Wilson Bull., 101(1), 1989, pp. 36–50

THE SINGING BEHAVIOR OF GOLDEN-WINGED WARBLERS

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ABSTRACT.—Golden-winged Warbler (*Vermivora chrysoptera*) males show distinct daily, seasonal, and social patterns in their use of two stereotyped song types. Type II song is used in an extended early morning bout, is sung at a rapid rate, and may be interspersed with flight song displays. Soon after sunrise, males switch to type I song, which is sung at a lower rate, often intermittently, throughout the morning. During actual or simulated agonistic encounters, long type I, short type I, and type II songs are used as a graded series. The amount of long type I singing, but not of short type I or type II singing, decreases upon attraction of a mate, and males were observed to sing only type I songs when consorting with females. These patterns of use support the view that song types in this species have special intrasexual (type II) and intersexual (type I) functions. The association of song types with specific singing behaviors suggests an organization of vocal behavior similar to that of parulines with much larger, more complex repertoires. *Received 19 May 1988, accepted 15 Oct. 1988.*

Unlike those songbirds that appear to use a variety of songs interchangeably, many wood warblers (Parulinae) have a repertoire of song types that are used in different ways in different contexts. In some warblers, the contexts in which songs are used suggest that song types are functionally distinct and carry predominantly intersexual (mate attraction) or intrasexual (territorial) messages (Chestnut-sided Warbler [*Dendroica pensylvanica*], Yellow Warbler [*D. petechia*], and American Redstart [*Setophaga ruticilla*], Ficken and Ficken 1965; Golden-winged Warbler [*Vermivora chrysoptera*] and Blue-winged Warbler [*V. pinus*], Ficken and Ficken 1967, Kroodsma 1981; Black-throated Green Warbler [*D. virens*], Morse 1970; and Grace's Warbler [*D. graciae*], Staicer 1982). In addition, observations of some species reveal that certain song types, or groups of song types, may be associated with distinct singing behaviors characterized by, for example, differences in rate of delivery or in sequential variety (Grace's Warbler, Staicer 1982; American Redstart, Lemon et al. 1985).

Golden-winged and Blue-winged warblers have a simple song system in which each male has a repertoire of two stereotyped songs, type I and type II (Lanyon and Gill 1964). An extensive literature, often with an emphasis on the role of vocalizations, documents within- and between-species behavioral interactions in this frequently hybridizing species pair (Gill and Lanyon 1964; Baird 1967; Ficken and Ficken 1967, 1968a, b,

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1969, 1973; Meyerriecks and Baird 1968; Gill and Murray 1972; Murray and Gill 1976). Despite this emphasis, only a very general picture of singing behavior has emerged; most authors note only that type I is the most frequently used song and that type II is restricted to particular situations. Only two studies attempt a more detailed analysis of patterns of song use. Ficken and Ficken (1967) found that levels of type I song activity are greater in unmated than in mated males of both species and that type II song is given most commonly during encounters with other males, suggesting mate attraction (type I) and territorial (type II) functions. Kroodsma (1988) provides a brief description of Blue-winged Warbler song use that is consistent with the view that different singing behaviors are used with the two song types.

I here present a comprehensive description of singing behavior in a population of Golden-winged Warblers that is currently and historically allopatric with Blue-winged Warblers. Through a series of early morning observations and song playback experiments, I investigated differences in the use of songs based on the behavioral context and on the time of day and season, and whether specific singing behaviors were associated with each song type.

METHODS

I studied Golden-winged Warblers in the Itasca State Park area, Hubbard and Clearwater Counties, of north-central Minnesota during May and June 1984–1986. Although Blue-winged Warblers nest only 300 km to the southeast, only one Blue-winged Warbler and one female hybrid have been reported from the area, both in 1986 (Highsmith 1987). Except for these individuals, the Itasca population appears phenotypically pure and shows no signs of genetic introgression with Blue-winged Warblers (Gill 1987). I performed all observations and experiments on active Golden-winged Warbler territories between 04:30 and 13:00 h CDT, with the help of several field assistants.

Song description.—Type I song (Fig. 1a) normally consists of a high frequency buzzy phrase followed by one to six buzzy phrases of lower frequency. Type I song length is referred to by the number of times each phrase type occurs in a song; a song with a single high frequency phrase followed by three lower frequency phases, for example, is a 1-3. Based on observations of song use by undisturbed males, I consider type I songs with four or more total phrases to be long type I songs, and songs with three or fewer total phrases to be short type I songs (see Results). Type II song (Fig. 1b) contains three to five syllable types and ends with a terminal buzzy phrase.

