searcy and Yasukawa 1996).

Repertoire overlap is a measure of the similarity between two birds' repertoires, or the fraction of song types they share. In principle, it can range from 0 to 1. Intraspecific differences in repertoire overlap have been documented for migratory versus sedentary populations of Sedge Wrens (*Cistothorus platensis*), Eastern Towhees (*Pipilo erythrophthalmus*), and Song Sparrows (*Melospiza melodia*). In each of these spe-

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cies, adjacent males in migratory populations shared less than 5% of their song types, whereas sedentary populations exhibited much higher song-type sharing (Kroodsma and Verner 1978, Ewert and Kroodsma 1994, Nielsen and Vehrencamp 1995, Beecher 1996, Kroodsma 1996, Nelson et al. 1996, Hughes et al. 1998). In age-restricted learners such as many wrens and sparrows, sedentary habits may allow birds to breed in the same area where they were born and learned their songs (Beecher et al. 1994). Song-type sharing may be an important strategic signal parameter in male-male territorial interactions. When two interacting birds share some but not all song types, a male can opt to sing a shared or an unshared song type. Depending on the song type being sung by the opponent, this may result in "song-type matching," "repertoire matching" (singing a shared song type but not the same one recently sung by the opponent), or "non-matching" (Beecher et al. 1996).

Singing mode refers to the sequential pattern of song-type presentation. Mode is often classified as "repeat" (singer repeats one song type a various number of times before switching to another type; also called "eventual variety" singing) or "serial" (singer switches to a new song type after each song; also called "immediate variety" singing). Less frequently documented is an intermediate or "subset" mode of presentation, in which a singer alternates among a small subset of song types and later sings a different subset of song types (Kroodsma 1975, 1977). Some repeat-mode singers increase their switching rate among song types during interactions (Kramer et al. 1985, Simpson 1985, Horn and Falls 1991). Other species increase their switching rate in the presence of females (Searcy and Yasukawa 1990, Langmore 1997). Among serial-mode singers, variation in mode of delivery has been described for Marsh Wrens, Sedge Wrens, and Rock Wrens (*Salpinctes obsoletus*; Kroodsma 1975, 1977; Verner 1976).

The Banded Wren (*Thryothorus pleurostictus*) belongs to a New World genus renowned for coordinated male-female duets (Farabaugh 1982; Levin 1996a, b; Morton 1996). However, in the Banded Wren, as well as the Sinaloa Wren (*T. sinaloa*), males are the primary songsters (Brown and Lemon 1979). Banded Wrens have been classified as repeat-mode or serial-mode singers by different observers (Brown and Lemon 1979, Stiles et al. 1989). In this paper, we describe the song system of this little-studied species by documenting the range of variation in song structure, repertoire size, repertoire overlap, and singing mode. We further show that population differences in repertoire overlap are associated with habitat structure in nesting territories, and that singing mode varies as a function of agonistic context. We also compare our results with the few existing studies of congeners and with other North American wrens and sparrows with similar song systems.

METHODS

The Banded Wren (20 g) is a resident of Neotropical dry lowland forests along the Pacific coast from central Mexico to Costa Rica. Our study was conducted in Sector Santa Rosa of the Area de Conservación, Guanacaste, at the southern end of the species' range in northwestern Costa Rica. Breeding is concentrated in the first half of the rainy season, approximately April to August. The nest is a bulky, covered chamber with a funnel entrance placed in the crotch of a thorny ant acacia (*Acacia* spp.) tree. Although nesting is fairly synchronized at the onset of the rainy season, it becomes more asynchronous as nests are lost to predation and pairs renest. Several nesting attempts may occur during a single breeding season. Despite the highly seasonal habitat, the birds remain paired on their territories year-round.

The study area consists largely of tropical deciduous forest in various stages of regeneration. Tracts of both open field and more humid evergreen forest also occur. Banded Wrens are common in the reserve and easy to detect because they sing loudly from high perches and often utter ticking and rattling sounds when disturbed by humans while foraging on or near the ground. We recorded and monitored clusters of adjacent territorial males located in three sites. Two of these sites were studied in two years each, for a total of five site-years and 36 individual males. The Centeno (CT-95 and CT-97) and Cerco de Piedra (CP-97) sites were situated in areas of recent regeneration bordering old pastures. The third area, Santa Rosa (SR-96 and SR-97), consisted of more mature and continuous regenerated forest. The SR and CP sites were located near the park's administrative headquarters and separated by about 500 m, whereas the CT site was located 8 km from the other two sites. Most (25 of 36) of the recorded males were banded with aluminum and colored plastic leg bands for identification. Whether banded or unbanded, however, birds could be identified by a combination of location and distinctive song types or versions of song types.

Recordings and observations were collected from July to August 1995, April to August 1996, and April to September 1997. We usually began recording with the onset of singing at dawn and continued for 45 min to 2 h after the first song was heard. We followed one or two males each morning. Songs were recorded on a TEAC DA-P20, Sony TCD-D7, or TASCAM DA-P1 DAT recorder with either a Sennheiser MKH 816 or Audiotechnica AT 4071 shotgun microphone. For each new male, we initially digitized every recorded song using Canary (Charif et al. 1995) on a Macintosh Powerbook in the field. We viewed the spectrogram of each song and printed exemplars of each new song type for reference. With practice, we found that song types were easy to distinguish by ear. Once a male's song types were identified, we transcribed subsequent tapes primarily by ear, logging all songs, tape times, and other observations into statistical spreadsheets. We confirmed the accuracy of our auditory song-type assignments back in the lab in San Diego using a Signal/RTS (Engineering Design 1996) or Canary Browser (Charif et al. 1995) real-time analyzer. Less than 1% of the songs were incorrectly assigned.

