

USE OF TWO SONG CATEGORIES BY GOLDEN-CHEEKED WARBLERS¹

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Abstract. I tape-recorded and counted the songs of color-banded Golden-cheeked Warblers (*Dendroica chrysoparia*) on Fort Hood, Texas in 1993 and 1994 to determine whether males use a two-category song system common to many wood-warbler species. More than 97% of all songs I documented belonged to two categories: A and B. A songs were higher in frequency, shorter, less complex, and were delivered at lower rates than B songs. Males used A songs primarily early in the nesting season, when near females, and from the interior of territories. In contrast, B songs were more common later in the nesting season, at dawn, and when males sang near territory boundaries. Songs delivered near territory edges were usually sung from one or two preferred perches on each male's territory that often coincided with the edge of a cliff or a break in the forest canopy. Based on these data, and in contrast to the implications of an early account of Golden-cheeked Warbler song use, this species shares the song system used by many wood-warbler species. Furthermore, the patterns of song use that I observed suggest that males do not sing randomly with respect to time or location on territory, and monitoring efforts that assume random singing across time and space may result in inaccurate or biased estimates of population sizes and habitat preferences.

Key words: *Dendroica chrysoparia*, *endangered species*, *Golden-cheeked Warbler*, *Parulidae*, *song*.

INTRODUCTION

Many species of North American wood-warblers (Parulidae) sing two categories of songs that differ in their patterns of temporal, spatial, and contextual use (Spector 1992). The first category songs of these species are often simple and highly stereotyped, sung at relatively low rates, and associated with singing early in the season, during daytime, and near females. In contrast, second category songs are usually more complex and variable, sung at higher rates, and are more frequently used later in the season, at dawn, and in male-male interactions. This two-category song system has been described for species in several genera, including *Dendroica* (Ficken and Ficken 1962, Kroodsma et al. 1989, Staicer 1989), *Mniotilta* (Tyler 1953), *Parula* (Morse 1967a), *Setophaga* (Ficken and Ficken 1965, Lemon et al. 1987), *Vermivora* (Kroodsma 1988, Highsmith 1989), and *Wilsonia* (Wiley et al. 1994).

Based on a largely anecdotal account of song use in the Golden-cheeked Warbler (*Dendroica chrysoparia*; Pulich 1976), Spector (1992) sug-

gested that this species might use its songs differently from other *Dendroica*. Two particular behaviors reported by Pulich—that Golden-cheeked Warblers do not sing at dawn, and that the song used early in the season is the same as that used in male-male interactions—seem inconsistent with the general parulid song system. The Black-throated Gray Warbler (*D. nigricens*), a species thought to be closely related to the Golden-cheeked Warbler within the Black-throated Green Warbler (*D. virens*) complex (Stein 1962, Mengel 1964), also has been reported to use one song type both early in the season and near neighbors (Morrison and Hardy 1983). This apparently shared behavior suggested that the pattern of song use by these two species might represent a shared derived character, but Spector warned that more detailed studies of song behavior were necessary to confirm the original reports of song use for each of these species.

Detailed knowledge about temporal and spatial patterns of song use is of practical concern for management of the Golden-cheeked Warbler. Most programs designed to monitor populations of this federally endangered songbird use standard methods that rely on the detection of singing males to determine habitat occupancy and relative abundances of breeding birds. A number

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of potential biases are associated with these census methods (Mayfield 1981, Verner 1985), including differences in vocal output relative to time of day (Robbins 1981), time of season (Best 1981), and mating status (Hayes et al. 1986). The data reported here thus provide information that will be useful in evaluating the assumptions of song-based monitoring programs as well as documenting the type of song system used by Golden-cheeked Warblers.

METHODS

STUDY AREA

I studied Golden-cheeked Warbler song behavior on the Fort Hood Military Reservation, Bell County, Texas during the 1993 and 1994 breeding seasons. Approximately 80% of my 85-ha study area was located on top of a relatively flat mesa, with the remainder occupying the steep slopes of a drainage containing a small, seasonal stream. Woody vegetation was dominated by a mix of mature Ashe juniper (*Juniperus ashei*), plateau live oak (*Quercus fusiformis*), and post oak (*Q. stellata*); other common tree species included Texas oak (*Q. buckleyi*) and Texas ash (*Fraxinus texana*). Understory vegetation consisted of locally dense thickets of shin oak (*Q. sinuata*) and Texas mountain laurel (*Sophora secundiflora*), particularly near woodland edges. Fort Hood Fish and Wildlife personnel have conducted research on various aspects of Golden-cheeked Warbler breeding biology in this study area since 1991.

I studied the song behavior of a core group of focal males ($n = 11$ in 1993 and $n = 14$ in 1994; 6 males were present both years, total $n = 19$ males) throughout each breeding season. I opportunistically recorded songs from additional males that were peripheral to this cluster of territories, but made no systematic attempt to sample their songs. Focal males (except for one in 1994) and most peripheral males were captured in mist-nests and banded with unique combinations of plastic colored bands and one numbered aluminum U.S. Fish and Wildlife Service band. I was unable to band most females because they did not respond aggressively to the tape-recorded songs I used to lure males to nets.

I monitored the territories of focal males from their arrival in March until singing ended in early June. Each day that I visited the study area, I mapped the locations where I observed each

individual on an aerial photograph with a 15×15 -m grid overlay, documented whether I had visually confirmed the band combination of each male I encountered, and made detailed behavioral notes. During afternoons and on days when high wind or noise prevented me from sampling songs, I searched for nests and other indications of nesting activity. Observations of females, nests, and fledglings provided information that I used to determine the dates for six stages of the nesting season on each male's territory: (1) pre-pairing, (2) the period from female arrival to egg-laying, including nest-building, (3) egg-laying, (4) incubation, (5) nestling care, and (6) fledgling care.