Observations of singing behavior.—Although the singing behavior of over 15 different males was observed, I here report data from the six color-banded males that were observed most intensively. Because previous accounts of Golden-winged Warbler singing behavior did not cover the early morning period, my assistants and I usually arrived on territories between 04:30 and 05:00 h to begin our observations before males started their singing activity each day. Males A, B, and C (1986), D and E (1985), and F (1984) were monitored continuously from the beginning of song activity to well after sunrise, and at various times later in the day. We used binoculars, stop watches, and data sheets, marked in minutes and seconds, to record the following: song type; song length; whether songs were loud or muted;

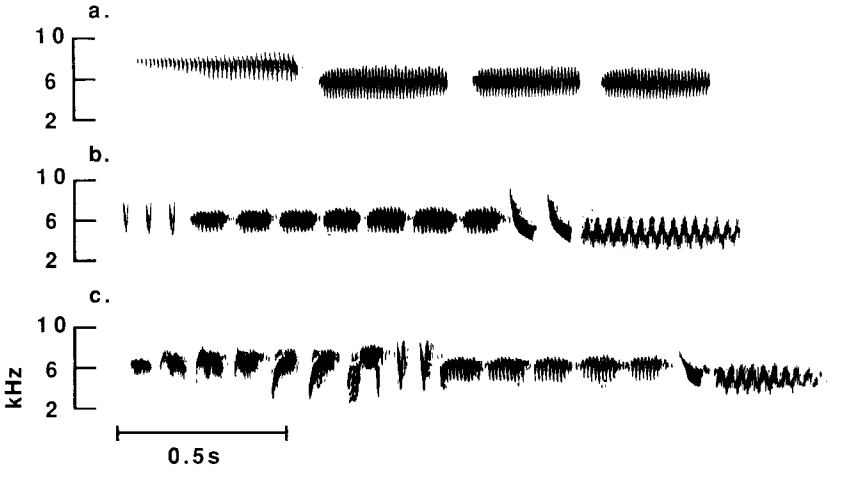

FIG. 1. Song repertoire of Golden-winged Warbler male A. Sonagrams were prepared on a Kay Elemetrics Co. Model 7029A Sonagraph (600 Hz filter). A. type I song. B. type II song. C. modified type II song used in flight song display.

the male's position on the territory; and the behavioral context of a male's singing, including any interactions with conspecifics.

The data from males A, B, and D that were used to compare singing behavior during the pair formation period were limited to those that were collected between the start of singing activity and 06:30 over the birds' first nineteen days on territory. I determined singing rate by counting the number of songs in each bout of continuous singing and dividing by the number of minutes of continuous song. I express the amount of type II song activity as the duration in minutes of the essentially continuous early morning type II bout, measured from the first type II song of the day to the last type II song given before the switch to pure type I singing. Because type I songs are sung more intermittently, the amount of type I song activity is best expressed as songs per minute of observation. Multiple linear regression analysis of male A's singing behavior was done using the Interactive Data Analysis Package (Wiedmann and Hosmer 1983).

Song playback experiments.—We noted responses to simulated territorial intrusions during the course of song playback experiments on species discrimination with over 250 different males. Pairs of song stimuli were played at a natural singing rate from two speakers placed on a male's territory. Each playback experiment consisted of five periods: 5 min of pre-playback observation, 5 min of stimulus presentation, a 3 min silent intermission, 5 min of stimulus presentation, and 5 min of post-playback observation. Males were scored on the basis of whether they sang any type I or type II songs during each period, and on the length of type I songs sung. If an individual sang both song types during a particular period, it was scored for both.

We used Uher 4200 or 4400 Report Monitor tape recorders and Olympus SP5 speakers (modified by Mineroff Electronics) to broadcast songs. Type II song stimuli (total of 8 different experimental tapes) consisted of natural Golden-winged and Blue-winged warbler type II songs. Type I song stimuli (total of 25 different experimental tapes) included various

TABLE 1
MEAN SINGING RATES OF TYPE I AND TYPE II SONGS (IN SONGS·MIN^{-1})

Male	Type I	Type II
A	3.9 ± 1.4 (10)[a]	6.5 ± 1.4 (7)[a]
B	3.7 ± 0.5 (6)	6.5 ± 1.9 (7)
D	4.3 ± 1.4 (5)	10.4 ± 1.6 (6)
E	4.5 ± 0.6 (6)	10.0 ± 1.9 (2)
F	3.2 ± 0.3 (6)	10.8 ± 2.6 (6)

[a] Mean ± SD (number of song bouts used to calculate mean).

combinations of natural Golden-winged Warbler type I, natural Blue-winged Warbler type I, and artificial type I songs composed of elements from both species. Some males also heard several type I songs during pre-playback or intermission from a separate tape used to attract males to the playback area. A small number of males received both a type I and a type II playback, but otherwise a male was used only once. Vocal responses of males to playbacks containing only natural or only artificial type I songs did not appear to differ, so all type I playbacks were lumped for analysis. Results from type I and type II playback experiments were analyzed separately. Statistical comparisons of changes in singing behavior between experimental periods were made using McNemar's test for significance of difference between two correlated proportions (two-tailed, Ferguson 1976).