Birds were recorded for two to five days until a plot of their cumulative song types versus the number of songs sampled reached an asymptote. Care was taken to collect additional recordings from birds who sang at relatively low rates or with low diversity during one or more sessions. Sampled songs ranged from 169 to 1,120 per bird. For the 15 males with 500 or more sampled songs, complete repertoires were obtained after a mean of 300 songs (range 109 to 495). The mean repertoire size of males with fewer than 300 sampled songs was similar to that of more extensively sampled males (19.70 vs. 19.54, respectively; $t = 0.184$, $P = 0.855$), and there was no correlation between repertoire size and the number of songs recorded ($r = -0.065$, $P = 0.702$). Additional song types did not turn up in males that were later subjected to playback experiments. Thus, we are confident that we obtained complete repertoires for all 36 subjects.

The spectrograms of song types for each male were compared visually with all other males in the study site to detect shared song types. Our criteria are comparable to those of other investigators for species with complex song structures (Kroodsma 1974, Verner 1976, Hultsch and Todt 1981, Morton 1987, Hughes et al. 1998). We use the term "note" to refer to a continuous trace on a spectrogram and "syllable" to refer to a 1-, 2-, or 3-note repeated element; a "trill" is a set of repeated syllables. A match was scored if the second half of the song, including the terminal trill and the loud notes, syllables, or trill preceding it, contained the same notes (based on shape, frequency, and duration) arranged in the same order. We ignored differences in the number of notes in trills, because this parameter varied even within males. Repertoire overlap was measured between each pair of males within a site using the similarity index

$$S = 2N_S/(R_1 + R_2), \qquad (1)$$

where N_S is the number of shared song types, and R_1 and R_2 are the total number of song types in the two males' repertoires (McGregor and Krebs 1982). We calculated repertoire overlap at three different levels: (1) between pairs of adjacent males (with a common territorial boundary); (2) as an average score for each male with all other males in his site; and (3) between populations using the total song types for males within each site. To determine whether repertoire overlap varied as a function of the distance between two males, we performed Mantel tests on each of the five sites separately. In these tests, matrices of repertoire overlap between all pairs of males in a site were correlated with corresponding matrices of male-male distances, as measured in the shortest possible number of territories separating the two males (distance = 1 for adjacent territories). The Mantel test is statistically superior to a parametric regression for analyzing distance effects because it corrects for spatial autocorrelation and the paucity of more-distant comparisons relative to close ones (Mantel 1967). It uses multiple random permutations of the observed data to generate the chance expectation and produces an r-value between -1 and $+1$ that can be interpreted like a correlation coefficient. We used the R Package (Legendre and Vaudor 1991) for the analyses, with 250 permutations per run.

We examined the association between singing mode and context in two ways. First, we took timed 5-min samples of song sequences by territorial males at random times throughout the morning. These samples were obtained either from recordings or from focal-bird samples taken by ear in the field. We counted total songs sung per 5 min and computed several measures of singing diversity (see below). Whenever possible, we classified the social context of the 5-min period as either: (1) dawn chorus (0500 to 0545), (2) post-chorus with no obvious interaction, (3) post-chorus countersinging with a neighbor, or (4) during and immediately after a close encounter with a neighbor. We also noted whether the male was nest building, foraging, or singing from a high perch and whether we detected the presence of the female. Of the 540 samples taken, many had uncertain context or song-type assignments, or too few songs for computing the diversity indices, so sample sizes differ depending on the variables being analyzed. The second method of analysis entailed examination of long song sequences from individual birds. These were recorded, along with commentary on context and location, during spontaneous singing bouts. We identified the song types used and plotted cumula-

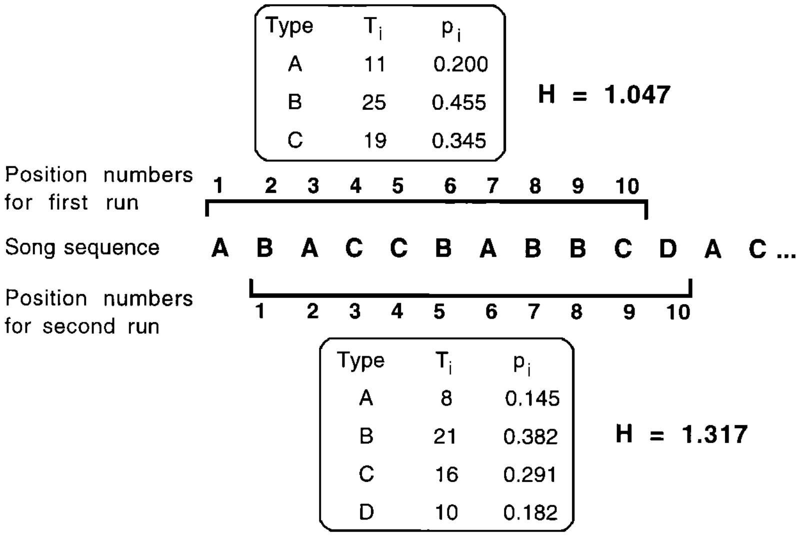

FIG. 1. Calculation of weighted song-type diversity index for a typical song sequence (center). The first 10 songs are assigned consecutive position numbers (top). The position numbers for each song type (i) are summed (T_i), and the weighted proportion of each song type, p_i, is given by T_i/T, where $T = 1 + 2 + \ldots + 10 = 55$ for a 10-song run. Diversity is $H = -\Sigma\, p_i \ln(p_i)$. The position numbers are then advanced by one song (bottom), and H is computed for the next run of 10 songs.

tive song types, intersong intervals (i.e. the difference in starting times between consecutive songs), and several running song-type diversity indices for the songs in each sequence.

