CHARACTERISTICS, USE, AND SIGNIFICANCE OF TWO SINGING BEHAVIORS IN GRACE'S WARBLER (*DENDROICA GRACIAE*)

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ABSTRACT.—Each male Grace's Warbler (*Dendroica graciae*) possessed two distinct subsets (*A* and *B*) of preferred songs and sang each subset with a different singing behavior. In singing behavior *A*,males sang subset *A* songs in a more repetitive manner (e.g. XXXX . . .); in singing behavior *B*, males sang subset *B* songs in a more variable, often alternating, manner (e.g. YZYZ . . .). Furthermore, singing behavior *B* was significantly higher in song diversity, rate, and complexity than singing behavior *A*; and the structure of *B* songs was more variable than the structure of *A* songs. The particular song types used in the two behaviors varied among males and, in several cases, the same song type was used in the opposite singing behavior by different males. I suggest that singing behaviors rather than song types are key features in song communication in this species.

Pairing status, time of season and day, location in the territory, and type of social interaction significantly affected the choice of singing behavior. Prior to pair formation and whenever males interacted with females, singing behavior *A* predominated. After pairing, singing behavior *B* predominated, particularly in countersinging between neighboring males, at songposts, and at dawn. Thus, in a relative comparison of functions, singing behavior *A* appears to have a stronger intersexual component, and singing behavior *B* a stronger intrasexual component. Presumably, the two singing behaviors differ in function and have been shaped by different selection pressures. They are used in ways parallel to, and thus functionally similar to, the two kinds of song identified in several other species of wood-warbler. *Received 8 February 1988, accepted 2 August 1988.*

UNLIKE many songbirds, male wood-warblers (Parulinae) of several species use different song types from their repertoire in different circumstances. Observers have long noted that certain wood-warblers sing different songs early vs. late in the breeding season (e.g. Saunders 1935, Kendeigh 1945, Ficken and Ficken 1962). Detailed descriptions of song use have since been made for the Golden-winged Warbler (*Vermivora chrysoptera*), Blue-winged Warbler (*V. pinus*), Yellow warbler (*Dendroica petechia*), Chestnut-sided Warbler (*D. pensylvanica*), Prairie Warbler (*D. discolor*), Black-throated Green Warbler (*D. virens*), Blackburnian Warbler (*D. fusca*), and American Redstart (*Setophaga ruticilla*) (Gill and Lanyon 1964; Ficken and Ficken 1965, 1967; Lein 1972, 1978; Morse 1966, 1967, 1970; Nolan 1978; Lemon et al. 1987). Each of these species has been reported to have two types or groups of songs distinguishable by the human ear (but see Lein 1978) that are shared by all males in the population (but see Lemon et al. 1985). Each species tends to use the two kinds of songs in the same set of divergent circumstances (e.g. one, when males are unpaired or near females; and the other, when males interact at territory borders).

Although various explanations for these vocal behaviors have been proposed (Ficken and Ficken 1965, Lein 1972, Morse 1970, Kroodsma 1981, Lemon et al. 1987), their functional significance remains unclear. All paruline species whose vocal behavior has been intensively studied breed in eastern North America and are sympatric with many other species. Some workers have suggested that the kind of song used early in the season may function in reproductive isolation among paruline species, because this song appears to be more species-specific (Ficken and Ficken 1962, 1965, 1967) and is more stereotyped geographically (Kroodsma 1981). Similarly, species in depauperate faunas, with few sympatric warbler species, may not possess two distinct kinds of song (Morse 1966). Grace's Warbler (*Dendroica graciae*), one of the least known parulines of North America (Webster 1961), is sympatric with relatively few paruline species throughout its range (A.O.U. 1983). It

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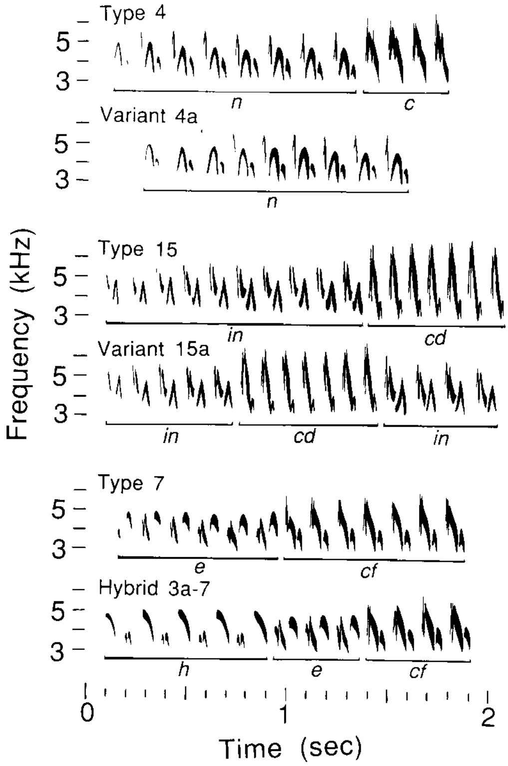

Fig. 1. Six songs recorded from male I-6. The spectrum of intra-individual variability in song structure is illustrated by these 3 pairs of songs. Upper pair: Variant 4a (*n*) resulted from omission of the second phrase (*c*) from a Type 4 (*n-c*) song. Middle pair: Variant 15a (*in-cd-in*) resulted from addition of the first phrase (*in*) to the end of a Type 15 song (*in-cd*). Lower pair: Hybrid 3a-7 (*h-e-cf*) resulted from combination of the first phrase (*h*) from a Type 3 song (*h-cd*)(Fig. 2, middle right) with a Type 7 song (*e-cf*). In Figs. 1–3, phrase types are denoted by the letter code for the syllable type in each phrase, and phrases are indicated by bars below each phrase, at a reference frequency of 2.5 kHz.

breeds in pine forests from the southwestern U.S. to Central America (Webster 1961) and is thought to have had no past affiliation with the eastern coniferous forest (Mengel 1964). Published descriptions of its songs do not suggest two distinct types (Bent 1953, Griscom and Sprunt 1957), and preliminary recordings I made in 1979 confirmed the lack of two types, distinguishable either by ear or by sound spectrogram, that were shared by males.

In order to describe the system of song communication of Grace's Warblers and to gain insight into the function and evolution of song in wood-warbler, I studied the details of song variation and use by members of this species. I tape-recorded samples of males singing throughout the breeding season and analyzed spectrographically every recorded song. This had two advantages over previous studies. I was able to describe and compare intra- and inter-individual song variation more quantitatively and to quantify certain aspects of singing behavior, song diversity, complexity, and variability. I found a dichotomy of singing behaviors for the individual male, apparently a critical organizing feature of Grace's Warbler song communication. I showed that the two singing behaviors were associated significantly with different circumstances. This implies that the signals have different functions and have been shaped by different selection pressures.