RESULTS

Daily Patterns of Singing Behavior

Undisturbed, mated Golden-winged Warbler males exhibited two distinct modes of singing behavior that were characterized by differences in song type and time of day.

Type II singing behavior.—Except for very early in the season, males began each day's singing activity with an extended and rapidly paced bout of type II songs. Many males began the bout from the same perch each day and sang continuously for 30–40 min, stopping around sunrise. Typically a male sat mid-level or high in a shrub or tree, often at an edge of his territory closest to conspecific neighbors with whom he counter-sang. Males frequently made short-distance perch changes.

Although most males began the bout with complete songs, others sang only the first two or three syllable types of their normal type II song for several minutes, and only gradually lengthened these songs to include the terminal buzz. Chip notes, similar in structure to the initial type II syllables, were used frequently between songs. Songs were delivered at a rapid rate throughout the bout, although the rate differed greatly both among males (mean = 8.8 ± 2.2 [SD] songs-min^{-1}, N = 5 males) and within individuals (Table 1). Male E, for example, was once observed

singing at the unusually high rate of 18–20 songs·min^{-1} for a two-minute period.

Interruptions of the type II bout were not uncommon, but their causes were difficult to observe because of low light levels and thick vegetation. Males sometimes paused to chase intruding males or to accompany females. In both cases, males and females uttered a low, buzzy "zzt," either singly or repeated in slow chatter-like strings. Following such disturbances, males typically returned to the same or a different perch and resumed type II singing.

Flight song displays can be given at any point in the type II bout, but five of the eleven males in which I observed it used it frequently as one of their very first songs of the morning. To perform the display a male flew up in an arching path, flapped his wings stiffly, gave the song at the peak of his ascent, and flapped or glided down to the same or a different perch (similar to description for other parulines in Ficken and Ficken 1962). The song itself was a modified version of the male's type II song, differing in the addition of two or three syllable types to the beginning of the song (Fig. 1C). I was able to obtain good recordings from only two males, but the structure of the syllables peculiar to the flight songs was similar in each individual. I frequently observed one to three flight song displays during a male's early morning type II bout, but on some days I heard none at all. The most I observed during a single bout was a total of nine given by male A in a 30-min period on 23 May 1986. Flight song displays were noted as early in the season as 17 May and as late as 20 June.

A male's early morning type II bout ended with a minute of intermingled type I and II songs, an abrupt switch to type I songs, or a cessation of singing activity. Type II songs were often used later in the morning, but with several notable differences. Rather than forming a distinct bout, strings of type II songs were likely to be mixed with strings of type I, usually preceding or following an interaction with another male. Although song rate remained high and some males sang incomplete songs, flight song displays were not used, chipping between songs was less frequent (although the "zzt" note was sometimes used), and males often sang at reduced volume.

Type I singing behavior.—Whether a male's first type I songs of the day were continuous with the end of his type II bout, or whether he stopped and began later in the morning, type I singing was characterized by a lower mean song rate (3.9 ± 0.6 [SD] songs·min^{-1}, N = 5 males), lack of chip notes between songs, and absence of flight song displays. Relatively little variation existed in type I song delivery rates among males (Table 1); even during counter-singing the highest type I rate I observed was 8 songs·min^{-1}, again from male E.

There was variation among males in the length of type I songs included in their individual repertoires. Individuals generally had a "preferred" type I rendition that was their most common song in bouts of undisturbed singing. This song was usually the longest or next longest type I song in a male's repertoire and contrasted with the shorter songs that a male sang during territorial disputes (see below). The "preferred" song for most males was a 1-3 (Fig. 1A), but I encountered a small number of males who sang predominantly 1-2's and another who sang predominantly 1-4's. Male A is typical of 1-3 singers; 57% of all songs observed over two seasons were 1-3's and less than 1% were 1-4's or longer. All of the six males that I intensively observed "preferred" 1-3's, except for male D, who sang mostly 1-2's (85% were 1-2's, only 3% were 1-3's).