The different measures of singing diversity used by previous investigators have their advantages and disadvantages (Kroodsma and Verner 1978). "Recurrence number" is the number of songs between successive renditions of a given song type. Although it is a useful tool for serial-mode singers, it is highly sensitive to sequence length and inappropriate for small samples and nonstationary contexts. "Switching rate" is the number of song-type transitions divided by the total possible number of transitions (total songs minus 1); it ignores total number of song types. "Number of song types per 10 songs" ignores switching rates and relative abundance of types. We computed all of these measures for our timed and long samples, and we also developed our own index of song-type diversity that we believe best captures the short-term changes in song-type use displayed by the Banded Wren. Essentially, our index is a running Shannon-Wiener diversity index, $H(w) = -\Sigma\, p_i \ln(p_i)$, with a moving window length of $w = 8$ or 10 consecutive songs, and where p_i = the proportion of the ith song type in the window (Shannon 1949). This index is preferable to song types per 10 songs because it gives a lower weighting to rare song types, produces a more smoothly varying running index, and provides an estimate of the uncertainty (inverse of predictability) of subsequent song types. We modified the index further with a linear weighting scheme that magnifies the influence of more recent songs in the sequence relative to earlier songs (Fig. 1). This modification enabled the index to respond more quickly to a sudden change in singing mode. For the 5-min samples, we used an 8-song run length because many of the samples had small numbers of total songs. In a random sample of 1,093 10-song runs, only 2 (0.2%) had 10 song types and 39 (3.4%) had 9 song types, whereas 97 (8.9%) had 8 song types. Therefore, the 8-song window was the smallest window length we could use without compromising the range of diversity. We averaged the H(8) values for all possible windows in the sample sequence. For the longer recorded sequences, we used a 10-song window and plotted the H(10) values for each song in the sequence. A plot of H(10) versus the number of song types per 10 songs gave a slightly decelerating curve, but when the types per 10 measure was square-root transformed to meet normality requirements, the two measures were linearly related ($r = 0.956$, $P < 0.0001$).

Standard statistical analyses were conducted with Statview 4.1. Variables for parametric tests were transformed as needed to meet the conditions of normality and homoscedasticity. Where multiple comparisons were made, significance levels for rejecting the null hypothesis were set at Bonferroni-corrected levels. All means reported in the text are presented ± 1 SD.

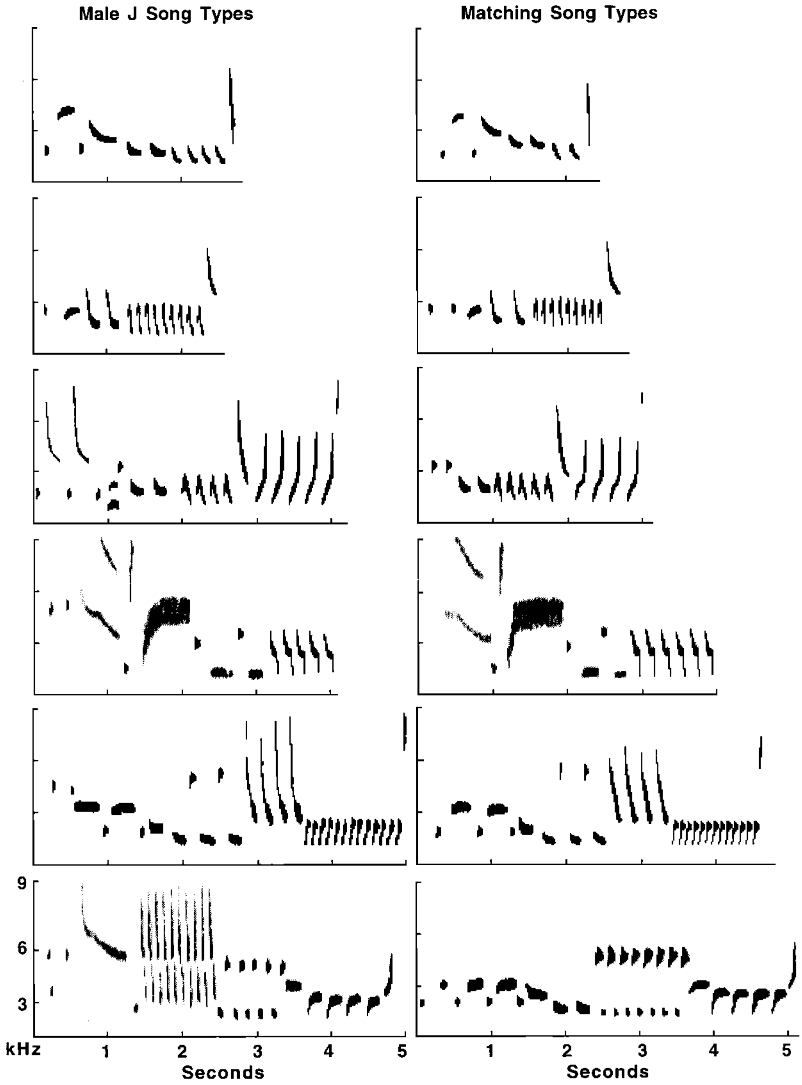

FIG. 2. Typical male Banded Wren song types. Left column shows six song types from male J's repertoire. Male J was recorded in the SR-96 site; he had a repertoire of 20 song types and an average overlap of 0.81 with other males at the site. Right column shows song-type matches to J's six song types from six different males.

RESULTS

Song structure.—Song structure in the Banded Wren is similar to that described for the conspecific Sinaloa Wren (Brown and Lemon 1979). The songs of an individual male can be easily classified into discrete song types. Song types are highly distinctive to the human ear and differ in duration (2.0 to 5.0 s), number of note and syllable types (5 to 10), and note shape and syntax. Males rarely introduce significant variation within song types during bouts, but the number of notes in the final trill may vary slightly, and introductory notes may be dropped. The left column of Figure 2 shows spectrograms of six song types from the repertoire of one male.

The right column of Figure 2 shows song types from six different males that we considered matches to songs in the left column. Examples include matches from males recorded in different sites and years. In some cases, the

TABLE 1. Repertoire size, repertoire overlap among males within a site, and Mantel correlation coefficient (r) for the association between repertoire overlap and distance between territories for Banded Wrens at five sites in Costa Rica. Repertoire values are $\bar{x}$ ± SD.