I tape-recorded singing males throughout each nesting season using a Marantz PMD cassette recorder with a Dan Gibson parabolic microphone in 1993, and a Nagra IV-L open-reel recorder with a Sennheiser MKH 816 shotgun microphone in 1994. During both years, I recorded songs 4–6 days each week from the arrival of the first male until nesting activity was completed in mid-May, after which I recorded songs 2–3 days each week until males quit singing for the year. On each recording day, I arrived on the territory of a randomly selected male 45–90 min before official sunrise (as reported by the National Weather Service) and recorded a 5–10 min sample of his song when he began singing. I visited the remaining territories in a predetermined sequence to record songs; in cases in which I was unable to hear a focal male sing when I arrived on his territory, I actively searched for the male for approximately 20 min before moving to the next territory. I documented the following information for each recording: the date, time of day, distance to singing male, whether a female was present, distance to nearest singing neighbor, and location on territory.

To document daily and seasonal patterns of vocal activity, I conducted timed song counts one or two days weekly throughout the 1994 nesting season. On each day that I counted songs, I visited the territory of every focal male once and tallied on data sheets all songs heard during a 20-min period. To ensure that I sampled songs from as many males as possible during the pre-pairing period, I performed an additional song count for each male on the day I first detected him (1–2 hr after initial detection) regardless of my sampling protocol for the day. At the

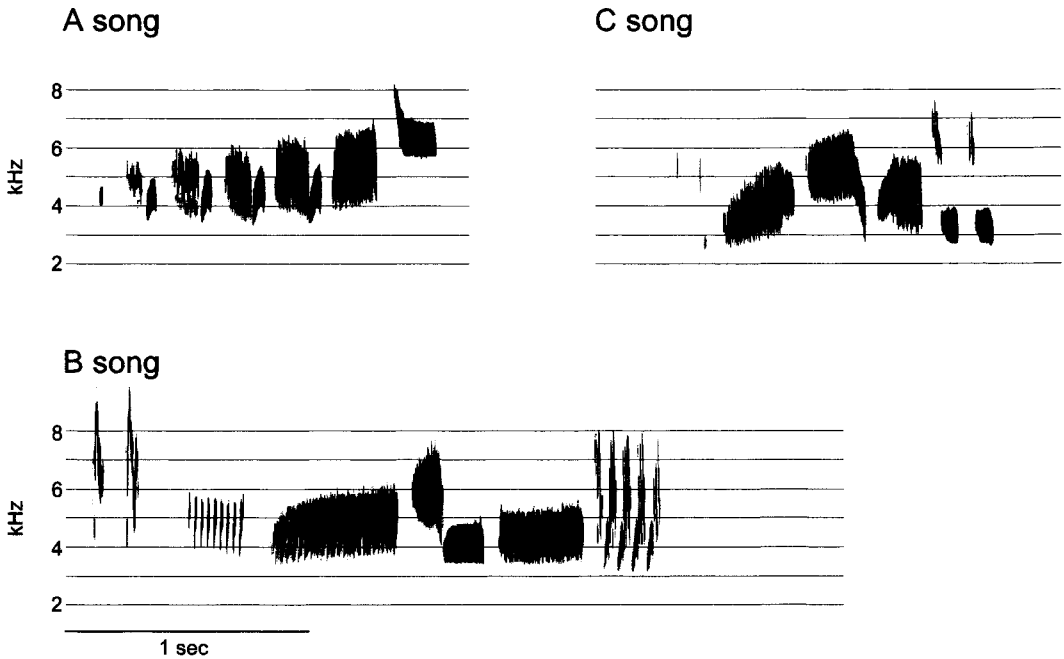


FIGURE 1. Male Golden-cheeked Warblers in the Fort Hood study area sang three stereotyped song forms. A and B songs were used by every study-area male; C songs were recorded from only five males in 1993 and three males in 1994. Call notes, such as the first two notes in the B-song sonagram, were used by males frequently before B songs but rarely before A songs.

beginning of every song count, I documented the time of day, identity of the focal male, and weather information. During each minute of each count, I documented the number of songs of each song form (easily distinguishable by ear) sung by the focal male, location of the male on his territory, distance from the nearest singing neighbor and the song form sung by that male, and when known, the distance to the nearest female and from the nest.

SONG TERMINOLOGY

Following Spector (1992), I refer to the two predominant song forms or behaviors in wood-warblers collectively as first and second category songs. Contrary to Spector, however, I do not use the terms originally used by Pulich (1976) for Golden-cheeked Warbler song—"prenuptial" and "subdued"—because these terms are misleading and possibly not based on real differences between songs of uniform type or delivery. The term "subdued" is particularly misleading as neither song form is characteristically sung in a subdued manner, although I did hear songs of each form whispered several times. The

only other original description of song types in Golden-cheeked Warblers I am aware of (Borror and Gunn 1985) clearly distinguishes at least two songs based on form, but I believe incorrectly attributes general patterns of song use to each form. As no accurate description of Golden-cheeked Warbler song types appears to be available, I use terms in existence for the songs of a number of other species: A for first category songs and B for second category songs.

DATA ANALYSIS

I analyzed nearly 11,000 songs recorded from study area males on a Kay Elemetrics DSP 5500 real-time spectrum analyzer set to simultaneously display broad-band sonagram and waveform representations of each song. For each male, I printed a sonagram of the first occurrence of each distinct song, which I then compared to all subsequent songs by the same male. Once I had printed examples of each unique song recorded from every male, I pooled all sonagrams and sorted them into major groups based on general similarities in song form (Fig. 1). Two of these groups—A and B—accounted for more than

97% of all songs I recorded each year, and were used by every study-area male. A third group of stereotyped songs (C) was recorded from ≤ 5 males each year and was not frequently used by any individual ($\leq 7\%$ of songs sampled from each male). I excluded C songs, along with rarely used hybrid A-B songs and unstereotyped songs, from subsequent analysis because I lacked sufficient samples of these songs to detect patterns in their use. I examined variation within each song form in another study (unpubl. data).