There was no distinct type I bout, analogous to the type II bout, that was predictable in time and place. Although an unmated male sometimes sang type I for hours from a single exposed perch, mated males were more likely to sing intermittently from a succession of perches around the perimeter of their territory, or not to sing at all for long periods. I have observed undisturbed males singing type I while preening or foraging, and from perches in thick vegetation where they were mostly obscured from view. Type II singing, at least during the pre-dawn bout, appeared to preclude preening or foraging, perhaps because of low light levels.

Seasonal Patterns of Singing Behavior

Type II singing behavior.—Analysis of samples from four males over the first nineteen days after their arrival on territory showed that the duration of the early morning type II bout tended to increase throughout this period (Fig. 2). Males did not begin singing these type II bouts until two to four days after arrival, and bouts were likely to be quite short (less than 15 min) for the first ten days or so. Some bouts eventually increased to 45 min in length as males began singing earlier before sunrise.

Type I singing behavior.—Type I singing activity decreased over the course of the breeding season. Following an abrupt drop from almost constant type I singing before males were paired in May, type I singing decreased more gradually until, by mid- to late June, songs were quite sporadic. Early in the season, before type II bouts were established, some males began their daily singing before sunrise with type I songs. In these instances, singing rate and behavior were the same as in typical later morning type I singing.

Social Patterns of Singing Behaviors

Singing behavior during song playback experiments.—Males used both their type I and type II singing behaviors during simulated territorial intrusions provided by song playback experiments. The most striking

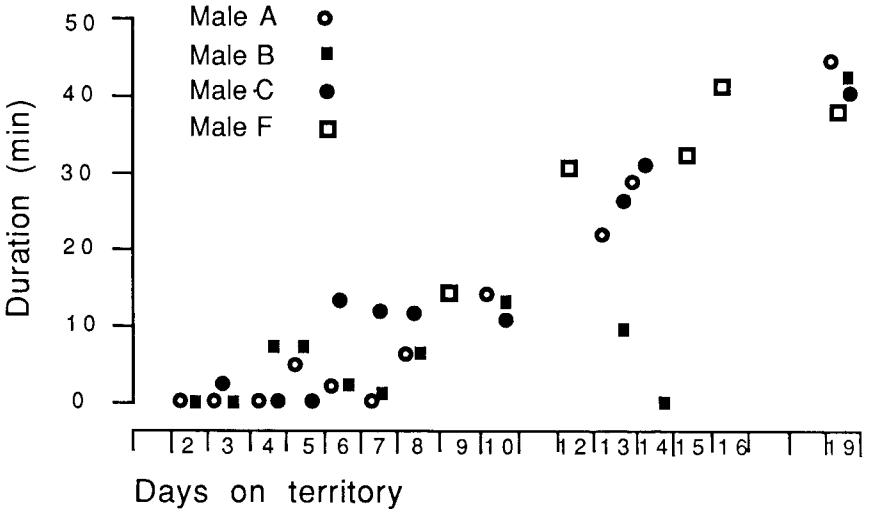

FIG. 2. Duration of early morning type II song bouts for four Golden-winged Warbler males over their first nineteen days on territory. Only those days on which data were taken are numbered on the abcissa. Date of arrival on territory (day one) for males A, B, and C is 10 May 1986; for male F, 17 May 1984. Spearman rank correlations (two-tailed): male A, $r_s = 0.91$, $P < 0.001$, N = 11; male B, $r_s = 0.54$, $0.05 < P < 0.1$, N = 11; male C, $r_s = 0.87$, $P < 0.001$, N = 10; male F, $r_s = 0.90$, $P = 0.05$, N = 5.

change in song type use occurred during the first stimulus presentation period, regardless of whether the experimental songs were type I or type II (Fig. 3). Although the number of males singing type I songs decreased slightly from the pre-playback to the first stimulus period, the number singing type II songs increased significantly. The same general pattern was evident over all five experimental periods: the number of males singing type II increased during periods of stimulus presentation and decreased during periods of silence, while the number of males singing type I decreased during stimulus periods and increased when the stimulus was withdrawn. These results agree with other playback experiments and observations of males in actual territorial encounters (Ficken and Ficken 1967, 1968b, 1969, 1973; pers. obs.). Responses to the playback experiments also showed that there was an overall increase in singing activity, in that more males were vocalizing after the experiments than before.