METHODS

Data collection.—I studied the behavior of 15 territorial male Grace's Warblers at 2 sites from 20 April to 17 July 1980. Sites I and II were located 17 km apart in *Pinus ponderosa* forest 50 km south of Flagstaff, Arizona (see Szaro and Balda 1979 and Staicer 1982 for more detail). I mapped the territory of each male, monitored his breeding status, and tape-recorded samples of his singing behavior throughout the study period. I continuously recorded a singing male for 5–10 min, then moved between territories to record as many singers as possible before returning to a previously recorded male. For each recording, I identified the male and noted the date, time, location, and type of social interaction, if any. I identified each male by location relative to territorial boundaries and by individual mannerisms such as unique song types (see Slater et al. 1981). I made all recordings with the same 46 cm Dan Gibson EPM-200 Parabolic microphone and Uher 4000 IC tape recorder at tape speed of 9.5 $\text{cm}\cdot\text{s}^{-1}$.

I concentrated on the population at Site I ($n = 9$ males), where territories were contiguous and breeding was relatively synchronous. Site II ($n = 6$ males) typically supported lower densities of Grace's Warblers (Szaro and Balda 1979), only some territories were contiguous, and 2 males remained unpaired throughout the 1980 breeding season. Otherwise, results for Site II were similar to those for Site I. Although I have included only data for 1980, results of observations and recordings at both sites in 1979 (nesting phase) and 1983 (courtship and nesting phases), and in several other populations in 1983, were consistent with those presented here.

Song terminology.—I used the following terminology to quantify the composition of songs so that I could compare objectively the song variation both within and among individuals (examples refer to Fig. 1 unless otherwise noted). A *syllable* was a repeated unit within a song and was symbolized by a letter (e.g. the Type 4 song was composed of 8 repetitions

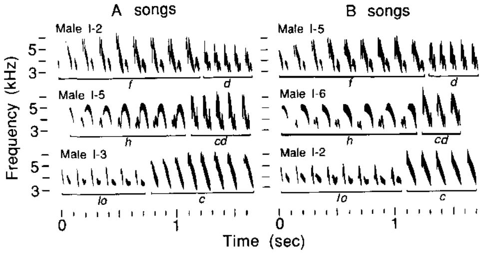

Fig. 2. Common song types used by a particular male as an *A* song (left) and by a neighboring male as a *B* song (right). Upper row, Type 2 (*f-d*); middle row, Type 3 (*h-cd*); lower row, Type 10 (*lo-c*). There were no consistent differences between examples of *A* and *B* songs of the same type from different males.

TABLE 1. Phrase patterns of male I-6 recorded in >1 sample.[a] Preferred songs (Types 3, 4, 7) occurred in nearly all samples and constituted the majority of his songs.

Designation and code	Phrase pattern	No. of samples	No. of songs
Type 4	*n-c*	29	491
Variant 4a	*n*	4	8
Type 3	*h-cd*	28	359
Hybrid 7a-3	*e-h-cd*	10	24
Type 7	*e-cf*	26	251
Hybrid 3a-7	*h-e-cf*	14	30
Type 15	*in-cd*	5	24
Variant 15a	*in-cd-in*	4	8
Variant 15b	*in-cd-in-cd*	2	12
Type 12	*k-r-c*	4	21
Type 2	*f-d*	2	5

[a] The 1,256 songs recorded for male I-6 from 55 separate samples represented 27 phrase patterns, 11 of which occurred in >1 sample. In addition, 16 phrase patterns occurred in only one sample: *ha-b, ha-b-g, ha-b-g-f-g, ha-b-e-b, g-b, g-b-f-g, g-b-h-b-g-f, f-g, h, h-b, h-b-g-f-g, b-h-e, b-g-f-g, n-h, n-h-cd,* and *k*. The first 13 occurred together in 1 recording of unstereotyped singing (see text) and contained 3 syllable types (*ha, b, g*) not recorded previously from the male, suggesting the phrase pattern *ha-b-g* may represent a seventh song type of male I-6.

of the syllable type *n* and 4 of the syllable type *c*). Syllable types shared among males were represented by the same letter code in the songs of different individuals (Figs. 2, 3). A *phrase* was a series of repeated syllables of one type and was symbolized by the code for the syllable type it contained (e.g. the *n* phrase contained a series of *n* syllables). A *song* was a general term for a series of syllables preceded and followed by silent intervals of relatively long duration (several seconds) in comparison to the silent intervals between syllables. A *phrase pattern* (e.g. *in-cd-in*) was the specific sequence of phrases of a given song and was symbolized by a numerical song code (e.g. 15a). A *song sequence* was a consecutive series of songs sung by a male during steady, continuous singing.

To describe song variation within individuals I defined *song type, song variation, variant,* and *hybrid* such that designation of songs to these categories was specific to each male (Table 1). Each male had a repertoire of relatively few discrete *song types* (5–9), as well as the ability to vary these types to produce many *song variations* (20–83) (Staicer 1982). The term "song type" usually refers to some basic song unit in the repertoire of a bird, so I incorporated this idea into a definition that permitted objective discrimination of the song types and song variations of a given male. I defined the *song types* of a male to be his most frequently used phrase patterns that contained, as a set, all his unique phrases, such that all his *song variations* could be derived from his song types (e.g. songs of male I-6: Fig. 1, Table 1). Each *song type* was, by definition, more frequent than its variations, and always contained 1 or more unique phrases. If the same phrase occurred in 2 song types of a given male, then it was usually represented by slightly different forms. Male I-6, for example, used noticeably different versions of the phrase *cd* in Type 15 (Fig. 1) and Type 3 (Fig. 2). In some cases, though, identical phrases occurred in >1 song type of a male (e.g. male I-8 had identical *in* phrases in 3 song types).

A *song variation* of a particular male differed from a type of the male by one or more phrases, but otherwise was more similar to that song type than to his other song types. *Variants* were variations that included phrases from only 1 song type and *hybrids* combined phrases from 2 or more song types. For example, Variant 15a of male I-6 (*in-cd-in*) was a variation of his Type 15 (*in-cd*) that included another repetition of the first syllable (*in*) of the song (Fig. 1), and Hybrid 3a-7 (*h-e-cf*) combined the first phrase (*h*) of his Type 3 (*h-cd*; Fig. 2) with his Type 7 (*e-cf*; Fig. 1). A given phrase pattern could be a song type of one male and a song variation of another male. For example, the phrase pattern *in-cd-in* (represented by the code 15a) was Variant 15a of male I-6, because he sang it less frequently than the phrase pattern *in-cd* (Type 15 of male I-6), but for his neighbor, male I-8, *in-cd-in* was Type 15a because he sang this frequently and *in-cd* (Variant 15 of male I-8) infrequently.

Song analysis.—I viewed all recordings using the continuous CRT display of a Unigon Model 4512 FFT Real Time Spectrum Analyzer. By playing tapes at half speed and freezing the CRT display for each song, I determined the exact sequence of phrases (i.e. the phrase pattern) for over 8,100 songs. I discriminated among syllable types by their form (time and frequency characteristics on wide-band spectrograms), and grouped forms if there was continuous variation among them. To document song repertoires and verify male identity, I made wide-band spectrograms of several hundred songs using a Kay Elemetrics Sona-Graph Model 6061-B. It was not possible to distinguish all pertinent details of songs by ear because, although I could detect transitions between phrases, I could not accurately identify syllable types.

Each recording contained a consecutive song series from a male during steady, continuous singing. The number of songs/recording varied, but singing behavior was usually homogeneous throughout the sample even in recordings of >50 songs. The samples I analyzed consisted of a subset of my recordings. I used the first 30 songs in each recording, but eliminated successive recordings from the same male that began <20 min apart (most recordings of a given individual were at least several hours apart), for a total of 294 samples. To compare song variation within and among individuals, I compiled a song profile of phrase patterns and their frequencies (Table 1) for each male at Sites I and II.