Using the Kay spectrum analyzer, I made structural measurements on the highest quality A and B songs that I recorded from each study-area male. To prevent differences in recording equipment from influencing the results of these analyses, I limited structural measurements to recordings made on the Nagra tape-recorder in 1994. I made temporal measurements by using cursors in "sonagram" mode. For frequency measurements, I used the "power between cursors" mode to generate a power spectrum for each song, from which I found the frequency with the greatest amplitude ("the frequency of modal intensity;" Spector 1991). "Song complexity" was a count of the number of distinct song elements or syllable types present in each song. I compared structural measurements of A and B songs for all males from which I measured both songs, including two males that occupied territories peripheral to my study area.

Tape recordings of continuously singing males with sequences of ≥ 10 consecutive songs of a single form ($n = 151$ in 1993 and $n = 141$ in 1994) were used to analyze song rates and the relative proportion of songs preceded by call notes. Recordings made within 20 min of a previous recording of the same male were not considered to be new samples and were excluded from analysis. For each sample, I calculated the song rate by dividing the time interval from the first to the eleventh song by 10 for recordings with > 10 songs, and the time from the first to the tenth song by 9 for recordings with exactly 10 songs (Scoville and Gottlieb 1978, Staicer 1989). I then computed mean A and B song rates and proportions of songs preceded by call notes for each male ($n = 11$ in 1993 and 14 in 1994; total = 19 males). These mean values were used for comparisons of song rates and call note use between A and B songs.

I used song count data to analyze song use in

relation to time of day, stage of the nesting season, and social interaction. For these analyses, I averaged the proportions of count minutes each male sang A-song, B-song, and all songs across samples within each relevant period (hour of day or nest stage) or social circumstance (neighboring male or female present or absent). I considered song use during the dawn hour (the hour beginning 30 min before sunrise) separately from daytime singing, and I divided the season into early (before incubation) and late (after the beginning of incubation) periods, as males appeared to behave differently within each of these daily and seasonal periods. I analyzed social patterns of song use by comparing the proportions of count minutes males sang A-song and B-song when females or neighboring males were present to when they were absent (Wiley et al. 1994).

To analyze song use relative to location on territory, I first mapped the locations males sang from at the beginning of each minute of each song count. These locations were compared to summary maps of territories compiled for each week of the season, and then classified as either territory edges or interiors. I generally defined territory edges as the portion of a male's territory within 30 m of where a neighbor regularly sang from or actively defended (most territories were 100–200 m across), but on some territories edges coincided with sharp habitat discontinuities, such as an abrupt change from woodland to grassland. I considered the remainder of each territory to be the interior. Once location data were summarized for all samples, I calculated the mean proportion of time A and B songs were sung from edges and interiors by each male. I compared the proportion of songs of each type used at territory edges and from interiors during daytime singing only, as I obtained few samples of A-song or interior singing before sunrise. Throughout the text, "Wilcoxon" refers to a Wilcoxon matched-pairs rank-sum test. All tests are two-tailed.

RESULTS

SONG TYPES

The two songs that dominated singing by male Golden-cheeked Warblers—A song and B song—were generally sung in prolonged sequences of a single form. Uniform sequences of either all A or all B song accounted for 87% of recordings made in 1993 and 1994 with ≥ 10

TABLE 1. A songs are shorter, higher in frequency, and less complex than B songs. Medians (and ranges in parentheses) are reported for the highest quality A and B song recorded from every male ($n = 16$) from which I sampled both songs during 1994. I used Mann-Whitney U -tests to compare variables between song forms.

Song	Song duration (sec)	Frequency of modal intensity (Hz)	Song complexity (elements/song)
A	1.5 (1.3–1.9) ***	5,140 (4,480–5,920) ***	3 ***
B	2.0 (1.4–2.5)	4,820 (4,000–5,640)	5 (4–6)

*** $P < 0.001$.

songs ($n = 335$), and 70% of all song counts in which focal males sang ($n = 190$). Most song counts during which males sang more than one song form involved one or two switches between extended bouts of uniform A or B singing, and actual mixed singing in which males regularly alternated between A and B songs occurred during only nine counts involving five males. These sequences of mixed singing each lasted ≤ 5 min, and occurred during transitions from longer sequences of one song form to the other (e.g., A to B) or during aggressive interactions with neighbors.

The A and B songs of Golden-cheeked Warblers differed in their relative degree of complexity, duration, and frequency of modal intensity. Every study area male sang just one A-song type, but most males sang two or more distinct B songs, of which only one was commonly used (the male's preferred B song; unpubl. data). Ev-

ery male from which I recorded both A and B songs ($n = 16$) sang a preferred B song that was longer and included more song elements than his A song, and only one male sang a preferred B song with a higher frequency of modal intensity than his A song (Table 1). B songs were not always longer or lower in frequency than A songs, however; the rarely used B songs of several males were shorter (six males) or had a higher frequency of modal intensity (three males) than the A song of the same male.

Males sang A songs at lower rates (songs min^{-1}) and with fewer call notes than B songs (Table 2), but within-type song rates varied substantially. For every male from which I recorded more than five bouts of each song form within a single season ($n = 6$), differences between minimum and maximum daytime song rates for A song (medians = 3.1 and 5.4 songs min^{-1} , respectively) and B song (medians = 4.1 and 9.1 songs min^{-1} , respectively) were greater than the difference between median A and B song rates. Despite overlap in the rates with which each male sang each song type, the rates at which five of these six males sang A songs were significantly lower than the rates at which they sang B songs (Mann-Whitney $U \leq 20.5$, $P < 0.05$ for five males, $P > 0.10$ for one male).