A pattern was also evident in the length of type I songs used by males during playback experiments (Fig. 4). Although the numbers of males singing short and long type I songs was approximately equal just before both type I and type II experiments, the number of males singing short songs increased significantly, and those singing long songs decreased sig-

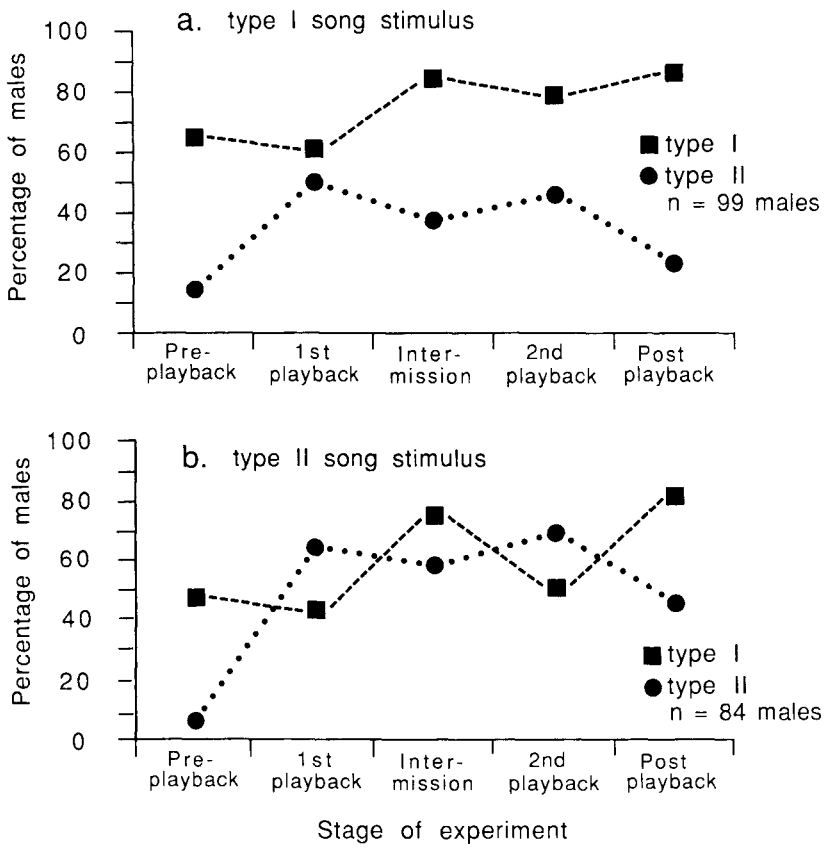

FIG. 3. Changes in song type use by male Golden-winged Warblers during song playback experiments. Graphs show the percentage of males that sang type I and type II songs in each of five experimental periods. Change in type II use between the pre-playback and first playback periods was statistically significant ($P < 0.01$) for both categories of stimuli. Change in type I use between the same periods was not significant ($P > 0.05$) for either type of stimuli. a. type I playback stimulus (median date 6 June, range 14 May–29 June). b. type II playback stimulus (median date 19 June, range 24 May–26 June).

nificantly, during the first stimulus period. Singers of short songs outnumbered singers of long songs throughout all but the pre-playback period.

Singing behavior during mate attraction and pair formation.—My assistants and I were able to follow three Golden-winged Warbler males through the process of mate attraction and pair formation. All three males engaged in a variety of visual courtship displays, which are well documented elsewhere (Baird 1967, Ficken and Ficken 1968a). Two of the males, B and D, successfully attracted and paired with single females. Male A, on