I quantified song rate, complexity, and diversity for each Site I sample ($n = 256$) that contained ≥ 10 songs (mean number of songs/sample = 22). To calculate song rates, I divided the time interval from the first to the eleventh song by 10 and converted to songs/min (Scoville and Gottlieb 1978; when $n = 10$, I divided the time interval from the first to the tenth song by 9). I defined song complexity as the average number of phrases/song. I computed the song diversity with the Brillioun Information Index, H (Pielou 1977), which permits the comparison of samples of different sizes. Song diversity is thus a measure of the uncertainty that any 2 songs drawn at random from the sample would be identical. I used the following formula: $H = \mathrm{n}^{-1} \log [n! \, (n_1!n_2!n_3! \ldots n_s!)^{-1}]$, where n = the number of songs in the sample, and s = the number of different kinds of phrase patterns, of which n_i are of the i^{th} kind. If 2 songs were composed of different phrase types or if phrase types appeared in different orders, the songs were, by definition, different phrase patterns.

To determine whether particular kinds of song sequences were associated with certain circumstances, I tallied the number of samples of particular song sequences that occurred during different times of season and day, at different locations within the territory, and in different types of social interactions. Contingency tables constructed in this way formed the basis for G-tests of association (Sokal and Rohlf 1981) between kinds of song sequences and circumstances. Although there was a multi-way classification for each sample, small totals in many cells precluded multivariate analysis of the data. I attempted to control for seasonal and diurnal effects on use of song by separating data by time of season and day prior to constructing contingency tables for effects of location and social interaction.

RESULTS

DESCRIPTION OF SONG VARIATION

Song structure.—Songs were composed of one or more phrases, and each phrase consisted of a particular syllable type repeated several times (Fig. 1). To the human ear, songs sounded like a series of chips that shift in pitch and quality with each phrase. Songs with 2 phrases were more common (63%) than songs with ≥ 3 phrases (32%). Songs with 1 phrase were uncommon (5%; based on 5,825 songs recorded at Site I). Songs usually contained as many syllable types as phrases, but sometimes the same phrase occurred twice in the same song, resulting in greater song complexity without an increase in the number of syllable types (Fig. 1, Variant 15a).

Variation within individuals.—Male I-6, for which I had the most recordings, illustrates song variation typical of paired males. This male had a repertoire of at least 6 song types (Table 1). He sang 3 song types (4, 3, 7) very frequently; 2 song types (12, 15), infrequently; and 1 song type (2), very rarely. The song profile of male I-6 indicates the distribution of his songs among these 6 song types and their variations (Table 1), plus a possible additional song type recorded on only 1 occasion (Table 1, footnote). Song variations included omission of a phrase, usually the end phrase (Fig. 1, Variant 4a), repetition of a phrase (Variant 15a), or recombinations of phrases from different song types (compare Types 3 and 7 and Hybrid 3a-7, Figs. 1, 2). The male had two sets of preferred song types: Type 4 songs tended to occur alone in recordings, whereas Types 3 and 7 tended to occur together in the same recordings. In addition, Types 3 and 7 were 6 times more likely to be varied than Type 4 songs, and their variations were usually hybrids. This male sang the same songs in similar proportions the previous year.

During one recording male I-6 sang a sequence of songs that was unusually unstereotyped in terms of song duration, structure, and cadence (time between songs). I termed this behavior *unstereotyped singing*. This sequence of 16 songs included 13 different phrase patterns, none of which were recorded either before or after this occasion (Table 1, footnote). These songs included three syllable types (*f*, *h*, and *e*) from Types 2, 3, and 7, plus 3 syllable types (*ha*, *b*, and *g*) not otherwise recorded from male I-6. I recorded unstereotyped singing from several other males on 1 or 2 occasions each, and these recordings usually contained syllable types or entire songs not observed in their normal singing.

Singing behaviors.—Based on the song profile of each male, it was clear that all paired males had 2 sets of preferred song types, *A* and *B*. The 2 sets of song types and their variations ac-

TABLE 2. Representative sequences of 10 consecutive *A* and *B* songs for Site I males, and the mean number of phrases per song for each sequence.[a] Note differences in sequential ordering of songs, song variability, and number of phrases/song in the 2 sequences, and variation among males in the songs used in each sequence.[b]

	A song sequence		*B* song sequence	
Male	Song codes	No. of phrases	Song codes	No. of phrases
I-1	4, 4, 4, 4, 4, 4, 4, 4, 4, 4	2.0	2c, 2b, 5-2, 2b, 2f, 5b, 2d, 2b, 2c, 2g	3.8
I-2	2, 2, 2, 2, 2, 2, 3, 3, 3, 3	2.0	1a, 10, 1a, 10, 1a, 10, 1a, 10, 1a, 1a	2.6
I-3	10, 10, 3, 3, 3, 4, 4, 4, 4, 4	2.0	1, 2a, 2-1, 2-5, 2-1, 2, 2-1a, 1, 2a, 1	3.2
I-4	4, 4, 4, 4, 4, 4, 4, 4, 4, 4	2.0	5, 5a, 5a, 3, 5a, 5a, 5a, 5a, 5a, 3	3.5
I-5	3, 3, 3, 3, 3, 3, 3, 3, 3, 3	2.0	9, 2, 2a, 9, 9, 2, 5c-9, 2, 9, 2	2.8
I-6	4, 4, 4, 4, 4, 4, 4, 4, 4, 4	2.0	7, 3, 7, 3, 7, 7a-3, 7, 3, 7, 3	2.1
I-8	4, 4, 4, 4, 4, 4, 4, 4, 4, 4	2.0	3b, 15a, 3b, 15a, 10b, 15a, 10b, 15, 10b, 3b	2.9
I-9	4, 4, 4, 4, 4, 4, 4, 4, 4, 4	2.0	2, 2e, 10a, 10c-15, 2, 10c-15, 2, 2, 2, 10c-15	2.6
I-10	3, 3, 3, 3, 3, 3, 3, 3, 3, 3	2.0	2e, 2e, 2e, 9a, 9a, 9b-2e, 9a, 9b-2e, 2e, 2e	1.5

[a] Phrase patterns of songs represented by above codes: 1: *ph-s-ph*, 1a: *j-s-ph*, 2: *f-d*, 2a: *f-d-b*, 2b: *f-b-d-in-g*, 2c: *f-d-in*, 2d: *f-d-in-g*, 2e: *f*, 2f: *f-b-d-in*, 2g: *in-g*, 2-5: *f-d-b-ha-b*, 2-1: *d-s-ph*, 2-1a: *d-s-ph-f*, 3: *h-cd*, 3b: *in-h-cd*, 4: *n-c*, 5: *ha-b-f*, 5a: *ha-b-f-d*, 5b-2c: *ha-b-f-d-in*, 5c-9: *b-ha-b-m-g*, 7: *e-cf*, 7a-3: *e-h-cd*, 9: *b-m-g*, 9a: *m-fi*, 9-2: *m-f*, 10: *lo-c*, 10a: *lo-t-in*, 10b: *in-lo-t*, 15: *in-cd*, 15a: *in-cd-in*, 10c-15: *lo-t-in-cd*.

