The Condor 93:12–18

THE FLIGHT SONGS OF COMMON YELLOWTHROATS: DESCRIPTION AND CAUSATION[1]

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Abstract. The flight songs of Common Yellowthroats (*Geothlypis trichas*) consist of three sections: 1) a series of short duration notes that extend over a wide range of frequencies, 2) a portion of the perch song, and 3) a complex series of notes and phrases that also extend over a wide range of frequencies. The initial and terminal sections provide information about the location of the singer while the inclusion of a portion of the perch song permits individual recognition by conspecifics. During these songs, males flew to a mean height of 5.5 m, enhancing the transmission of the vocal signal. Flight songs were uttered at similar rates throughout the breeding season, with no difference in rates before and after pairing. Most flight songs were performed when males were not interacting with conspecific males, suggesting that such songs play little or no role in territorial defense. Male yellowthroats did perform significantly more flight songs when I was present in their territories, suggesting that these songs are performed in response to the presence of potential predators. Such songs may simultaneously warn mates and direct the attention of the predator to the male.

Key words: Flight song; Common Yellowthroat; Geothlypis trichas; *individual recognition; warning mate; distraction display.*

INTRODUCTION

Flight songs have been described in a variety of species, many of which nest in open habitats. Among warblers, flight songs have been reported for 11 species, including the Common Yellowthroat (*Geothlypis trichas*). As a rule, the flight song in each of these species is accompanied by a peculiar flight pattern: a rising flight on slowly flapping or quivering wings (with tail bobbing in some species) and typically a direct and silent descent. These songs may contain elements of the individual's normal perch song. Bent (1953) described the flight song of the yellowthroat as "an outburst of ecstasy consisting of short, confused, and sputtering notes, but generally including phrases of the common song."

Ficken and Ficken (1962) observed that the function of flight songs in warblers remains undetermined. Lein (1981:39) examined the singing behavior of Ovenbirds (*Seiurus aurocapillus*) and, regarding its flight song, observed that "its rare occurrence and peculiar situation of use . . . make it difficult to suggest its function." Kowalski (1983) examined the factors affecting the performance of flight songs by Common Yellowthroats in Indiana and suggested that such songs functioned to maintain territorial boundaries after those boundaries had been established. The objectives of my study were 1) to describe the flight songs of Common Yellowthroats and 2) to determine the function of such songs.

METHODS

Seven male Common Yellowthroats located on contiguous territories were observed for 220 hours from 21 April through 15 August 1987 at the Central Kentucky Wildlife Management Area, located 17 km SSE of Richmond, Madison County, Kentucky. Each male was observed approximately once every nine days, thus averaging about 13 times throughout the study. Males were captured in mist nets and individually marked with colored leg bands and plastic tape attached to the tail (Ritchison 1984). Daily observation periods were 2–3 hr in duration. Although most observations were made during the period from sunrise to 10:00 hr, some observations were also made from 18:00 hr to sunset. Territory boundaries were delineated by following males and by noting the location of interactions with neighboring males. I followed one male per observation period and remained within that focal male's territory. Because territories were small ($\bar{x} = 0.8$ ha) and flight songs so audible, I was able to hear the flight songs of males on territories immediately adjacent to the focal male's. Thus, during

[1] Received 23 May 1990. Final acceptance 16 October 1990.

each observation period I also noted the number of flight songs uttered by one adjacent male. For each flight song uttered by a focal male, I noted the date, time of day (am or pm), and nesting stage. The nesting period was divided into five stages: pre-pairing, pre-nesting, nest building, incubation/brooding, and post-fledging. I further noted whether or not conspecific males were singing and, if so, the location of the singing conspecific(s). On that basis, I recognized three possible situations: spontaneous song (no other males singing), close exchange (perch songs being uttered by one or more conspecific males with territories contiguous to that of the focal male), and distant exchange (perch songs being uttered by one or more conspecific males with territories not contiguous to that of the focal male, i.e., at least one territory removed from the focal male). I also noted the location of males relative to females and the nest at the beginning and end of flight songs. Finally, I estimated the height of the male at the apex of his flight (using nearby vegetation of known height as a guide) and also noted the position of the male relative to the boundary of his territory at the end of a flight song compared to his position at the initiation of the flight song. Thus, the focal male could have moved closer to the boundary, further from the boundary, or remained the same distance from the boundary.