The use of call notes differed more sharply between A and B songs. Every study-area male used call notes prior to B songs, particularly at dawn, but I recorded A songs that were preceded by call notes from just three males, and I heard only one male call during A singing more than once. The call notes that preceded A songs differed in character from those used between B songs; males often uttered two call notes in rapid

TABLE 2. Song rates (songs min^{-1}) and the proportions of songs preceded by call notes were highest for dawn B song, intermediate for daytime B song, and lowest for A song. Reported values are medians for all males (with ranges in parentheses). Asterisks between the rows designate significance levels for Mann-Whitney U -tests comparing A and B songs within daily periods; asterisks within the B-song row are for comparisons of dawn and daytime song rates.

Song	Number males sampled		Song rate		Proportion of songs preceded by call notes	
	Dawn	Day	Dawn	Day	Dawn	Day
A	3	14	3.9 (3.0–4.3) **	4.7 (2.5–6.6) **	0.0 (0.0–1.0)	0.0 (0.0–0.9) ***
B	12	13	6.8 (5.5–8.2)	5.4** (4.2–7.8)	1.0 (0.7–1.0)	0.6*** (0.0–1.0)

** $P < 0.01$, *** $P < 0.001$.

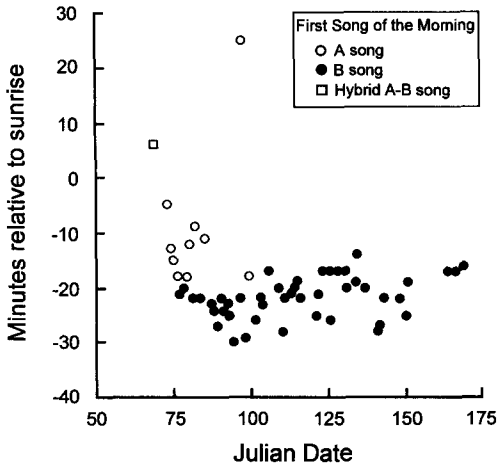


FIGURE 2. Male Golden-cheeked Warblers used B song as the first song of the day throughout the 1994 nesting season, but used A song as the first song of the day during only the earliest part of the season. Time relative to sunrise is represented on the vertical axis; zero represents sunrise, and negative and positive values represent the number of minutes before and after sunrise, respectively. Excluded are two days in early March on which the first song I heard was later than 30 min after sunrise. Julian date 50 = 19 Feb.

succession during B singing, especially at dawn or during interactions with other males, but only single call notes preceded A songs.

TEMPORAL PATTERNS OF SONG USE

Dawn song. The first one to two males to arrive in the study area each season did not sing before sunrise during the week after I first detected them. During the subsequent two weeks, singing began progressively earlier in the morning, and by the time the latest males arrived in the study area, the first songs of the day were often sung more than 20 min before sunrise (median = 20.5 min before sunrise on 56 mornings in 1994; Fig. 2). Once males began singing before sunrise, they generally delivered songs continuously at a high rate until approximately sunrise, at which time males either became silent or changed the song type used and/or the rate of song delivery.

Males sang both A and B songs before sunrise early in the nesting season, but almost entirely B songs for the remainder of the season. During the first half of the 1994 nesting season, the first song I heard on 40% of mornings ($n = 25$) was an A song, and 59% of dawn samples ($n = 13$ recordings and 9 counts) included A songs. Also within the early season, males that used A song

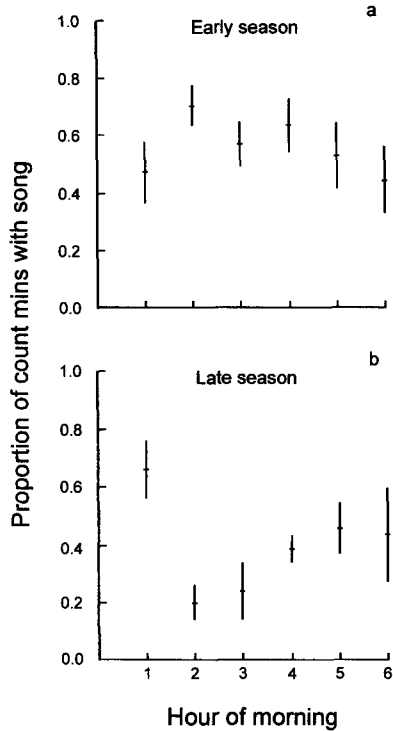


FIGURE 3. The proportion of count minutes that male Golden-cheeked Warblers sang was highest during the first hour of the day within the late nesting season (b) but not during the early season (a). Dashes represent the mean of individual male's means; vertical bars represent standard error. Hour "1" began 30 min prior to sunrise. Number of males sampled during each hour are (early season, late season): hr 1 (10, 9); hr 2 (11, 9); hr 3 (10, 8); hr 4 (9, 9); hr 5 (9, 10); hr 6 (10, 4).

as the first song of the day began singing later in the morning than males that used B song (median of 12 min compared to 22.5 min before sunrise, Mann-Whitney $U = 0.0$, $n_1 = n_2 = 6$, $P < 0.01$). During the second half of the nesting season, the first song I heard every morning I was in the field at dawn ($n = 31$) was a B song, and just one recording ($n = 24$) and no song counts ($n = 7$) included A songs.