[b] Phrase patterns 2, 3, and 10 occurred in the *A* sequence of 4 males (I-2, I-3, I-5, I-10), and occurred in the *B* sequence of 6 males (I-2, I-3, I-4, I-5, I-6, I-9). Phrases characteristic of these songs (*f*, *h*, *lo*) occurred in the *B* sequence of all males.

counted for about 95% of the songs recorded from each male, and were associated with 2 distinct singing behaviors. In *singing behavior A* a male sang *A* song types in repetitive sequences, and in *singing behavior B* the same male sang *B* song types in more variable sequences. For example, most recordings of male I-6 contained either repetitions of Type 4 songs (singing behavior *A*) or a mixture of Type 3 and 7 songs, in which the two types were alternated (singing behavior *B*) (Tables 1, 2). Most males tended to sing one *A* song type with no variation (79% of *A* sequences contained a single phrase pattern), and those tending to sing >1 *A* song type (e.g. males I-2 and I-3) sang each repeatedly before switching to another (Table 2). Males typically used 2 or 3 song types in singing behavior *B*, often alternating song types (e.g. males I-6 and I-8) and also varying the combinations of phrases in song types (e.g. male I-1; Table 2).

I grouped each male's infrequently used song types into an artificial category *X* because I could not determine unambiguously whether these song types were associated with either *A* or *B* singing behaviors. Although *X* songs may be important, they accounted for few of the total number of songs recorded per individual. Because *A* and *B* songs together accounted for >95% of all songs recorded, I excluded *X* songs from further analysis.

I found significant differences between *A* and *B* sequences in song diversity, complexity, and rate. In all comparisons, the medians for *B* sequences were higher than for *A* sequences (Table 3). The higher diversity of *B* sequences was due to the inclusion of both more song types and more song variations. Because the diversity measure (*H*) was based on the proportions of different phrase patterns, it is not identical to sequential variety. Some males tended to sing *A* sequences with high diversity (*H*) but low variety (e.g. the *A* and *B* sequences for male I-2 in Table 2 differ in sequential variety but not diversity).

I compared the *A* and *B* samples from Site I at 3 levels—within individuals, among individuals, and for the population—each of which yielded similar results (two-tailed Mann-Whitney *U*-tests). Within individuals, for each male with >6 sequences of each type (males I-1, I-2,

TABLE 3. Comparison of *A* and *B* song sequences. Medians (and ranges in parentheses) for the measured parameters of singing behavior for Site I males.[a]

Type of sequence	Samples/male	Song diversity (H)	Song complexity (phrases/song)	Song rate (songs/min)
A	10 (2–23)	0.0 (0.0–1.8) ***	2.0 (1.5–2.4) **	4.6 (3.1–5.7) ***
B	10 (6–26)	1.2 (1.0–2.1)	2.6 (1.9–4.3)	8.9 (6.7–10.3)

[a] ** = $P < 0.01$, *** = $P < 0.001$; Mann-Whitney *U*-test, $n_1 = n_2 = 9$, two-tailed, comparing medians of *A* and *B* samples for the 9 Site I males.

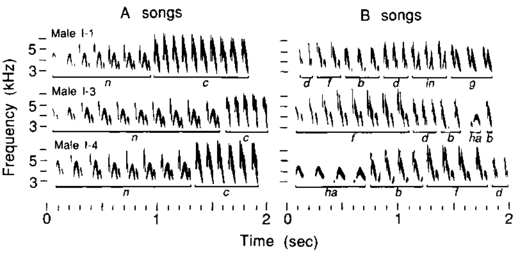

Fig. 3. Comparison of typical *A* (left) and *B* (right) songs from 3 neighbors, arranged by row. These males shared a simple (two-phrase) *A* song of Type 4 (*n-c*) but sang unique and more complex *B* songs (examples here range from four to six phrases; see also Table 2). Although each of these males used syllables *f*, *d*, and *b* in their *B* songs, each arranged the syllables in a different order (male I-1, *f-b-d*; male I-3, *f-d-b*; male I-4, *b-f-d*).

I-3, I-4, I-5, and I-6), *A* and *B* sequences differed for all 3 parameters (separate tests for each male were significant at $P < 0.001$). Among individuals, the median values of *A* and *B* sequences for the 9 Site I males were significantly different for all 3 parameters (Table 3). For the population (data pooled for all males) *A* ($n = 102$) and *B* ($n = 120$) sequences were also significantly different for all 3 parameters ($P < 0.001$). In addition, the variability in song complexity (measured by the standard error of the mean number of phrases/song of each sample) was significantly higher ($P < 0.01$) for *B* sequences in similar tests at all 3 levels.

Variation among individuals in A *and* B *songs.*—Males used their song types in consistent but individually specific ways (Table 2; Fig. 2). For example, 5 of the 9 song types used only in singing behavior *A* by certain males were used in singing behavior *B* by other males. Three of these song types, used by neighbors as either *A* or *B* songs, are illustrated in Fig. 2. The most common song, Type 4 (*n-c*; Fig. 1), was used by 11 males as an *A* song type, but male II-9 used it as a *B* song type and male II-8 had the phrases incorporated into a *B* song type (*ha-b-ha-b-n-c*). The second most common song, Type 3 (*h-cd*; Fig. 2), was used by 5 males as an *A* song type, by another 5 males as a *B* song type, and male I-8 incorporated the phrases into a *B* song type (*in-h-cd*; Table 2). Type 2 (*f-d*) was a common *B* song type but male I-2 used it as an *A* song type (Fig. 2). Of the Type 10 or similar phrase patterns (*lo-c*, *lo-t*, or *lo-g*), 3 males used one as an *A* song type whereas 2 males used one as a *B* song type (Fig. 2), and 3 males had some of the phrases incorporated into a *B* song type (e.g. *in-lo-t*, Table 2). Male I-2 used Type 11 (*ba-cd*) as an *A* song type whereas males II-5 and II-6 had the phrases incorporated into *B* song types.

Despite such variation among individuals, there was an overall tendency for *A* song types to be more similar among individuals than were *B* song types, as seen when comparing a common *A* and *B* song of three neighbors (Fig.3). All males sang a unique set of *B* song types, and at least one of each male's *B* song types was unique, though neighbors often shared one or more phrases (Fig. 3, right; Table 2). Conversely, at least 2 males shared 8 of the 9 *A* song types, and about half of the males shared the most frequently recorded *A* song, Type 4 (Fig. 3, left; Table 2).

PATTERNS OF USE OF THE TWO SINGING BEHAVIORS

Classification and analysis of samples.—I placed each sample into 1 of 4 categories based on detailed knowledge of each male's repertoire: *A* (singing behavior *A*), *B* (singing behavior *B*), *M* (mixture of *A* and *B*), or *X* (only *X* songs). In the few cases where *X* songs occurred within a sequence of definite *A* or *B* songs, I classified the sample as *A* or *B*, reasoning that those particular *X* songs were less preferred songs of the *A* or *B* category. The data (Tables 4, 5; Figs. 4, 6) are from Site I males only (the 9 intensively studied males plus a few samples from 4 additional males on adjacent territories). I combined sequences and analyzed data for Site I males at the population level because reproduction was relatively synchronized. All Site I birds paired and initiated nesting at about the same time and each had one clutch.