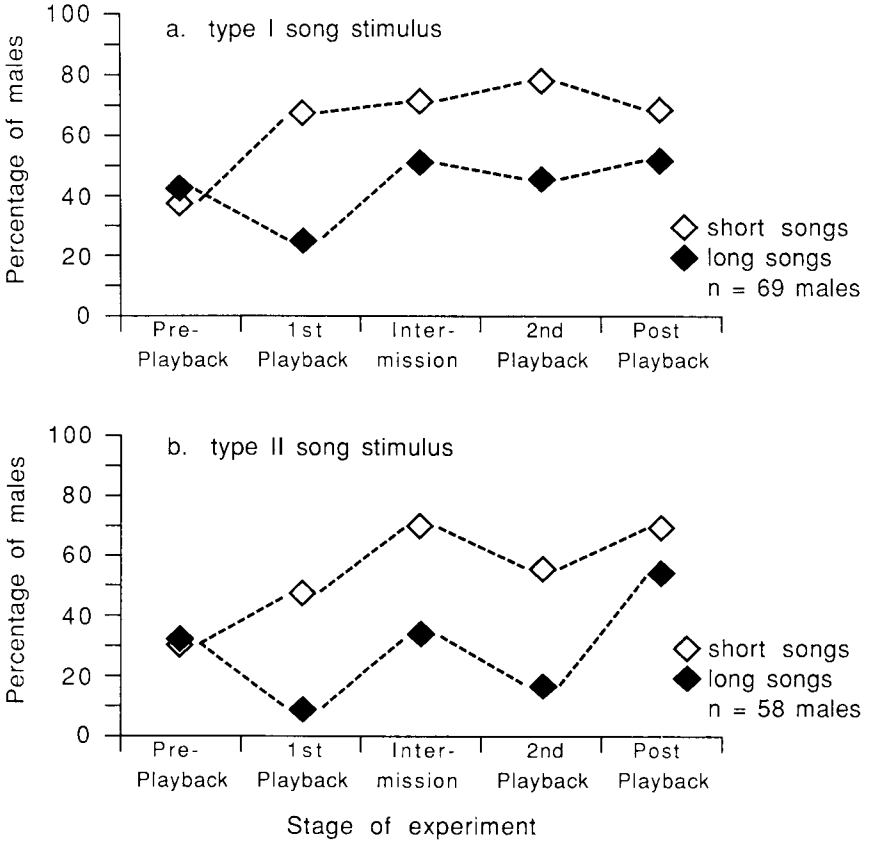

FIG. 4. Changes in the length of type I songs sung by male Golden-winged Warblers during song playback experiments. Graphs show percentage of males which sang short (1-0, 1-1, 1-2) or long (1-3, 1-4, 1-5) type I songs in each of five experimental periods. Changes in the use of both short and long songs between the pre-playback and first playback periods were statistically significant ($P < 0.01$) for both categories of stimuli. a. type I playback stimulus. b. type II playback stimulus.

the other hand, provided a natural mate-loss experiment. Male A's first potential mate, a female Blue-winged Warbler, remained on his territory for only three days, during which time she was closely attended by male A and appeared to prospect for nest sites. After her disappearance, male A remained unpaired for five to seven days until he finally attracted a Golden-winged Warbler female. Although male A's circumstances were unusual in this study population, I believe his behavior may be considered representative of a normal Golden-winged Warbler male. Interspecific

pairing of Golden-winged and Blue-winged Warblers is not uncommon in areas of more extensive sympatry and, except for song morphology, courtship displays of the two species are essentially identical (Ficken and Ficken 1968a). Also, male A's behavior with the two females did not differ in any notable way, nor did it differ from that of the other two males under observation.

The presence of a female on a male's territory had no consistent effect on the type II singing behavior of the three males during pair formation. Male A sang progressively longer type II bouts throughout this period (Fig. 2). Analysis by multiple linear regression showed that the number of days since he arrived on territory contributed significantly to explaining variation in the amount of his type II singing ($t = 6.89$, $P = 0.0001$), but female presence did not ($t = 0.86$, $P = 0.41$; female presence and days together: $F = 25.3$, df = 2,7, $R^2 = 0.88$, $P = 0.0006$). Male B (Fig. 2) showed a smaller increase in type II bout length before and after female arrival, and male D's bouts decreased in length the first two days on which he was closely attending his female. Males appeared to cut short or abandon their type II bouts in order to closely attend the females on some days, but I never observed males to sing type II while in close association with females.

All three males showed a dramatic change in long type I singing activity with the arrival of the female. In general, males sang extended, uninterrupted bouts of long type I songs before attracting a female, but sang very few long type I's once a female was present. For male A (Fig. 5), long type I activity decreased with the arrival of the Blue-winged Warbler female, rose when she disappeared, and fell off again with the arrival of the Golden-winged Warbler female. Regression showed that female presence contributed significantly ($t = -4.09$, $P = 0.003$) to explaining variation in the amount of his long type I singing, but number of days on territory did not ($t = -0.217$, $P = 0.83$; female presence and days together: $F = 7.43$, df = 2,7, $R^2 = 0.68$, $P = 0.018$). Males B and D (Fig. 5) also showed a sharp drop in the amount of their long type I activity immediately after attracting females.

Males showed no corresponding variation in the amount of their short type I singing, although they did use sporadic, usually muted, short type I songs when close to a female. The amount of short type I activity varied little before and after female arrival for male A (Fig. 5; female presence: $t = 0.136$, $P = 0.89$; number of days on territory: $t = -0.590$, $P = 0.57$; female presence and days together: $F = 0.177$, df = 2,7, $R^2 = 0.04$, $P = 0.84$) and for male D (Fig. 5). Male B's short type I singing did increase on the first day of his female's presence, but returned to previous levels the following three days (Fig. 5).