Site	n	Repertoire size	Repertoire overlap	r	P
CT95	6	19.2 ± 1.84	0.625 ± 0.045	−0.421	0.124
CT97	6	21.0 ± 0.89	0.599 ± 0.071	−0.882	0.024
CP97	5	21.4 ± 2.07	0.639 ± 0.050	−0.807	0.108
SR96	10	18.0 ± 1.63	0.769 ± 0.033	0.014	0.498
SR97	12	20.1 ± 2.90	0.779 ± 0.040	−0.469	0.004

entire song matched that of another male's song perfectly, but often consistent (though subtle) individual differences existed in the types and shapes of soft notes in the introductory portion of the song. Other songs exhibited different introductions but shared the main loud notes; these were considered full matches. Finally, a few songs seemed to combine the first part of a song type of one neighbor with the second part of a song type of another neighbor. To maintain consistent criteria, these were considered matches based on the second part of the song.

Female Banded Wrens sing, but pairs do not perform antiphonal duets. Female songs resemble male songs in general form but are lower in amplitude, and the trill notes lack the consistency of male song (as for female Northern Cardinals [*Cardinalis cardinalis*]; Yamaguchi 1998). Females occasionally insert or overlap their songs with those of the male and participate in vocal boundary disputes along with their mates. On rare occasions, females give brief bouts of solo song.

Repertoire size.—Repertoire size averaged 19.7 ± 2.4 songs types per male (range 15 to 24 song types, $n = 36$ males). Averages by site are shown in Table 1. Repertoire size differed slightly among sites (one-way ANOVA, $F = 3.12$, df = 4 and 34, $P = 0.027$), but no post-hoc pairwise comparisons met the Bonferroni critical significance level of $P = 0.005$.

Repertoire overlap.—The fraction of song types shared by adjacent territorial males averaged 0.769 ± 0.111 (range 0.476 to 0.895, $n = 38$ pairs). The average repertoire overlap among males within sites was 0.711 ± 0.089, but repertoire overlap varied among sites ($F = 26.24$, df = 4 and 34, $P < 0.0001$). Overlap was very high (0.77 to 0.78) in the forested SR site and lower (0.60 to 0.64) in the secondary growth CP and CT sites. Several between-site/year differences met the Bonferroni criterion of $P = 0.005$; all comparisons between either of the SR site-years and both CP and CT were significant ($P < 0.0001$), whereas none of the comparisons between the two SR site-years, or between the CP and CT sites, were significant ($P > 0.015$ in all cases).

Repertoire overlap tended to decline with distance between birds, but the trend was only significant in two of the five site-years (Table 1). In the SR area, the relationship between repertoire overlap and distance changed from being flat in 1996 (Mantel $r = 0.014$) to significantly negative in 1997 (Mantel $r = -0.469$). This change was associated with unusually high mortality in the intervening nonbreeding season, during which 60% of the SR-96 males disappeared and were replaced by new males. Finally, the 1997 population-level overlap of song types averaged 0.776 between the two nearby SR and CP sites (26 shared types out of 31 + 36 total types, respectively), and 0.102 between these two sites and CT (4 of the 45 types at this site were shared). Every male recorded had at least two of these four common song types in his repertoire. Between years, the index of sharing for the SR-96 and SR-97 sites was 0.807.

Singing mode.—Banded Wrens usually sing in serial mode, switching to a new song type after nearly every song. However, serial mode can entail the sequential use of many song types (i.e. large recurrence numbers), alternation between a subset of two or three song types (recurrence numbers of 1 to 2), or repetition of the same song type from one to many times (recurrence number of 0). The two most useful variables we found for describing this variability were switching rate and song-type diversity.

Singing patterns changed conspicuously during the morning hours. Bivariate regression analyses indicated that the total number of songs, switching rate, and song-type diversity decreased significantly as a function of time of

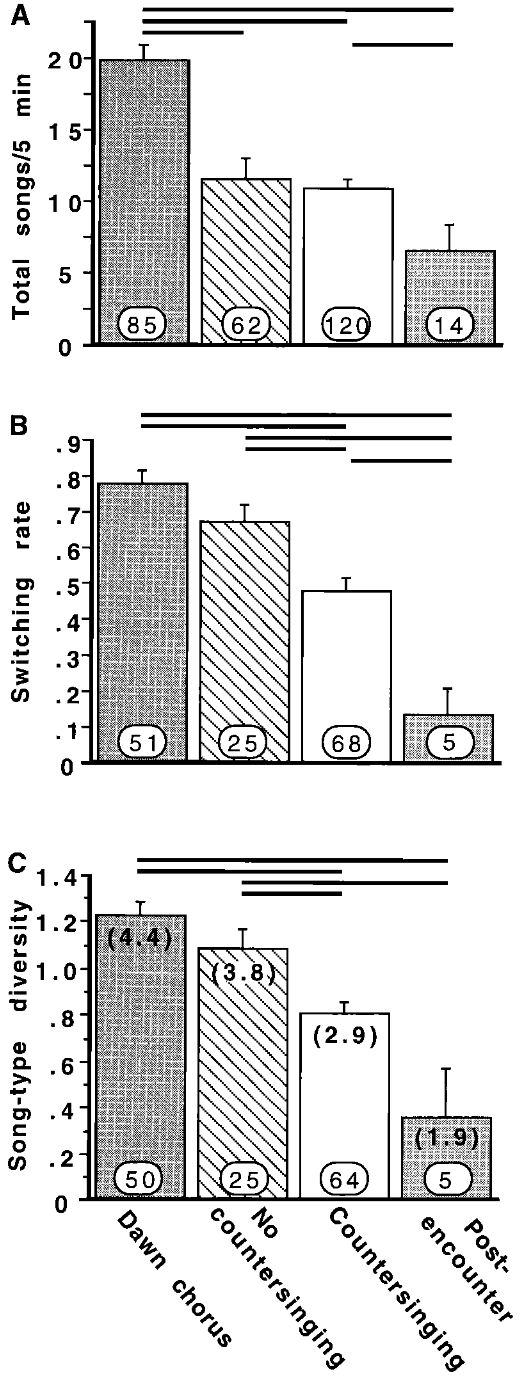

FIG. 3. Song variables ($\bar{x} \pm$ SE, with n in ovals) during four social contexts sampled for 5-min periods. (A) Total songs per 5 min ($F = 16.59$, df = 3 and 278, $P < 0.0001$). (B) Switching rate, including only samples with eight or more songs ($F = 18.15$, df = 3 and 146, $P < 0.0001$). (C) Average song-type diversity H(8), including only samples with eight or more songs ($F = 13.35$, df = 3 and 141, $P < 0.0001$). Bold numbers in parentheses are average number of song types per 8 songs. Horizontal bars connect contexts with significant differences by the Bonferroni/Dunn post-hoc test criterion of $P < 0.008$. ANOVAs were performed on transformed data.