I separated the season into 6 periods (prepairing, courtship, nest building, incubation, nestling, and fledgling), based on observations of activities during these time periods which have been recognized as distinct periods previously (e.g. Ficken and Ficken 1965, Morse 1966). I separated the day into dawn and daytime periods, as singing is likely to be different at these times (e.g. Nolan 1978, Kroodsma in press). To control for seasonal and diurnal effects on use of song, I separated data by time of day (dawn vs. daytime) and time of season (early vs. late) before I analyzed patterns of song use at different locations and in different social

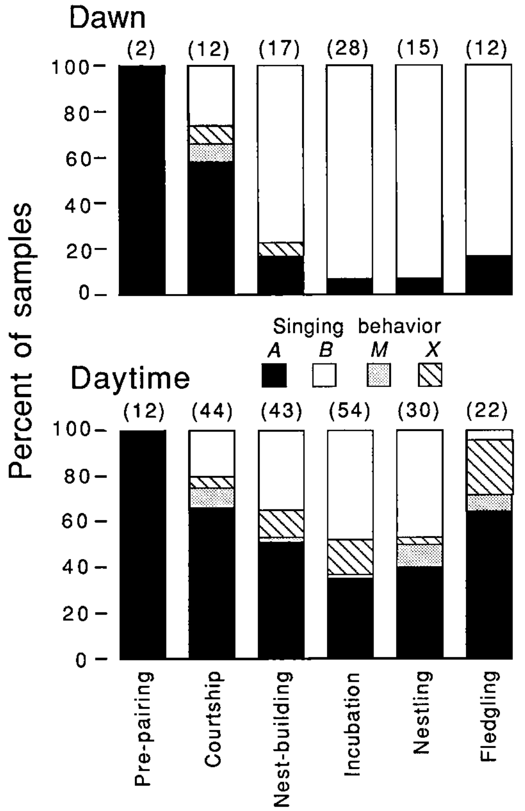

Fig. 4. Seasonal trends in dawn and daytime use of the singing behaviors. Dawn was the hour before sunlight appeared on trees, and daytime was the remainder of the day. Dates of sampling periods which corresponded to 6 distinguishable phases of the breeding cycle were: 20-28 April (pre-pairing), 3-15 May (courtship), 18-28 May (nest building), 31 May to 14 June (incubation), 18-28 June (nestling), and 1-15 July (fledgling). For Figs. 4-6: Each sample was a separate sequence of 10-30 consecutive songs recorded from a particular Site I male. The number of samples per period appears above each bar. I classified each sample to one of the following categories based on detailed knowledge of the male's repertoire: *A* (singing behavior *A*), *B* (singing behavior *B*), *M* (a mixture of *A* and *B* songs), or *X* (songs that were neither *A* nor *B*).

circumstances. Separating data by time of day allowed comparison with results of previous studies which have focused on daytime patterns of song use. I divided the season into halves—early (weeks 1-6) and late (weeks 7-12)—at the start of incubation because this seemed to represent an important change in the behavior of paired birds (males and females spent less time together after this point).

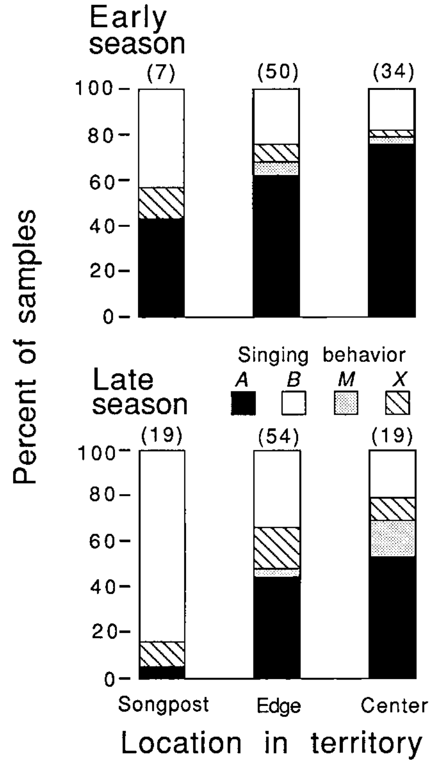

Fig. 5. Effects of location in the territory on daytime use of the singing behaviors. The location categories were: songpost (song perches from which males sang at dawn, usually on territory edges), edge (≤30 m from border and not at songpost), and center (>30 m from border and not at songpost). As in Fig. 6, seasonal effects are examined by dividing the season into halves, early (weeks 1-6) and late (weeks 7-12).

To test whether singing behavior was significantly dependent upon circumstance (time of season or day, location in territory, and type of social interaction), I used *G*-tests for association (Sokal and Rohlf 1981). Calculations were based on contingency tables in which rows were represented by the different circumstances and columns were represented by the different singing behaviors. Because behaviors *A* and *B* were of primary interest, and because cell totals for categories *M* and *X* were often very small, I included only data for categories *A* and *B* when calculating the test statistic.

Dawn song.—Males typically sang their first songs of the day about 40 min before sunrise from particular trees or *songposts.* The male sang while perched inside the upper branches, at heights of 15-25 m, of a single tree or stand of

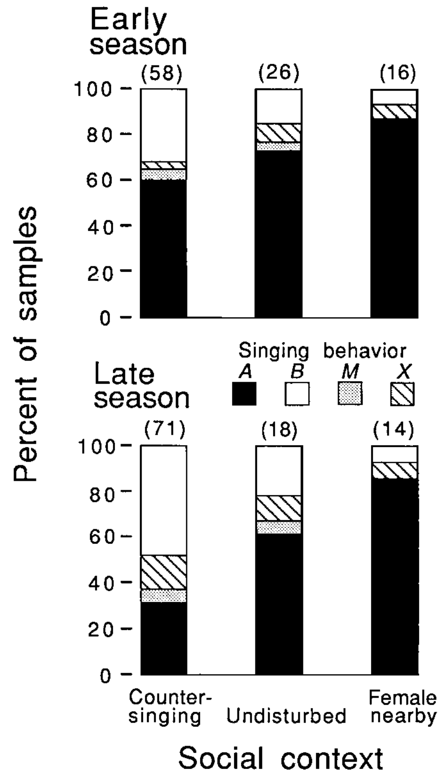

Fig. 6. Effects of social context on daytime use of the singing behaviors. The social contexts were: countersinging (singer interacting vocally with conspecific male by exchanging songs), undisturbed (singer not interacting with or nearby a conspecific), and female nearby (conspecific female ≤15 m away, usually interacting with the singer).

trees, which were often the largest pines on his territory. Although territory boundaries were contiguous, songposts were often clustered on the edges of territories, such that males were nearer to and interacted vocally with certain neighbors. Distances between songposts of neighbors were significantly less than distances between nearest territory centers (median of 67 m compared to 164 m; $P < 0.001$, one-tailed Mann-Whitney U-test) for Site I males with three or more neighbors ($n = 8$).

The continuous and intensive singing initiated at dawn usually ceased by the time that sunlight first appeared on treetops (about 20 min after sunrise for Flagstaff, Arizona). I therefore used the time "sunrise + 20 min" to separate samples into "dawn" and "daytime" periods. Diurnal patterns in singing behavior varied through the season (Fig. 4). Early in the season (pre-pairing and courtship periods) there was no significant association between singing and time of day ($G = 0.3$, df = 1, NS). For nest-building through fledgling periods, however, there was a significant association between time of day (dawn or daytime) and singing ($G = 39.5$, df = 1, $P < 0.001$).