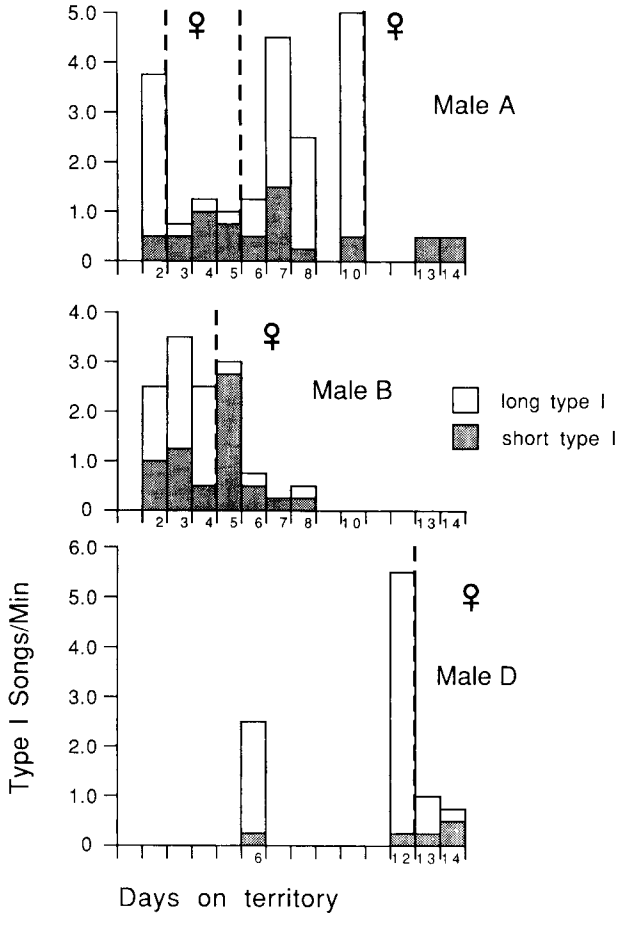

FIG. 5. Changes in the type I singing behavior of three Golden-winged Warbler males in response to the presence or absence of a resident female on their territories. Songs were sampled continuously from the first song of the morning (usually between 04:50 and 05:00 h) until 06:00–06:30 h. Song activity is expressed as type I songs-min^{-1} of observation after the early morning type II bout. Vertical dashed lines separate periods of female presence and absence. Only those days on which data were taken are numbered on the abcissa. Male A's long type I songs are 1-3's and 1-4's; short type I songs are 1-2's and 1-1's. Male B's long type I songs are 1-3's; short type I songs are 1-2's and 1-1's. Male D's long type I songs are 1-2's and 1-3's; short type I songs are 1-1's.

DISCUSSION

My results generally support the descriptions of Golden-winged Warbler singing behavior made by Ficken and Ficken (1967) but provide a more complete picture of the ways in which males use their two song types.

Although previously considered an infrequently used song, type II song constitutes a substantial part of a male's vocal behavior and is not limited to use during conflicts between males. Except at the very beginning of the season, type II makes up a distinct and lengthy bout of songs, performed daily at the same time and place, that initiates a male's daily singing activity. Especially late in the season, when most mated males are singing type I only sporadically, the early morning type II bout may be the only predictable element of a male's singing behavior on a particular day.

Singing in flight has been noted in a number of *Vermivora* (Bent 1953, pp. 42, 84; Pitelka 1939; Ficken and Ficken 1962; Gilbert 1983), but modification of both the song and pattern of flight has been previously reported only in the Nashville Warbler (*V. ruficapilla,* Bowles and Bowles 1906, Chapman 1907). Golden-winged Warblers occasionally sing normal type II songs in flight, especially during song playback experiments, but their flight song display is distinctly different. The range of dates and time of day of my observations do not strongly support the suggestion that these displays are primarily given late in the day and late in the season (Ficken and Ficken 1962). I observed all but one of more than 30 displays during the early morning type II bout, and the other one around 07:00 h. Although I have not made extensive observations in the evening, others have noted flight song displays during a brief type II bout at that time (T. Will pers. comm.).

Both observational and experimental data show that a male's song repertoire exists as a graded series. A male sings long type I songs when he is relatively undisturbed, and shortens these when presented with either a real or simulated male intruder (Fig. 4), or when closely accompanying a female. If an interaction with another male escalates, males switch to type II songs, although I never observed males to use type II songs when in close contact with females. Responses to song playback show that males often switch songs in stepwise fashion, up or down the series (e.g., 1-3 to 1-1 to type II), but they may also switch directly from long type I to type II or vice versa. Ficken and Ficken (1967) obtained similar results for Golden-winged Warblers from a population sympatric with Blue-winged Warblers in New York.