Recordings were made with a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic reflector and microphone. Sonagrams of flight songs were produced with a Kay Elemetric Sonagraph (Model 6061A). All analyses were performed using procedures found in the Statistical Analysis Systems Guides (SAS Institute 1985). Differences in song rates (number of flight songs per hour) were analyzed for variance (GLM procedure) and post hoc comparisons were made using the Student-Newman-Keuls (SNK) test. Paired comparisons were made using either Wilcoxon or Mann-Whitney U tests. Chi square tests were used to test for non-random distributions.

I use the terminology of Borror (1967) and Wunderle (1979) to describe the songs of Common Yellowthroats. A "note" is used to designate a sound that produces a continuous mark on a sonagram. A group of notes, repeated two or more times, make up a phrase. I defined a bout as a series of songs separated in time from each other by intervals of 60 sec or less.

RESULTS

The flight songs of Common Yellowthroats began with a series of short duration notes that extended over a wide range of frequencies, continued with phrases from the male's perch song, and terminated with a complex series of longer notes and phrases (Fig. 1). The mean number of introductory notes was 4.77 ± 0.11 (SE) (n = 48). Males (n = 7) exhibited significant variation (F = 5.56, df = 6, 41, $P < 0.0003$) in the mean number of introductory notes, ranging from four to six. The introductory notes were followed by a mean of 2.49 ± 0.04 (n = 94) phrases from the male's perch song. Again, males (n = 7) exhibited significant variation (F = 14.96, df = 6, 87, $P < 0.0001$), with the mean number of phrases per flight song ranging from 2.00 to 2.86. Flight songs ended with a complex series of notes and phrases (Fig. 1). Although individual variation was apparent in the structure of the introductory and perch song portions of flight songs, all seven males used notes and phrases that were similar in structure in the terminal section (Fig. 2). The mean number of notes and phrases was 5.52 ± 0.16 (n = 95), with significant variation among males (F = 5.23, df = 6, 88, $P < 0.0001$). The mean number of terminal notes and phrases per flight song among the seven males ranged from 3.9 to 6.3. Infrequently (14 of 95; 14.7 percent), additional phrases ($\bar{x}$ = 1.45 ± 0.17) from a male's perch song followed the usual terminal notes. These additional phrases were added to flight songs by only two of the seven males, with one male adding these phrases to 11 of 12 flight songs.

Although I found significant inter-individual variation, it appeared that each male yellowthroat had but one flight song that was reproduced with only minor variation. Males sometimes: 1) omitted the first one or two introductory notes, 2) varied the number of phrases from their perch song, and 3) omitted one or two terminal notes or phrases. For example, the flight song of one male (top sonagram in Fig. 2) typically consisted of five introductory notes, two complete phrases from his perch song, and six terminal notes and phrases. This male exhibited no variation in the number introductory notes, all flight songs included five (n = 13 songs). Some variation was found in the number of phrases from this male's perch song, with five flight songs including two complete phrases (as in Fig. 2) and 15 including two complete phrases plus the first