day (total songs vs. time, $r = -0.352$, $n = 540$, $P < 0.0001$; switching rate vs. time, $r = -0.374$, $n = 255$, $P < 0.0001$; average 8-song diversity vs. time, $r = -0.396$, $n = 188$, $P < 0.0001$). Much of this time-of-day effect appeared to be associated with changing contexts. Figures 3A–C show the mean values of total songs, switching rate, and song-type diversity in four contexts: dawn chorus (all pre-0545 samples except encounters), post-chorus without obvious countersinging, post-chorus with countersinging, and close encounters. The dawn chorus was characterized by high singing rates, high switching rates, and high song-type diversity. In the post-chorus period, song rates declined significantly, and males often countersang with specific neighbors. Switching rate ($P = 0.003$) and song-type diversity ($P = 0.006$) were lower during countersinging compared with the social context of no countersinging. In the few samples that followed a close encounter or fight between two males at their common boundary, singing mode differed drastically. One male usually remained at the boundary and sang repetitively (i.e. low switching rate and low song-type diversity), while the other male gave rattle calls or became silent and retreated.

The longer sequences we analyzed for single birds showed how singing mode varied over short time periods and changed during the course of an interaction. Figure 4A illustrates a typical dawn chorus bout recorded for 15 min. This male was not interacting or countersinging in an obvious way with any of his neighbors during the recording period and remained at the same singing perch in the central part of his territory. Most song types used were introduced during the first few minutes of the bout and were repeated from 1 to 12 times in a random-like pattern. Diversity decreased slightly ($r = -0.375$, $P = 0.0014$), and intersong interval increased ($r = 0.368$, $P = 0.0009$) during the bout. Figure 4B illustrates a sequence in which a male sang a similar cumulative number of

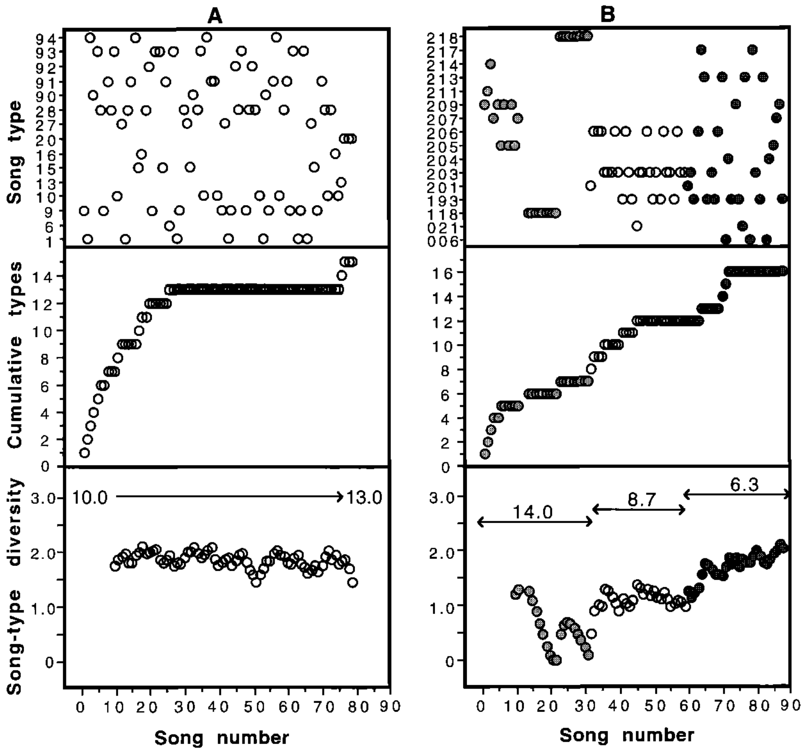

FIG. 4. Song sequence of two male Banded Wrens during 15 min of dawn chorus (before 0530) plotted from three perspectives. Top panel shows song types used, middle panel shows cumulative number of song types, and bottom panel shows song-type diversity H(10) versus song number (the position of the song in the bout). Arrows and numbers in bottom panel show changes in intersong interval (s) during the bout. (A) Typical singing bout by male K/c, who did not interact with neighbors during the bout. Song-type diversity decreased gradually, whereas intersong interval increased. (B) Singing bout of male J, who interacted with three different birds during the sequence. He first approached neighbor D (light gray circles) and engaged in a brief encounter with him after song 11. D retreated, making rattle noises, while J continued to sing. Neighbor H began countersinging with J at song 28 (open circles). Countersinging continued until song 37, when neighbor D and his mate each sang short songs. J continued to sing, loudly and from a high perch, until song 60, when he joined his mate near the ground (dark gray circles). After this point, his songs were sung softly and at a significantly higher rate.

song types, but in a much different fashion. The bird first participated in a brief boundary dispute with one neighbor that he appeared to win, then countersang with another neighbor, and approached his mate at the end of the bout. Changes in his singing pattern occurred concurrently with changes in position and activity. As he approached the first neighbor, he changed from high-diversity singing to alternation between two song types. After the encounter, he sang repetitively from the boundary. He then moved to a high perch and began countersinging with a second neighbor using a high-switching but low-diversity mode (alternation between three song types). High-diversity singing, like that shown in Fig. 4A but at a low amplitude, was associated with approach to the male's mate near the ground. Intersong interval was significantly shorter during this female phase compared with the prior-male-interaction phase (6.30 ± 5.16 s vs. 11.3 ± 5.99 s; *t*-test on ln-transformed data, $P < 0.0001$). It therefore appears that slower, low-diversity, repetitive singing is used in more aggressive contexts, whereas the faster, high-diversity, high-switching mode is used in nonaggressive contexts. Furthermore, switching rate and song-type diversity can be varied somewhat independently of each other; a reduction in diversity is associated with the initial stages of a countersinging contest, and a subsequent reduction in switching rate is associated with more escalated stages.