This pattern of song use resembles the "motivational continuum" Lein (1972) has proposed to explain the use of song types by Black-throated Green Warblers. Territorial Black-throated Green Warbler males, Lein suggests, spontaneously produce type B songs when undisturbed, but switch to type A in the presence of a variety of external stimuli including other males, low light levels, or proximity to the territory boundary (but see Morse 1970). Similarly, Chestnut-sided Warblers (Lein 1978) switch up or down within a series of accented and unaccented ending song types depending on the singer's "mood," location on his territory, and the

likelihood of a dispute with a neighbor. Lein argued that song in these and other warbler species functions primarily in territorial establishment and defense. While he notes that the message a song type carries may well have different meanings for male and female conspecifics, he concludes that any intersexual function of song is supplementary to the intrasexual (Lein 1978). Although song use by Golden-winged Warblers appears consistent with Lein's "motivational continuum," observations of the contexts in which songs are used do not support his functional explanation. There appears to be a major functional distinction between the two extremes of the graded series, type II songs and long type I songs.

Patterns of song use by Golden-winged Warblers early in the season suggest that long type I songs, but not short type I or type II, are particularly important in mate attraction. The early morning type II bout is absent, or of short duration, during this period (Fig. 2), although type II is used during encounters with other males at that time. The presence of a female on a male's territory had no consistent effect on the amount of short type I (Fig. 5) or type II singing. In contrast, female presence correlated strongly with a sharp drop in long type I singing activity, and one male who lost his first mate reverted to a high level of long type I activity until he attracted another (Fig. 5). Further, although both song types are used in agonistic situations, songs from the middle of the graded series (short type I) are used with conspecifics of either sex; daytime type II songs appear to be reserved for use during interactions with other males.

The data thus support the general view that type I and type II songs carry inter- and intrasexual messages, respectively (Ficken and Ficken 1967, Kroodsma 1981), but with two important qualifications. First, the mate attraction function appears limited to a male's long type I song. Second, each song type has a specific, but not a solitary, message: despite type I song's special mate attraction function, it is also used by males in territorial disputes, and despite type II's special territorial function, it may also carry information about species or individual identity that is available to listening females.

Differences between type I and II songs are further underlined by the distinctive behaviors associated with the delivery of each song type. Type I and type II singing behaviors differ in song rate, use of chip notes between songs, use during flight displays, and use during well defined, ritualized song bouts. It is likely that Blue-winged Warblers share many of the patterns of behavior, if not specific behaviors, that I have described for Golden-winged Warblers. Blue-winged Warbler males sing an early morning type II bout and singing rates of type I and type II songs differ in ways parallel to those of Golden-winged Warblers (mean rate of type I songs = 4.6 ± 0.8 [SD] songs·min^{-1}, mean rate of type II songs = 11.9 ± 1.7

[SD] songs·min^{-1}, N=5; Massachusetts Blue-winged Wargler males). There is also evidence that modified type II songs are used in a flight display (pers. obs.; Kroodsma, unpubl. data).

This correlation of particular behaviors and particular song types is also seen in some parulines with much larger, more complex repertoires. Species may sing specific song types, or groups of song types, with consistent differences in rate or pattern of delivery. Male American Redstarts (mean repertoire size = 4.4 songs per adult male), for example, consistently repeat one of their song types over and over (repeat mode) but sing the others with high immediate variety (serial mode) (Lemon et al. 1985). For Grace's Warblers, which typically have repertoire sizes of six or more song types per male (Staicer 1982), similarities with Golden-winged Warblers are pronounced both in how the songs are sung and in what contexts they are used. Group A songs, used prior to pairing and in the presence of females, are sung with low or no sequential variety and at a slow rate. Group B songs, used primarily during an early morning bout and in interactions with other males, are sung with immediate variety and at a high rate (Staicer 1982).

These comparisons among warbler species suggest that the complexity of singing behavior may depend as much on how the repertoire is used as it does on repertoire size. Despite the limitation of two stereotyped song types per male, the flexibility of Golden-winged Warbler singing behavior serves to create a larger effective repertoire. Golden-winged Warbler males use songs as a continuous series and as discrete song types. Distinctions between mate attraction and agonistic functions are apparent both between the two song types and within a single song type (type I).

ACKNOWLEDGMENTS

I thank S. Householder, D. Pranke, P. Rodewald, P. Rosel, and T. Seabolt for their able and eager field assistance. J. Ross and D. Parmelee of the Univ. of Minnesota Forestry and Biological Station provided invaluable help and orientation in the Lake Itasca area. J. Gifford offered patient statistical advice. The article was greatly improved by the comments of T. Armstrong, C. Blem, F. Gill, D. Kroodsma, T. Sargent, D. Spector, and C. Staicer. The work was supported, in part, by the Itasca Field Biology Program, the Josephine Herz Foundation, the Zoology Department of the University of Massachusetts, and the National Science Foundation (to D. Kroodsma, BNS-8506996).

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