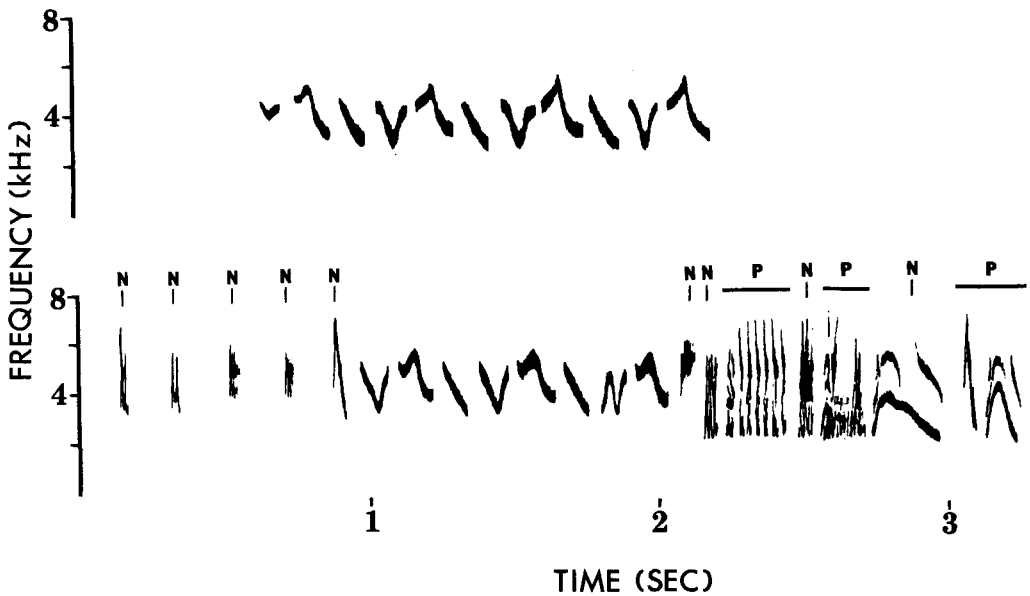

FIGURE 1. The perch song (above) and flight song (below) of a Common Yellowthroat. In this perch song, each phrase consists of three notes. This flight song includes two complete phrases and two notes of a third phrase from the perch song. The initial section of the flight song consists of a series of notes and the terminal section consists of a series of notes (N) and phrases (P). Notes and phrases in the initial and terminal sections are not included in perch songs.

two notes of a third phrase. Minor variation was also found in the number of terminal notes and trills, with 14 flight songs including six notes and phrases (as in Fig. 2) and six including all but the last phrase. The other six males exhibited similar degrees of variation in their flight songs.

During flight songs, male yellowthroats flew to a mean estimated height of 5.5 ± 0.35 m (n = 47). The mean distance between take-off and landing points was 5.2 ± 0.48 m (n = 90). Significantly more (χ^2 = 18.3, df = 2, $P < 0.001$) flight songs were directed away from territory boundaries (51/99) than toward territory boundaries (16/99). Flight songs were rarely (only 12 of 156) uttered during bouts of perch songs. The mean time since the last perch song by males uttering flight songs was 22.01 ± 2.05 min (n = 156), while the mean time until the next perch song after a flight song was 6.13 ± 0.82 min (n = 164).

No significant variation was found between morning (prior to 10:00 hr) and evening (after 18:00 hr) in the number of flight songs per hour of observation (Mann-Whitney U test, $P = 0.779$), with songs being uttered at a rate of 0.24 per hour (n = 197 hrs) during the morning and 0.27 per hour (n = 23 hrs) during the evening. Most flight songs were given at times when no conspecifics (either neighboring or more distant) were singing perch songs (χ^2 = 45.08, df = 2, $P <$ 0.0001). Nearly 58 percent (95 of 164) of the flight songs were given "spontaneously," while 19 percent (31 of 164) were given when one or more neighboring males were singing perch songs ("close exchanges") and 23 percent (38 of 164) were given when one or more males at least one territory removed ("distant exchanges") were singing perch songs. All seven males performed most of their flight songs when no conspecifics were singing (χ^2 = 13.93, df = 12, $P = 0.305$).

The mean distance between males and their mates at the beginning and end of flight songs (n = 22, with females at a nest on 8 occasions and not at a nest on 14 occasions) was 22.07 ± 3.52 and 34.41 ± 3.36 m, respectively, with this difference not significant (Wilcoxon test, Z = 1.38, $P = 0.165$). The mean distance between males and their nest at the beginning and end of flight songs (n = 17, with the female known to be at a nest on 8 occasions and the location of the female not known on 9 occasions) was 39.76 ± 4.19 m and 45.29 ± 3.01 m, respectively, with this dif-