During the pre-pairing period males used singing behavior *A* exclusively, both at dawn and in the daytime (Fig. 4). During the courtship period males began to use singing behavior *B* both at dawn and in the daytime, though singing behavior *A* remained predominant. During the next few weeks, the duration of the dawn bout of singing behavior *B* lengthened, and by the beginning of nesting, a strong diurnal pattern emerged: males used singing behavior *B* at the dawn period and switched to singing behavior *A* approximately at the start of the daytime period. From nest-building through courtship periods, males typically returned to singing behavior *B* again later in the morning. Daytime use of singing behavior *A* peaked during the first 2 h of daytime (Staicer 1982).

Seasonal patterns in daytime song.—The relative proportions of the singing behaviors changed seasonally in relation to phase of the breeding cycle (Fig. 4). Upon arrival on the study sites on or before 20 April, and continuing through the pre-pairing period, males sang *A* songs persistently throughout the day. The two males at Site II that did not obtain a mate (II-9 and II-10) continued this behavior throughout the breeding season (over 90% of each male's recorded songs were a single *A* song type). All other males obtained mates by early May and, for the next two weeks, spent much time associating with mates but singing little. Singing behavior *A* predominated, but singing behavior *B* was becoming more common.

In late May or early June, females began to incubate and, until young fledged in late June, males spent much less time associating with their mates. Song activity was consistently high and singing behavior *B* predominated (Fig. 4). By early July, most young had fledged, and territorial interactions, general song activity, and use of singing behavior *B* had decreased markedly. During the fledgling period, males used singing behavior *A* intermittently while feeding young, and the relative frequency of *X* songs (primarily those not previously recorded from individuals) increased. I terminated observa-

TABLE 4. Association between location in the territory and singing behavior (*A* or *B*). Results of *G*-tests indicate whether there were significant differences in singing behaviors used when comparing different locations.[a] Number of samples (song sequences) are in parentheses.

	Dawn			Daytime			Total day (all season)
Locations	Early[b]	Late	All	Early	Late	All	
Songpost vs. edge	2.71[c] (16)	1.41 (46)	5.74** (62)	1.13 (49)	15.44*** (59)	17.17*** (108)	51.09*** (170)
Edge vs. center	0.32 (13)	0.27 (15)	0.79 (28)	0.86 (75)	0.93 (56)	2.67 (131)	1.73 (159)
Songpost vs. center	6.43** (19)	4.01* (47)	14.60*** (66)	2.40 (38)	15.97*** (31)	24.47*** (69)	58.17*** (135)
Songpost vs. edge vs. center	6.95* (24)	4.48 (54)	16.22*** (78)	2.59 (81)	19.35*** (73)	25.20*** (154)	70.28*** (232)

[a] This table summarizes 28 separate tests for association. Each entry is the result of a R × C test of association in which the *G* statistic given was obtained. The *G* statistic is based on a 2 × 2 or 3 × 2 contingency table, where the number of rows = number of locations compared (either 2 or 3), and the number of columns = 2 for the 2 singing behaviors.

[b] Time of season: early = weeks 1-6, late = weeks 7-12, all = weeks 1-12.

[c] * = $P < 0.05$, ** = $P < 0.025$, *** = $P < 0.001$; *G* values for 2 × 2 tests of association, df = 1, or (bottom row) 3 × 2 tests of association, df = 2.

tions in mid-July because persistent territorial behavior and song activity had apparently ceased for the season.

Location effects.—I analyzed the use of singing behaviors with respect to 3 categories of location relative to an individual's territorial borders: songpost (in songpost trees), edge (≤30 m from border and not at songpost), or center (>30 m from border and not at songpost). There was a significant association between location and singing behavior, but diurnal and seasonal effects on this association were evident (Table 4). For both dawn and daytime periods, the relative proportions of the singing behaviors used at the songpost were significantly different from those used at other locations (Table 4), and these differences were more pronounced in the second half of the breeding season. There were no significant differences in the relative proportions of singing behaviors used at territory centers and edges at any time (Table 4).

Singing behavior *B* was strongly associated with songposts, whereas singing behavior *A* was used at both territory edges and centers that were not near songposts. At dawn, most sequences (64%) occurred at songposts while few occurred at edges (16%) or centers (20%); singing behavior *B* predominated at songposts in early season and in all locations in late season. Singing behavior *A* was common at dawn only in early season at territory edges and centers. Daytime patterns showed that singing behavior *A* was least common at songposts and most common in territory centers all season, but was much less common in all 3 locations and was rarely used at songposts in late season (Fig. 5). Singing behavior *B* was most common at songposts and least common in territory centers. In late sea-

TABLE 5. Association between social context and singing behavior (*A* or *B*). *G*-tests indicate whether there were significant differences in singing behaviors used in different social circumstances.[a]

	Dawn			Daytime			Total day (all season)
Contexts	Early	Late	All	Early	Late	All	
Countersinging vs. undisturbed	0.20 (25)	6.13* (54)	4.26* (79)	2.28 (76)	5.89* (72)	9.12** (148)	12.35*** (227)
Undisturbed vs. female nearby	2.80 (9)	2.39 (12)	5.77* (21)	0.99 (38)	2.06 (29)	2.80 (67)	11.01*** (88)
Countersinging vs. female nearby	4.01* (20)	6.77* (44)	12.00*** (64)	5.29* (68)	15.18*** (71)	19.70*** (139)	39.22*** (203)
Countersinging vs. undisturbed vs. female nearby	4.02 (27)	11.12** (55)	14.56*** (82)	6.37* (91)	18.17*** (86)	24.45*** (177)	44.96*** (259)

[a] Format as in Table 4.

son, singing behavior *B* became increasingly common in all locations, and predominated at songposts. Considering that most songposts were on territory edges, singing behavior *B* was strongly associated with territory edges. Mixed singing behaviors occurred mostly in territory centers (Fig. 5) and, in 2 males, *X* songs occurred mostly along the territory edge most distant from their songposts.

Effect of social interactions.—I analyzed the use of singing behaviors with respect to 3 social contexts: countersinging (singer interacted vocally and exchanged songs with another male, at variable distances but often <50 m), undisturbed (singer was neither near nor interacting with any other individual), and female nearby (female often interacted vocally, followed, or engaged in courtship with singer ≤15 m away). Overall, there was a significant association between social context and singing behavior for combined diurnal and seasonal periods, and social context had significant effects on singing behavior during most time periods (Table 5). The behavior of countersinging males was strikingly different from undisturbed males and especially from males near females, but there was less difference between the singing of undisturbed males and those near females (Table 5).

For the dawn period, patterns of song use were relatively invariable. Countersinging predominated (73% of sequences) and most recordings were *B* sequences (87%). I never observed females near males during dawn sequences of *B* songs. When females were nearby during the dawn period ($n = 5$), males sang *A* songs. Males usually began to associate with their mates at the beginning of the daytime period. Most sequences of singing behavior *A* in the dawn period were either by paired males near females, by unpaired males, or by paired males who switched from singing behavior *B* to *A* before the end of the dawn period.