Daytime song. Males spent proportionately more time singing during the dawn hour than during the subsequent 2 hr within the late season (Wilcoxon $T = 1$, $n = 8$, $P < 0.02$), but not within the early season ($T = 13$, $n = 10$, $P > 0.10$; Fig. 3). On most days I did not hear any mated male sing for 20–60 min at a time during the 2 hr following sunrise, and I did not detect focal males on 36% of counts ($n = 36$ counts

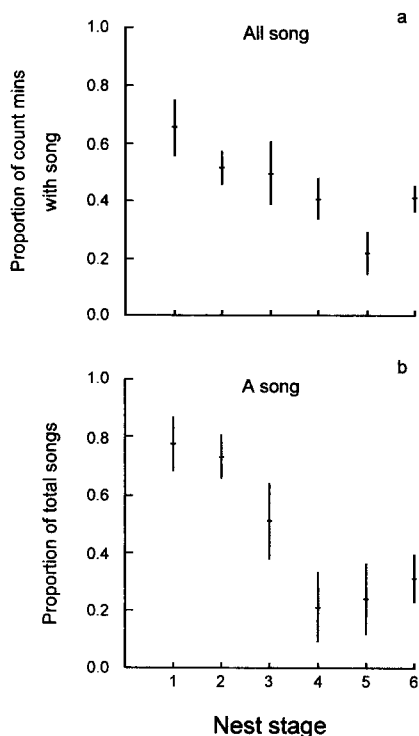


FIGURE 4. The proportion of daytime count minutes that male Golden-check Warblers sang (a) and the proportion of all songs that were A song (b) were highest during the pre-pairing period and declined as the season progressed. The proportion of B songs used within each stage of nesting was exactly the reverse of that shown in graph b. Numbers of males sampled (graph a, graph b) are as follows: stage 1 (12, 11); stage 2 (13, 13); stage 3 (9, 8); stage 4 (11, 9); stage 5 (11, 6); stage 6 (10, 10); see text for descriptions of nest stages. Counts in which focal males sang < 10 songs were excluded from graph b so that proportions are based on bouts of continuous singing and not isolated songs. Symbols are defined in Figure 3.

on the territories of 11 males) during this portion of the morning. During other periods of the morning (dawn or mid-morning), I detected focal males on $\geq 89\%$ of song counts.

Daytime vocal activity was highest during the early stages of nesting and declined as the season progressed (Fig. 4a). Males generally sang a high proportion of the time during the pre-pairing period, but early season vocal activity differed according to arrival date. During 1994, males that arrived on or before 17 March spent less time singing prior to mate acquisition than did males that arrived after 17 March (median

= 45% of count minutes compared to 93%; Mann-Whitney $U = 1.0$, $n_1 = n_2 = 6$, $P < 0.01$). Differences in the proportion of time males sang were not significant between successive nest periods (i.e., pre-pairing vs. courtship, or incubation vs. nestling), but males sang significantly more often during the first half of the nesting season than during the second half (Wilcoxon $T = 2$, $n = 12$, $P < 0.002$).

Males sang primarily A song early in the nesting season, but the proportion of A song declined after courtship, and this song type was used infrequently during the later stages of nesting (Fig. 4b). B songs exhibited the reverse pattern; B songs were rare prior to pairing, and increased in occurrence during subsequent stages until the incubation period, when B song became the predominant song used. Overall, males sang a higher proportion of A songs before the beginning of incubation than later in the season (Wilcoxon $T = 5$, $n = 12$, $P < 0.01$), and sang more B songs after incubation had begun than earlier in the season ($T = 6$, $n = 12$, $P < 0.01$). One exception was the only focal male that appeared to be unmated for the entire 1994 nesting season; this male sang A songs persistently during daytime from his arrival in late March until he stopped singing for the year in late May.

SPATIAL PATTERNS OF SONG USE

Dawn song. Each male sang at dawn from one or two preferred locations on his territory, which were generally at territory edges near the preferred song post of a neighbor. The distance between song posts on neighboring territories was significantly closer than the distance between the centers of adjacent territories (median of 63 m compared to 175 m; Mann-Whitney $U = 0.0$, $n_1 = n_2 = 10$, $P < 0.001$), so that males typically had one or two neighbors toward which their songs appeared to be directed. Every male that occupied a territory in or adjacent to the drainage during 1994 ($n = 8$, including three males peripheral to this study) also sang his dawn bout from a location at the immediate cliff edge that formed the uppermost reaches of the drainage slopes, even though the territories of all but one of these males appeared to be entirely on a slope ($n = 3$) or on the flat ridgetop ($n = 4$). Most males that occupied territories away from the drainage sang their dawn bouts from locations near openings in the forest canopy, such as along

trails or small clearings. Two of these latter males expanded their territories late in the season (after 15 May) to include portions of the cliff edge above the drainage, from which they sang their dawn bout for the remainder of the season.

Daytime singing. The relative amount of time males sang from territory interiors and edges was different before and after the start of incubation. During the early season, males sang mostly from the interior of their territories (median = 80% of count minutes, $n = 13$ males) and moved frequently between songs. After females began incubating, males decreased the amount of time they sang from territory interiors (Wilcoxon $T = 14$, $n = 13$, $P < 0.01$) and increased the amount of time they sang from territory edges ($T = 7$, $n = 12$, $P < 0.01$). Males sang primarily from territory edges throughout the remainder of the season (median = 74% of count minutes, $n = 13$ males), and most sustained bouts of song were sung from or near preferred song posts.

The association between song form and relative territory location also differed between the early and late nesting season. Before incubation, males spent more time singing A song than B song from the interior of territories (Sign test, $n = 13$, $P < 0.01$), but exhibited no preference for either song type when singing along territory edges ($n = 11$, $P > 0.10$). During the late season, there was no difference in the amount of time males sang A and B songs from territory interiors (Sign test, $n = 10$, $P > 0.10$), but males spent significantly more time singing B song than A song at territory edges ($n = 12$, $P < 0.02$). Overall, males spent much of the early season singing A song from locations throughout their territories, and most late-season singing consisted of bouts of B song delivered near territory boundaries.