Discussion

Song structure, repertoire size, and primary singing mode.—The Banded Wren has a relatively complex song structure with many note and syllable types per song, a moderately sized repertoire of highly distinctive song types, and serial mode style of singing with a tendency to use subsets of types in a bout of singing. These song traits are very similar to one of the Banded Wren's congeners, the Sinaloa Wren (Brown and Lemon 1979). Song structure in this species is also characterized by long duration, moderate internal repetition, a variety of note types, and a loud terminal trill. Repertoire size is approximately the same; Brown and Lemon (1979) counted 15 to 17 song types per male *T. sinaloa,* which they did not believe represented complete repertoires. In addition, they documented that the two species share the following singing strategies: (1) occasional song-type matching; (2) occasional multiple-song utterances; (3) high singing perches; (4) no coordinated duetting; and (5) female songs that are male-like but shorter, softer, and infrequent. The distributional range of the Sinaloa Wren extends along the Pacific coast of Mexico, and it is largely allopatric with the Banded Wren, suggesting that the two are recently diverged sibling species.

Repertoire size for the Banded Wren is slightly smaller than that described for several other congeners (e.g. 32 for Carolina Wren [*T. ludovicianus*], 29 for Happy Wren [*T. felix*], and 16 for Bay Wren [*T. nigricapillus*]; Brown and Lemon 1979, Morton 1987, Levin 1996a). However, the song structure and singing behavior of these three species are markedly different. All three commonly produce coordinated male-female duets. Songs are shorter and consist of a single repeated multinote syllable that alternates with a different syllable by the mate. Furthermore, all are repeat-mode singers. This simpler song structure facilitates duetting, and the repetitive song structure and singing mode may aid in song-type recognition (Brown and Lemon 1979). Other wrens (Troglodytidae) with serial-mode singing have much larger repertoire sizes than the Banded Wren. Males in Washington populations of the Marsh Wren have more than 100 song types that they largely share with their neighbors and, like Nightingales (*Luscinia megarhynchos*), they tend to cycle through their entire repertoire in a predictable order (Todt 1971, Verner 1976). We have no evidence for this kind of ordered cycling in the Banded Wren (see Fig. 4A) but have not undertaken a formal analysis of song sequences. Marsh Wrens in Illinois, in contrast, exhibit a strategy similar to that of Banded Wrens, with smaller repertoires (40) and a mixture of subset-mode and repeat-mode singing (Kroodsma 1977). Rock Wrens also employ subset-mode singing and have somewhat smaller repertoire sizes (69 to 119; Kroodsma 1975). Finally, Sedge Wrens in the temperate zone have very large repertoires (110 or more) of unshared song types (Kroodsma and Verner 1978).

At least three selective factors seem to affect repertoire size in songbirds: (1) female preference for larger song type repertoires has been documented for several species in the laboratory and in the field, suggesting a mate-attraction function for repertoires (Catchpole 1980, Searcy and Marler 1984, Searcy 1992, Mountjoy and Lemon 1996, Hasselquist et al. 1996); (2) competitive interactions among males involving leader-follower roles and anticipated matching of song types seems to result in large repertoires of ordered song-type sequences (Kroodsma 1979, Todt and Hultsch 1996); and (3) competitive interactions among males involving variable switching rates among song types and/or strategic use of shared and unshared song types favors a smaller repertoire of highly distinctive song types to facilitate type recognition (Horn and Falls 1996). In the Banded Wren, the third factor appears to be the primary process leading to a moderately small repertoire size, but female preference for large repertoires may have favored high-diversity singing when in close proximity to the female and perhaps during the dawn chorus (see Figs. 4A, B).

Repertoire overlap.—Repertoire overlap was relatively high in the Banded Wren, averaging 71% for males within a site and 77% for adjacent males. The variation in repertoire overlap among adjacent males was also high, ranging from a low of 47% to a high of 90%. Some of this variation was explained by site differences, with significantly higher overlap in forested habitat compared with the patchy, broken-canopy habitats. Song-type sharing decreased with distance between males and dropped to 10% between sites separated by 8 km.

The two best-studied congeners also show high levels of song sharing with intriguing intraspecific variation. In the Carolina Wren, repertoire overlap between neighbors of mainland populations averages 64%, and song-type sharing between populations decreases much more slowly with the distance between populations (56% overlap at 20 km) compared with the Banded Wren. Island populations of the Carolina Wren have somewhat higher repertoire overlap between neighbors (69%), and song-type sharing between island and adjacent mainland populations is very low (Morton 1987). These population differences are believed to be a consequence of the water gap acting as a significant dispersal barrier. In the Bay Wren, females exhibit higher song-type sharing levels than males (ca. 84% vs. 23%, respectively; Levin 1996a). Females lead the duets in this species; it is believed that females sing primarily for territory defense, whereas males sing to guard their mates against other males.

These patterns of repertoire overlap (partial but variable overlap between neighboring males, gradual decline in song-type sharing with distance) are consistent with the song-learning model developed by Beecher et al. (1994, 1996) for western populations of Song Sparrows. In this species, memorization of song types by young birds is restricted to a critical period of two to three months following nutritional independence. During this time, the young birds float among the territories of several adults who serve as song tutors. Sometime before the next breeding season, yearlings attempt to acquire a vacated territory as close to their floater range as possible. If they succeed in obtaining a territory near some of their tutors, males end up sharing a large fraction of song types with their neighbors, but if they obtain a territory farther away they share fewer or no song types. Age-restricted learning has been demonstrated in the lab for both Carolina Wrens and Bay Wrens (Morton et al. 1986, R. N. Levin pers. comm.). We also found no evidence for postdispersal learning of new song types by Banded Wrens.