For the daytime period, singing behavior *B* was most frequent in countersinging, less frequent when undisturbed, and least frequent near females. Singing behavior *A* showed the opposite pattern (Fig. 6). Males near females used singing behavior *A*, regardless of time of season. When courtship activity was most frequent (13–26 May), there was a female nearby during half of the daytime recordings; and, in all but one case, males used *A* songs. Singing behavior *A* was common in undisturbed males but less so in late season. Singing behavior *A* was used in countersinging during the pre-pairing period, but singing behavior *B* was typically used in countersinging after nesting began. No contextual effects were evident for use of *X* songs and mixed singing behaviors, except that the latter did not occur near females.

The first recording I have of *B* songs for each Site I male occurred in his second or third week on territory and during the daytime period. In each case the male was countersinging and, in half of the cases, the other male was also using singing behavior *B*. The two unpaired males on Site II used singing behavior *A* almost exclusively and did not exhibit the seasonal shift to singing behavior *B* typical of paired males. These unpaired males used singing behavior *B* only during territorial encounters ($n = 3$). Once both males switched to *B* songs upon approaching one another at a common border, and male II-9 twice responded to an intruder with singing behavior *B*. Of 21 samples during close-range territorial interactions between paired males at Site I, most (76%) involved singing behavior *B* and some (24%) involved *X* songs.

Discussion

Each male Grace's Warbler preferred certain of the song types in his repertoire, and different individuals often preferred different song types, even in cases where song types were shared (see also Lein 1978 and Nolan 1978). Males have two distinct singing behaviors in which they use their preferred song types (Table 6). The more repetitive (by definition) singing behavior *A* was significantly lower in song diversity, rate, and complexity than singing behavior *B*. Although individual males are consistent in the use of a particular song type in one singing behavior, other males may use the same song type in the other singing behavior. This, combined with the association between singing behaviors and particular circumstances (Table 6), results in use of shared song types in completely different circumstances by different birds (see also Lemon et al. 1985). Therefore, among individual Grace's Warblers, organization of song variation seems to be based on singing behaviors rather than song types, suggesting that singing behaviors convey key information.

Males consistently use the same singing behavior in the same time period, location, and social circumstance (Table 6). Unpaired males

TABLE 6. Characteristics and temporal, spatial, and social correlates of *A* and *B* singing behaviors in Grace's Warbler.

Character	Singing behavior	
	A	*B*
Individual variation	Songs often shared	Songs often unique
Song structure	Simple and stereotyped	More complex and variable
Aspects of singing behavior		
Sequential variety	Repetitive	Alternating
Diversity of song sequences	Lower	Higher
Rate of song delivery	Slower	More rapid
Temporal patterns of use		
Seasonal predominance	Before nesting	During nesting
Diurnal predominance	Daytime	Dawn
Location in territory	Center to edge	Songpost (often at edge)
Social circumstance		
Use in countersinging	Before pairing	After pairing
Type of interaction	Male-female	Male-male

use singing behavior *A* almost exclusively, but sometimes switch to singing behavior *B* in territorial encounters. Paired males use singing behavior *B* at dawn, then switch to singing behavior *A* around sunrise. Later in the day, choice of singing behavior depends on location and social interactions. Singing behavior *A* is more likely if the male is undisturbed or interacting with a female, whereas singing behavior *B* is more likely if the male is at his songpost or countersinging, i.e. interacting vocally with another male. The singing behavior used for countersinging depends on pairing status. Unpaired males usually use singing behavior *A* but paired males usually use singing behavior *B*.

Five closely related wood-warbler genera share characteristics of repertoire organization and patterns of use. At least 12 species of *Dendroica*, four species of *Vermivora*, and one species each of *Parula*, *Mniotilta*, and *Setophaga* have two "kinds" of songs that tend to be used at different times of the season (Ficken and Ficken 1962). Detailed studies of several species have demonstrated that the two kinds of songs are used in the same manner that Grace's Warblers use their two singing behaviors, which implies functional similarity (Table 7). Unfortunately, standardized terminology to facilitate species comparisons of song variation and use in wood-warblers is lacking. For convenience, I will use the term *A songs* to refer to vocal signals that appear functionally similar to singing behavior *A* of Grace's Warbler, and the term *B songs* to refer to vocal signals that appear functionally similar to singing behavior *B* (Table 7).

Interpretations of song variation in warblers have focused primarily on the proximate effects of circumstance on song use, particularly the

TABLE 7. Functionally similar vocal signals of some wood-warbler species, based on similar patterns of use in various circumstances and identified by the terminology of each author.[a]

A songs	*B* songs	Species (and principal references)
Singing behavior *A*	Singing behavior *B*	Grace's Warbler (this study)
Group-A	Group-B	Prairie Warbler (Nolan 1978)
Type B	Type A	Black-throated Green Warbler, Blackburnian Warbler (Morse 1967, 1970)
Accented (AE)	Unaccented (UE)	Chestnut-sided Warbler (Ficken and Ficken 1965, Lein 1978),[b] Yellow Warbler (Ficken and Ficken 1965, Morse 1966), American Redstart (Ficken and Ficken 1965)[c]
Repeat Mode	Serial Mode	American Redstart (Lemon et al. 1987)[c]
Type I	Type II	Golden-winged Warbler, Blue-winged Warbler (Gill and Lanyon 1964, Ficken and Ficken 1966)

[a] *A* songs predominate early in the season; *B* songs are more common later in the season, especially at dawn.

[b] Lein (1978) actually recognized 5 categories of songs, 3 AE and 2 UE variants.

[c] Song variation in the American Redstart has been described in terms of song types (Ficken and Ficken 1965) and singing behaviors (Lemon et al. 1987).

motivation of the singer (e.g. Ficken and Ficken 1965, 1967; Morse 1966, 1967, 1970; Lein 1972, 1978). Ultimate effects have been explained by two general hypotheses. In the first, different songs have different functions, one primarily intersexual (female attraction and pair bond maintenance) and one primarily intrasexual (territory maintenance) (Morse 1970, Nolan 1978, Kroodsma 1981). In the second, all songs function primarily intrasexually in territory maintenance by representing a graded series of signals (Lein 1972, 1978). The two hypotheses may not be mutually exclusive, because information for a given species may support aspects of both hypotheses.

The widespread tendency among species for *A* and *B* songs to be used in different circumstances is consistent with the first hypothesis (see below). On the other hand, data from the same studies may be interpreted as supporting the second hypothesis, which consists of two ideas: all songs function in territory defense, and song variation represents a graded series of messages (Lein 1978). First, males of all species sing *A* songs during the time they are unpaired when they are also establishing their territory. Also, males do sing *A* songs when undisturbed even after paired. Thus, *A* songs must play some role in territory defense. Second, there is evidence in several species that graded signals are associated with different circumstances. For example, Golden-winged Warblers vary the number of repetitions of part of their *A* song (Ficken and Ficken 1967), Yellow Warblers sing intermediate songs (Morse 1966), Chestnut-sided Warblers use different song endings (Lein 1978), and Grace's Warblers vary the complexity of singing behavior *B*.