Singing relative to nest location. The perches from which males preferred to sing were usually far from nests, and I rarely observed males singing near nests. Most nests that I found were > 100 m from preferred song posts (median = 140 m, $n = 14$), and five of the nine nests I found in 1994 were at or near the extreme opposite edge of a male's territory. In 1994, the year in which I had the best information about nest location and status, I obtained just 15 samples (10 of 89 song counts and 5 of 44 recordings collected on territories with active nests) from eight

males that sang < 25 m from nests. In every case, males sang briefly when approaching the nest, but were silent at the nest site, and flew away after ≤ 2 min and ≤ 5 total songs. Six of these males sang entirely ($n = 5$) or primarily ($n = 1$) A song as they approached the nest, one male sang entirely B song, and one male sang A song during one sample and C song during another sample.

SOCIAL PATTERNS OF SONG USE

Song use near females. My analysis of song type use with respect to female presence was restricted to daytime singing during the courtship and egg-laying phases of nesting, as this was the only portion of the nesting season in which I regularly encountered males and females near one another. Within this period, males spent more time singing A song when females were nearby than when males were alone (Wilcoxon $T = 0$, $n = 10$, $P < 0.01$), but did not increase their use of B song near females ($T = 14$, $n = 11$, $P > 0.1$). Of the 12 males that I observed near females during this period (median = 51 count min male⁻¹), A songs accounted for all of the songs used by eight males, and more than 90% of songs used by three additional males. The one male that sang more B songs than A songs when near his mate generally used his songs differently from other study area males (see below).

Male-male song behavior. During the late nesting season, males spent more time singing B songs when nearby male neighbors sang than when neighbors were silent or sang in the distance (Table 3). Males also appeared to prefer B songs when nearby neighbors sang during the pre-pairing period (median proportion of min spent singing B song = 93% near neighbors compared to 0% when no neighbors sang, $n = 4$), but my sample during this period was insufficient for statistical analysis. The proximity of neighboring males had no apparent effect on the use of A song during any part of the nesting season; males sang A songs often early in the season and infrequently late in the season whether neighbors sang or were silent.

Males sang both A and B songs during most aggressive interactions that I observed in 1993 and 1994, but B songs were usually more common. The frequent movement of chasing males often prevented me from determining which male sang a given song, so my description of

TABLE 3. During the late nesting season, the proportion of count minutes males sang B song was higher when nearby neighbors (<25 m) sang than when neighbors sang in the distance (>25 m) or were silent. Values in table are median proportions of count minutes males sang each song when in each situation, with the number of males sampled in parentheses. The Wilcoxon test was used to compare the proportion of time males sang each song when nearby and distant neighbors sang to when no neighbors were audible.

Period	Focal male sang A song			Focal male sang B song		
	No neighbor audible	Neighbor audible		No neighbor audible	Neighbor audible	
		>25 m	<25 m		>25 m	<25 m
Early season	0.51 (13)	0.44 (12)	0.48 (9)	0.03 (13)	0.12 (12)	0.20 (9)
Late season	0.04 (12)	0.06 (12)	0.00 (9)	0.19 (12)	0.25 (12)	0.86 (9)*

* $P < 0.05$.

song use during territorial conflicts is based on all songs used by every male in each interaction. Within the early season, both A and B songs were used by every unique pair of chasing males that I observed ($n = 9$ unique pairs); B songs were generally more common than A songs in these interactions (medians = 69.5% vs. 26.5%), but this difference was not statistically significant (Sign test, $n = 9$, $P > 0.1$). During late season chases, B songs were used significantly more frequently than A songs (medians = 90.5% vs. 9.5%; Sign test, $n = 8$, $P < 0.01$), and five of eight unique pairs of chasing males used only B songs. Throughout the nesting season, I observed no aggressive interactions in which A song was the only song type used.

The presence of nearby females may have influenced song choice during territorial conflicts. I detected females near chasing males during 50% of early season chases in which males sang, and during two of the three late-season encounters in which both A and B songs were used. I detected no females during the five late season chases in which males sang entirely B songs. For the entire season, chasing males sang a higher percentage of A song when females were present than when females were absent (medians = 38.8% vs. 18.6%, Mann-Whitney $U = 13.0$, $n_1 = 6$, $n_2 = 11$, $P < 0.05$, where n_1 and n_2 = unique pairs of neighboring males); I lacked sufficient samples to test for differences in song use within each seasonal period.

One male that occupied a territory in the study area during both 1993 and 1994 used his songs differently from other males. During both years this male sang primarily B song during all stages of the nesting season, including pre-pairing and courtship, and when near females or

from the interior of his territory. The only time I heard him sing A songs early in the season was during a territorial conflict, when he sang entirely A song. This male's B song delivery differed according to context; he sang slowly and with no call notes when near a female or from the interior of his territory, and more rapidly and with call notes at dawn, near neighboring males, and from the edge of his territory. This male also included a small number of A songs mixed in with B songs during dawn singing, and modestly increased his use of daytime A song as the season progressed. Despite this male's atypical use of song types, he successfully acquired mates and raised young during both years that I monitored his territory.

USE OF C SONG

The rarity of C song prevented me from sampling this song sufficiently to analyze patterns of use statistically, but potential patterns were evident. During the two years of this study, I documented 29 occurrences of C song by eight males, excluding two short bouts from males of unknown identity. Of these bouts of C song, 69% occurred during the nestling and fledgling periods, although I did hear at least one bout of C song during every nest stage. Of 25 bouts of C song for which I was close enough to the singing male to observe the circumstances under which he sang, 21 (84%) were sung by males ($n = 8$) approaching nests or fledglings, and just 2 bouts, sung by two different males, occurred when a second male was singing nearby. C songs were rare during all portions of the nesting season, however, and I heard only four males use this song on more than two occasions.