Given that this model is correct, what factors might explain the different sharing levels we observed in the forested SR site compared with the patchy second-growth CP and CT sites? Continuous mature forest appears to be a more preferred, higher-quality habitat for Banded Wrens than is second-growth habitat for two reasons: (1) forest territories are smaller than those in second growth; and (2) second-growth areas contain ample densities of ant acacia trees for nesting, but encompass more uninhabitable grassy areas and less forest understory that the wrens require for foraging. High-quality habitats could foster higher repertoire overlap in several ways. First, adult survival and territory tenure may be higher in good habitat such that the few vacancies that occur always are filled by local floaters rather than by long-distance dispersers. Second, high-quality habitats may produce more offspring and be net exporters of young males. In this case, territory vacancies in source populations would be filled by local offspring, whereas many vacancies in sink populations would be filled by dispersers from the source populations. Third, offspring may hatch earlier on average in forest compared with second-growth habitat; early hatching allows young males to memorize more total songs and thereby achieve a higher fraction of shared song types. We do not have sufficient data on mortality, reproductive success, and dispersal distances to test these ideas quantitatively. However, because repertoire overlap remained high in SR-97, even after very high adult mortality during the previous dry season, the differences in overlap were more likely to have resulted from the effects of habitat quality on immature floaters (second and third scenarios) than from the effects on territorial adults.

Even if variation in repertoire overlap is a byproduct of habitat features, it serves a territorial function in many species by allowing repertoire and song-type matching. Matched-type countersinging has been shown to occur in escalated aggressive contexts, or is followed by close aggressive approach, in several species with partial repertoire overlap (Lemon 1974, Krebs et al. 1981, Simpson 1985, Nielsen and Vehrencamp 1995). Repertoire matching may direct mild threats to specific neighbors without escalating the encounter (Beecher et al. 1996). We have observed Banded Wrens to use different song types and song-type matching in spontaneous interactions and in response to playback, suggesting that these behaviors have value as signals in territorial interactions.

Singing modes.—The basic daily singing pattern of Banded Wrens during the breeding season appears to be typical of dawn-chorus singers (Staicer et al. 1996), with early, intense song activity tapering to occasional and shorter bouts by mid-morning. Switching rate and song-type diversity also decline from dawn to mid-morning. A similar diurnal decrease in singing diversity was also described in the Sedge Wren (Kroodsma and Verner 1978). Although we found a strong positive correlation between song rate and song-type diversity, we believe this is a spurious consequence of opposing singing strategies in different contexts. When Banded Wren males are undertaking general territorial advertisement (dawn chorus) and singing to females, they use a large number of song types in random order and deliver songs at high rates. When males are interacting with other males, they use fewer song types in more predictable patterns and reduce their song rates, perhaps to allow them to listen for their opponent's song-type choice and respond appropriately. Repeat-mode singers also often exhibit the positive correlation between song-type diversity and song rate, but they have reversed the contextual rule. Here, general advertisement singing involves low switching and singing rates, whereas intense interactions, either with encroaching male neighbors or with females, cause an increase in switching and singing rates (Simpson 1985, Kramer et al. 1985, Falls et al. 1990, Searcy and Yasukawa 1990, Horn and Falls 1991, Langmore 1997). Repeat-mode and serial-mode singing thus seem to represent two stable alternative antithetical signaling systems for conveying graded agonistic information (Hurd et al. 1995).

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LITERATURE CITED

ARCESE, P. 1989. Territory acquisition and loss in male song sparrows. Animal Behaviour 37:45–55.

BEECHER, M. D. 1996. Birdsong learning in the laboratory and field. Pages 61–78 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

BEECHER, M. D., S. E. CAMPBELL, AND P. K. STODDARD. 1994. Correlation of song learning and territory establishment strategies in the Song Sparrow. Proceedings of the National Academy of Sciences USA 91:1450–1454.

BEECHER, M. D., P. K. STODDARD, S. E. CAMPBELL, AND C. L. HORNING. 1996. Repertoire matching between neighbouring Song Sparrows. Animal Behaviour 51:917–923.

BROWN, R. N., AND R. E. LEMON. 1979. Structure and evolution of song form in the wrens *Thryothorus sinaloa* and *T. felix*. Behavioral Ecology and Sociobiology 5:111–131.

CATCHPOLE, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74: 149–166.

CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. Bird song: Biological themes and variations. Cambridge University Press, Cambridge, United Kingdom.

CHARIF, R. A., S. MITCHELL, AND C. W. CLARK. 1995. Canary 1.2 user's manual. Cornell Laboratory of Ornithology, Ithaca, New York.

ENGINEERING DESIGN. 1996. RTS Real-time Spectrogram user's guide, version 2.0. Engineering Design, Belmont, Massachusetts.

EWERT, D. N., AND D. E. KROODSMA. 1994. Song sharing and repertoires among migratory and resident Rufous-sided Towhees. Condor 96:190–196.

FALLS, J. B., T. E. DICKINSON, AND J. R. KREBS. 1990. Contrast between successive songs affects the response of Eastern Meadowlarks to playback. Animal Behaviour 39:717–728.

FARABAUGH, S. M. 1982. The ecological and social significance of duetting. Pages 85–124 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma, E. H. Miller, and H. Ouellet, Eds.). Academic Press, New York.

HASSELQUIST, D., S. BENSCH, AND T. VON SCHANTZ. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the Great Reed Warbler. Nature 381:229–232.

HORN, A. G., AND J. B. FALLS. 1991. Song switching in mate attraction and territory defense by Western Meadowlarks (*Sturnella neglecta*). Ethology 87:262–268.