Location in the territory affects songs used in all species studied. In general, *A* songs tend to be used at territory centers or near nests, and *B* songs tend to be used along territory borders, especially at locations where males often interact. Lein (1978) suggests that choice of song reflects willingness to defend the territory, as he found position relative to the territory center and edge was an important predictor of song use. Other studies have found other features to be more relevant in determining song use. Some examples are position relative to neighbors and nests rather than the geographic center of the territory (Lemon et al. 1987), location relative to the nest and territory boundaries (Morse 1966), and proximity to songposts (specific locations where males tend to interact) rather than to territory edges per se (this study). Slight differences among studies probably reflect differences in methods rather than actual species differences.

Lein argues that the primary function of all Chestnut-sided Warbler songs is to inform other individuals of the singer's mood and location, and that the primary function of accented songs (AE) cannot be intersexual because males spend little time associating with and rarely sing near females. Most (17 of 19) records of song given near females were AE (Lein 1978), and a female need only be within earshot of the singer for the signal to function intersexually (Kroodsma 1981). In all species studied, *A* songs declined after pairing and were usually least common during nesting (Ficken and Ficken 1965, 1967; Lein 1978; Morse 1966, 1967; Nolan 1978), although a second peak in *A* songs may appear during incubation (e.g. Lemon et al. 1987; Kroodsma et al. in press). Males used *A* songs before obtaining a mate, after losing a mate (Nolan 1978), and in the presence of females (Ficken and Ficken 1965, 1967; Morse 1966, 1967; Nolan 1978). In experiments where mates of paired males were removed, Chestnut-sided Warblers sang more AE songs than control-paired males (Kroodsma et al. in press), indicating importance in mate attraction. Thus, patterns of use of *A* songs among all species suggest a specialized function of pair bond establishment and maintenance.

In contrast, *B* songs were rarely used by unpaired males or by males near females, even though these songs were commonly used through much of the breeding season. *B* songs were often used in territorial interactions between paired males, suggesting a specialized function for territory maintenance. *B* songs were also used by paired males countersinging at dawn (Kroodsma in press; Lein 1972, 1978; Nolan 1978). Although the functions of the two signals may overlap somewhat, *A* songs have a stronger intersexual component and *B* songs have a stronger intrasexual component. Characteristics of singing behaviors *A* and *B* in Grace's Warbler (and for *A* and *B* songs of other species where data are available) were consistent with this hypothesis.

Song variation was strikingly similar among the few species for which comparative descriptive data exist. The structure of *B* songs and the associated behavior were apparently more variable within and among individuals than those of *A* songs. Songs used in behavior *B* by Grace's Warblers were more variable both within and among individuals, Prairie Warbler group-B songs were "more numerous and less stereotyped" and "less easily described" (Nolan 1978: 60), and Chestnut-sided Warbler unaccented songs were more variable and diverse in form (Lein 1978). Sequential variety was higher in sequences of *B* songs than in sequences of *A* songs for American Redstarts (Lemon et al. 1987) and Grace's Warblers. Comparative data are lacking for other warbler species with repertoires of more than two songs.

Signals that differ in function may be expected to differ in their characteristics in predictable ways (Marler 1960). The more stereotyped *A* songs of warblers tend to be used by undisturbed males or males singing near females, whereas the more variable *B* songs tend to be used in territorial interactions. Species-specificity requires clarity and stability in vocalizations, whereas the transmission of additional information demands an increase in complexity as well as individual and contextual variability (Becker 1982). Accordingly, the characteristics of warbler *A* songs, relative simplicity and relative stereotypy suggest species-recognition features. In *B* songs, the variability and relative complexity suggest the encoding of additional information, such as individual identity and motivational state. A parallel situation has been documented in treefrogs (*Hyla* spp.) where advertisement calls, used to attract females, were more stereotyped and species-specific than aggressive calls, used in interactions among males (Schwartz and Wells 1984).

I suggest selection for species-specificity could have played an important role in the evolution of North American wood-warblers (but see Payne 1983, West-Eberhard 1983). During paruline radiation, climate and habitat shifts likely produced highly dynamic assemblages of sympatric species (Mengel 1964). Even at present, several species typically breed sympatrically, especially in eastern North America (e.g. Lemon et al. [1983] found19 species breeding at one locale). Species-distinct, stereotyped songs may enable a male to stand out more effectively from the acoustic background of sympatric species and may also function as ethological isolating mechanisms.

In several wood-warbler species, including Grace's Warbler, stereotyped *A* songs and associated simple singing behaviors contribute to the species-specific potential of this signal. Ficken and Ficken (1962) suggested that *A* songs were more species-specific because warbler species were more easily distinguished on the basis of their *A* songs than *B* songs. In the Chestnut-sided and Blue-winged warblers, *A* songs were stereotyped over wide geographic areas while *B* songs varied among localities. This is consistent with the hypothesis that *A* songs function as pre-mating isolating mechanisms (Kroodsma 1981). The stereotypy of *A* songs could be maintained through female preference for simpler, more species-specific signals. For example, Swamp Sparrow (*Melospiza georgiana*) females court preferentially in response to songs with more species-typical temporal patterns, but males respond strongly to both typical and more variable songs (Searcy et al. 1981). It is plausible that a similar mechanism has been important in the evolution and maintenance of the relative stereotypy of *A* songs and singing behaviors of wood-warblers.

Grace's Warblers exhibit more interindividual variability in *A* songs than described previously for other wood-warblers. Grace's Warbler has one to four *A* song types that may be completely different in neighboring males. Some species (e.g. Chestnut-sided Warbler) have more than one *A* song type all males share (Lein 1978), some (e.g. American Redstart) have one *A* song type that is usually, but not necessarily, shared (Lemon et al. 1985), and others (e.g. Blue-winged Warbler) have essentially one *A* song type shared by all males (Kroodsma 1981). If *A* songs were important in species recognition in warblers, it is possible that the greater variation in *A* songs in Grace's Warblers is related to their occurrence in areas with relatively few wood-warbler species. Selection for stereotyped species signals would be less intense in these areas.

The more complex and variable *B* songs and singing behaviors in territorial contests suggests these signals are important in intrasexual competition for territory (Morse 1970, Kroodsma 1981). The switch to *B* songs in dawn countersinging after pairing provides an additional intrasexual function, defense of mates against extra-pair copulations at a time of day when the female is particularly fertile and apart from the male (Mace 1987). The increase in *B* songs during nesting may also be related to increased trespassing by neighbors and "explorers," which appears to be more frequent when opportunity to associate with a female is limited (Nolan 1978). Furthermore, the frequency of use of *B* songs seems to be related to intensity of territorial interactions in different populations of some species (Morse 1966, 1970).

Intrasexual competition presumably leads to the elaboration of vocal signals due to advantages conferred by more complex repertoires (Howard 1974, Yasukawa et al. 1980, West-Eberhard 1983; but see Catchpole 1980). In wood-warblers more complex and variable singing behaviors may represent a signal that is higher in perceived threat than simpler singing behaviors (Staicer 1982, Lemon et at. 1987). In other groups of songbirds (e.g. parids, wrens, and sparrows) where males interacted at closer distances, males switch between song types more frequently, and the complexity or variety of the song sequence increases (Lemon 1968, Dixon 1969, Kroodsma and Verner 1978, Kramer et al. 1985, Simpson 1985). Although the specific mechanisms are unclear, perhaps intrasexual interactions have been important in shaping the relative complexity of *B* songs and singing behaviors of wood-warblers.

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