DISCUSSION

SIMILARITY TO PATTERNS OF SONG USE IN OTHER WOOD-WARBLER SPECIES

The A and B songs of Golden-cheeked Warblers differ from one another in their structure and manner of delivery much like the first and second category songs of other parulid species. Many wood-warblers sing second category songs at higher rates than first category songs (Highsmith 1989, Staicer 1989, Spector 1991), use call notes between second category but not first category songs (Morse 1967b, Highsmith 1989, Spector 1991), and emphasize relatively higher frequencies in their first category songs (Spector 1992, Staicer 1996a). Based on these features of song form and delivery, the A and B songs of Golden-cheeked Warblers conform to the first and second song categories used by other wood-warbler species in *Dendroica* and related genera.

Patterns of song use by Golden-cheeked Warblers also conform to the generalized parulid song system. The dominance of first category songs early and second category songs later in the nesting season is widespread among species that use this song system (Ficken and Ficken 1965, Morse 1970, Staicer 1989). Similarly, the preference for second category songs during dawn singing has been documented for most wood-warbler species that use two song categories (Highsmith 1989, Morse 1989, Spector 1991). Many species use first category songs from territory interiors or near females, and second category songs near territory boundaries or neighboring males (Morse 1967b, Lemon et al. 1987, Byers 1996). I observed no aspect of A or B song use that was inconsistent with the manner with which other wood-warbler species use their first and second category songs.

My observations contradict Pulich's (1976) conclusion that Golden-cheeked Warblers do not sing before sunrise, but it is not clear to me that the males he studied lacked a dawn bout. Sample data reported by Pulich (1976) suggest that the males he observed began singing approximately 15–19 min after official sunrise in March ($n = 2$), but 24–38 min before sunrise in April and May ($n = 3$). The contradiction between the times these late season males began singing and Pulich's conclusion that males did not sing before sunrise leads me to suspect that he defined sunrise differently than I did, perhaps as the time

when light is first noticeable on the horizon. Regardless of his definition of sunrise, it seems likely that the males Pulich studied did sing before sunrise, and our contrary conclusions regarding the use of dawn song reflects a difference in semantics rather than a difference in the bird's behavior.

Pulich's assertion that the song males use early in the season is the same as that used in male-male interactions is not entirely consistent with the behavior of males on Fort Hood. Although both A and B songs were used in many chases that I observed, males appeared to prefer B songs during conflicts with neighbors. When I observed chasing males singing A songs, I frequently saw or suspected females nearby. Similar use of first category songs by fighting males in the presence of females has been reported for at least two other wood-warbler species that normally sing second category songs in agonistic situations (Nolan 1978, Kroodsmma et al. 1989). Two additional species—Black-throated Gray Warbler and Kirtland's Warbler (*Dendroica kirtlandii*)—have been reported to regularly use their first category songs during aggressive interactions (Morrison and Hardy 1983, Spector 1992), but it is not clear whether females were near the fighting males whose behavior was described. Based on the males I studied, it would not be inaccurate to conclude that Golden-cheeked Warblers use A songs in fights, but B songs appear to be more characteristic of aggressive behavior.

Considering the conformity of Golden-cheeked Warbler song use to the generalized wood-warbler song system, I find little evidence that members of the *Dendroica virens* complex differ in their use of songs. The apparent preference for first category songs by male Black-throated Gray Warblers responding to approaching males or tape-recorded conspecific song (Morrison and Hardy 1983) is not typical of wood-warbler behavior, but this species otherwise appears to exhibit a "normal" pattern of seasonal song use. Substantial observational evidence suggests that Black-throated Green Warblers also use their song types like other wood-warblers (Morse 1967b, 1989). The two remaining members of the complex, Hermit (*D. occidentalis*) and Townsend's Warblers (*D. townsendi*), sing two distinct songs (Borror and Gunn 1985), but the manner with which these songs are used has not been thoroughly de-

scribed. The divergent use of first category song (confusingly described as Type 2 song by Morrison and Hardy 1983; Spector 1992) by Black-throated Gray Warblers is difficult to explain, but does not seem to represent sufficient evidence that this species or species-complex behaves in a different or unique manner with respect to overall song use.

FUNCTIONS OF SONG TYPES

Most authors who have studied wood-warblers with two category song systems have invoked one of two functional explanations for the use of these categories. The most frequently cited explanation is that first and second category songs are specialized for inter- and intrasexual communication, respectively (Morse 1970, Nolan 1978, Kroodsma 1981). According to this explanation, first category songs are directed toward potential mates and are used in maintenance of the pair bond, and second category songs largely function in territorial defense. The predominant use of A songs by male Golden-cheeked Warblers early in the season and when near their mates supports the idea that this song is directed primarily toward females. Similarly, the dominance of B song by males singing near neighbors at dawn, and the relatively high proportion of B songs used when nearby neighbors sang late in the season and during many territorial conflicts suggests an intrasexual function of this song.