HORN, A. G., AND J. B. FALLS. 1996. Categorization and the design of signals: The case of song repertoires. Pages 121–135 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

HUGHES, M., S. NOWICKI, W. A. SEARCY, AND S. PETERS. 1998. Song-type sharing in Song Sparrows: Implications for repertoire function and song learning. Behavioral Ecology and Sociobiology 42:437–446.

HULTSCH, H., AND D. TODT. 1981. Repertoire sharing and song-post distance in Nightingales (*Luscinia megarhynchos* B.). Behavioral Ecology and Sociobiology 8:183–188.

HURD, P. L., C. A. WACHTMEISTER, AND M. ENQUIST. 1995. Darwin's principle of antithesis revisited: A role for perceptual biases in the evolution of intraspecific signals. Proceedings of the Royal Society of London Series B 259:201–205.

KRAMER, H. G., R. E. LEMON, AND M. J. MORRIS. 1985. Song switching and agonistic stimulation in the Song Sparrow (*Melospiza melodia*): Five tests. Animal Behaviour 33:135–149.

KREBS, J. R., R. ASHCROFT, AND K. VAN ORSDOL. 1981. Song matching in the Great Tit, *Parus major.* Animal Behavior 29:918–923.

KROODSMA, D. E. 1974. Song learning, dialects and dispersal in the Bewick's Wren. Zeitschrift für Tierpsychologie 35:352–380.

KROODSMA, D. E. 1975. Song patterning in the Rock Wren. Condor 77:294–303.

KROODSMA, D. E. 1977. Correlates of song organization among North American wrens. American Naturalist 111:995–1008.

KROODSMA, D. E. 1979. Vocal dueling among male Marsh Wrens: Evidence for ritualized expression of dominance/subordinance. Auk 96:506–515.

KROODSMA, D. E. 1996. The ecology of passerine song development. Pages 3–19 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

KROODSMA, D. E., AND R. A. CANADY. 1985. Differences in repertoire size, singing behavior, and associated neuroanatomy among Marsh Wren populations have a genetic basis. Auk 102:439–446.

KROODSMA, D. E., AND J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. Auk 95:703–716.

KROODSMA, D. E., AND J. VERNER. 1987. Use of song repertoires among Marsh Wren populations. Auk 104:63–72.

LANGMORE, N. E. 1997. Song switching in monandrous and polyandrous Dunnocks, *Prunella modularis.* Animal Behaviour 53:757–766.

LEGENDRE, P., AND A. VAUDOR. 1991. The R package: Multidimensional analysis, spatial analysis. Département de sciences biologiques, Université de Montréal, Montreal, Quebec.

LEMON, R. E. 1974. Song dialects, song matching, and species recognition by Cardinals *Richmondena cardinalis.* Ibis 116:545–548.

LEVIN, R. N. 1996a. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiments. Animal Behaviour 52:1093–1106.

LEVIN, R. N. 1996b. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments. Animal Behaviour 52:1107–1117.

MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209–220.

MCGREGOR, P. K., AND J. R. KREBS. 1982. Song types in a population of Great Tits (*Parus major*): Their distribution, abundance, and acquisition by individuals. Behaviour 79:126–152.

MORTON, E. S. 1987. The effects of distance and isolation on song-type sharing in the Carolina Wren. Wilson Bulletin 99:601–610.

MORTON, E. S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. Pages 258–258 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

MORTON, E. S., S. L. GISH, AND M. VAN DER VOORT. 1986. On the learning of degraded and undegraded songs in the Carolina Wren. Animal Behaviour 34:815–820.

MOUNTJOY, D. J., AND R. E. LEMON. 1996. Female choice for complex song in the European Starling: A field experiment. Behavioral Ecology and Sociobiology 38:65–71.

NELSON, D. A., C. WHALING, AND P. MARLER. 1996. The capacity for song memorization varies in populations of the same species. Animal Behaviour 52:379–387.

NIELSEN, B. M. B., AND S. L. VEHRENCAMP. 1995. Responses of Song Sparrows to song-type matching via interactive playback. Behavioral Ecology and Sociobiology 37:109–117.

READ, A. F., AND D. M. WEARY. 1992. The evolution of bird song: Comparative analyses. Philosophical Transactions of the Royal Society of London Series B 338:165–187.

SEARCY, W. A. 1992. Song repertoire and mate choice in birds. American Zoologist 32:71–80.

SEARCY, W. A., AND P. MARLER. 1984. Interspecific differences in the response of female birds to song repertoires. Zeitschrift für Tierpsychologie 66:128–142.

SEARCY, W. A., AND K. YASUKAWA. 1990. Use of the song repertoire in intersexual and intrasexual contexts by male Red-winged Blackbirds. Behavioral Ecology and Sociobiology 27:123–128.

SEARCY, W. A., AND K. YASUKAWA. 1996. Song and female choice. Pages 454–473 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

SHANNON, C. E. 1949. The mathematical theory of communication. University of Illinois Press, Urbana.

SIMPSON, B. S. 1985. Effects of location in territory and distance from neighbours on the use of song repertoires by Carolina Wrens. Animal Behaviour 33:793–804.

STACIER, C. A., D. A. SPECTOR, AND A. G. HORN. 1996. The dawn chorus and other diel patterns in acoustic signaling. Pages 426–453 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

STILES, F. G., A. R. SKUTCH, AND D. GARDNER. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York.

TODT, D. 1971. Aquivalente und konvalente gesangliche Reaktionen einer extrem regelmässig singenden Nachtigall (*Luscinia megarhynchos* B.). Zeitrshrift Vergleichende Physiologie 71:262–285.

TODT, D., AND H. HULTSCH. 1996. Acquisition and performance of song repertoires: Ways of coping with diversity and diversity. Pages 79–96 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.

VERNER, J. 1976. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. Living Bird 14:263–300.

YAMAGUCHI, A. 1998. A sexually dimorphic learned birdsong in the Northern Cardinal. Condor 100: 504–511.

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