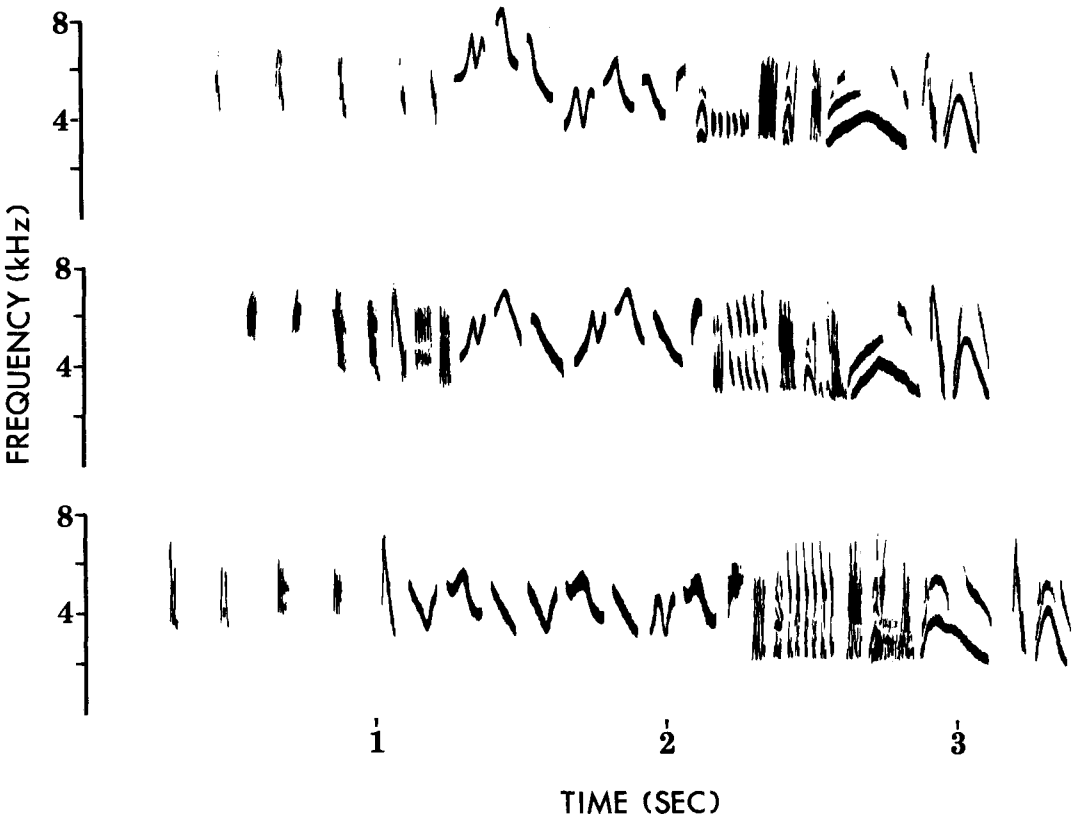

FIGURE 2. The flight songs of three male Common Yellowthroats. Note the similarity of the terminal portions.

ference again not significant (Wilcoxon test, $Z = 0.639$, $P = 0.523$). Prior to nesting or when females were known to be away from nests ($n = 14$), males began and ended flight songs at mean distances of 23.82 ± 4.31 m and 28.93 ± 3.80 m, respectively, from their mate. Again, this difference was not significant (Wilcoxon test, $Z = 1.04$, $P = 0.299$).

Although I found no significant variation in use of flight songs among months ($F = 1.95$, df = 4, 266, $P = 0.103$), rates were lower in April (no songs in 12 hours of observations) and August (Fig. 3). Although no significant relationship was noted between the number of flight songs per hour and nesting stage ($F = 0.34$, $P = 0.852$), males did utter fewer flight songs after the young fledged (Fig. 4).

Male yellowthroats uttered flight songs at a significantly higher rate when I was in their territory (Mann-Whitney U test, $P < 0.0001$). Flight songs were uttered at a rate of 0.51 per hour of observation by focal males and at a rate of only 0.11 per hour of observation by non-focal males.

The seven males exhibited significant variation in the number of flight songs uttered per hour of observation ($F = 2.56$, df = 6, 84, $P = 0.025$). Rates varied from 1.00 to 0.12 per hour of observation, with one male uttering significantly fewer flight songs than the other six males (SNK; $P < 0.05$).

DISCUSSION

The flight songs of male Common Yellowthroats appear to convey information about both location and identity. Both the introductory and terminal portions of these songs include notes of short duration that extend over a wide range of frequencies. Such notes make a caller relatively easy to locate (Marler 1955). Wunderle (1978) demonstrated that both male and female Common Yellowthroats were able to recognize the perch songs of different individuals. Thus, the

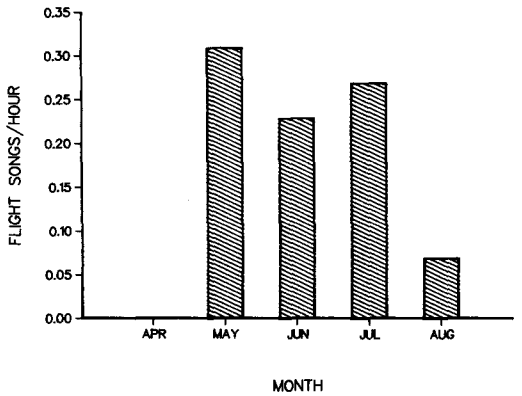

FIGURE 3. Flight songs per hour of observation by month.