Contrary to the idea that each song is specialized for communication with members of a different sex, Lein (1972, 1978) argues that all songs serve a primarily intrasexual function, and are used in a graded series representing different motivational states. The motivational continuum that Lein described for Chestnut-sided Warblers (*Dendroica pensylvanica*) included five song types that males cycled through in a predictable sequence. Kroodsma et al. (1989) and Byers (1995) did not find this pattern of song use in the same species, and few authors have reported such a continuum in other species (Staicer 1989, Spector 1992). Highsmith (1989) described a song continuum used by Golden-winged Warblers (*Vermivora chrysoptera*), in which first category songs varied in length according to social stimulus, but he attributed different functions (intersexual and intrasexual) to songs at either extreme of the continuum. I observed no predictable continuum of song use by Golden-

cheeked Warblers, but the potential for one exists; males varied the duration of their A songs (unpubl. data), and also used several infrequent song types or behaviors (C, hybrid, unstereotyped) that could potentially represent different motivational levels. Regardless of the potential existence of a song continuum, however, the patterns of A-song use that I observed do not support the idea that both songs are directed primarily toward other males.

The role of C song in the repertoire of Golden-cheeked Warblers is unclear, but at least two possibilities are apparent. C song may represent a type of B song, and my identification of C song as a distinct song form may be a function of the subjective manner with which I classified songs. C songs did not appear to be used in the same types of situations as B songs, however; the apparent pattern of C song use I observed on Fort Hood suggests a role in communication with young or females caring for young. Perhaps such a specialized song could be of importance in reducing feeding time or disturbance at the nest, or in helping males to find their fledglings, but this explanation for C song is highly speculative. Also, although C songs were rarely used by Fort Hood males, I visited one location (Colorado Bend State Park, San Saba County, Texas) where C songs were the most frequently used songs by three neighboring males, each of which sang this song in fights or during countersinging with one another (unpubl. data). Although males at Colorado Bend and Fort Hood appeared to use C songs differently, I did not sample this song frequently enough to determine whether either behavior represents a common pattern of use.

IMPLICATIONS FOR MONITORING EFFORTS

Seasonal and daily patterns of vocal activity are relevant to monitoring efforts, as differences in song levels between nest stages or hours of the day may affect the results of song-based censuses. Unfortunately, during no period of the nesting season did I observe uniformly high levels of song output, and vocal activity was particularly low late in the season and during the two hours following sunrise. If the low song levels during these periods translate into a decrease in detectability of males, then censuses conducted at these times may result in substantial underestimates of the number of males present, and may not be comparable to the results of censuses conducted at other times (Skirvin 1981,

Best and Petersen 1982). As accurate density estimates are vital to successful monitoring of this endangered songbird, detailed studies of the degree to which differences in detectability affect indices of Golden-cheeked Warbler abundance, and of how to control for such differences when designing census methods and analyzing results, are warranted.

Although I monitored just one male that was unmated throughout the 1994 season, this male's behavior and that of most males prior to pairing suggest that Golden-cheeked Warblers sing most often when they are unmated. Higher levels of vocal activity for unmated vs. mated males have been documented for many songbird species (Johnson 1983, Cuthill and Hindmarsh 1985, Staicer 1996b). Differences in singing between unmated and mated males could significantly bias detection on censuses toward unmated males, particularly if song output of mated males is very low (Hayes et al. 1986), as was the case on Fort Hood for much of each season. As a result of this bias, relatively low intensity census methods (such as point counts) are likely to result in the detection of a relatively higher proportion of unmated males than mated males, potentially compromising population estimates and assessments of habitat quality (Gibbs and Faaborg 1990, Gibbs and Wenny 1993). More detailed studies of the efficiency with which point counts or other census methods detect mated males would be of great importance in evaluating the degree to which censuses reliably estimate densities of breeding individuals.

The pattern of spatial song use that I observed suggests that some conclusions about Golden-cheeked Warbler habitat requirements made by other researchers merit reconsideration. One such conclusion is that Golden-cheeked Warblers prefer or require habitat edges for nesting (Pulich 1976, Kroll 1980, Ladd 1985), an idea that is largely based on studies in which territories were determined from the locations of singing males. Throughout much of the season, most males that I studied sang a high proportion of their songs from preferred perches near territory edges, but many other aspects of breeding biology, such as courtship and nesting, often occurred far from territory boundaries. I suspect that the tendency for males to sing from the edges of their territories, which often coincide with breaks in the woodland habitat, has contributed to the view that Golden-cheeked Warblers prefer

edge habitat. Golden-cheeked Warblers restrict their activity to woodland habitat, however, so this species does not seem to represent a true edge species (U.S. Fish and Wildlife Service 1992).

The reliance on point locations of singing males to describe Golden-cheeked Warbler habitat also may have led to an overly restrictive view of the importance of steep slopes for nesting habitat. Several authors have noticed that Golden-cheeked Warblers are often found in steep terrain (Chapman 1917, Oberholser 1974, Pulich 1976), and Ladd (1985) concluded that males prefer areas with high relief to those that are less rugged. Within the Fort Hood study area, males seemed to prefer singing from the edge of a cliff if such a site was available to them, perhaps because of acoustic properties associated with the cliff edge. Males on either the slope or hilltop can probably best monitor each other from these locations, and can also broadcast their songs to the largest area, and presumably the greatest number of individuals, from these sites. These cliff edges were at territory boundaries, however, and most other territorial behavior occurred away from the edge of the cliff. These observations suggest that descriptions of Golden-cheeked Warbler habitat based on point locations of singing males may exaggerate the importance of steep terrain and underestimate the use of upland areas.

Although point locations of singing males may not provide a complete picture of territory size or habitat use by individual Golden-cheeked Warblers, cautious evaluation of song behavior may be useful when monitoring territories. For instance, the proportions of A and B songs used by individual males may provide clues to mating status or nesting stage. Such clues can help biologists decide when and where nests or fledglings are likely to be found, or in estimating other facets of breeding biology. I should emphasize, however, that because of the probabilistic nature with which songs of each category are used, song behavior should be evaluated in conjunction with other observational data and not relied on exclusively to determine any aspect of nesting or territorial behavior.

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