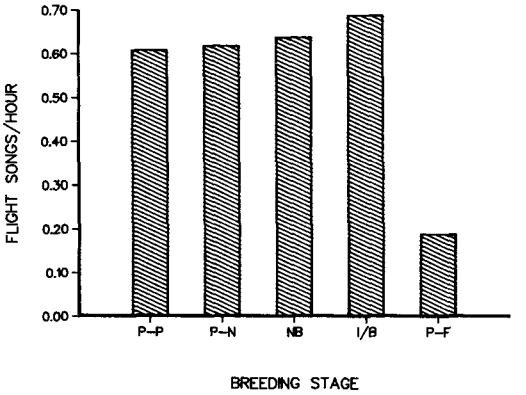

FIGURE 4. Flight songs per hour of observation by breeding stage (P-P = pre-pairing, P-N = pre-nesting, NB = nest building, I/B = incubation/brooding, and P-F = post-fledging).

inclusion of these phrases in flight songs permits conspecifics to determine the identity of the individual performing the flight song. The transmission of the signal is further enhanced by uttering these songs well above the ground. Previous studies have noted that increased height tends to decrease attenuation of vocal signals (Morton 1975, Martin and Marler 1977, Brenowitz 1986, Wilczynski et al. 1989).

Several factors suggest that the flight songs of Common Yellowthroats play little or no role in territorial interactions. Male yellowthroats first arrived on my study area on 18 April and detailed observations began on 21 April. The first flight song was heard on 2 May, at least 11 days after arrival of the males. Kowalski (1983) observed only that the use of flight songs by yellowthroats increased with time of year. Stewart (1953) suggested that yellowthroat flight songs were more frequent in late July and early August. Hofslund (1959:156) noted that among yellowthroats "the season for the flight song is the period between mating and the end of nesting." This apparent absence of flight songs immediately after arrival at the breeding grounds suggests that flight songs play no role in the establishment of territories. Further, most flight songs were uttered when no conspecifics were singing. Similarly, Kowalski (1983) noted no significant difference in the number of flight songs uttered by "disturbed" (i.e., neighboring males singing or displaying) versus "undisturbed" males. In addition, I found that most flight songs were directed away from territory boundaries.

The flight songs of male yellowthroats also appear to play little or no role in mate attraction. Flight songs were uttered at similar rates throughout the breeding season, with no difference in rates before and after pairing. Further, Stewart (1953) indicated that yellowthroat flight songs were more frequent well after pairing (late July and early August). Kowalski (1983) reported that yellowthroat flight songs were more frequent later in the breeding season. In addition, male yellowthroats in the present study typically initiated flight songs some distance from females (usually more than 20 m) and males were usually further away from females at the end of flight songs than they were when the flight was initiated.

Previous investigators have reported that the flight songs of Common Yellowthroats are uttered more frequently during the late afternoon and evening. For example, Bent (1953) observed that "the flight song is more often heard in the late afternoon or toward evening than it is during the early part of the day." Similarly, Kowalski (1983) noted that "flight-song performance increased with time of day . . ." Lein (1981) also reported an increased use of flight songs at dusk in Ovenbirds. None of these investigators provided an explanation for this behavior. I found no significant differences between morning and evening in the number of flight songs per hour of observation.

My presence in a territory had a significant influence on the rate at which flight songs were uttered, with male yellowthroats uttering flight

songs at rates nearly five times higher when I was in their territory. Similarly, Hofslund (1959:156) observed that the yellowthroat flight song was "heard most frequently when I first entered a territory . . ." Although apparently uttered in response to my presence, males rarely flew either toward me or over me when uttering flight songs. These observations suggest that the flight songs of male Common Yellowthroats are given in response to the presence of potential predators. Similar behavior has been reported in Bobolinks (*Dolichonyx oryzivorus*; Wittenberger 1983). Wittenberger (1983) observed that the flight songs of Bobolinks did not represent true mobbing behavior because they are not oriented toward the predator. Similarly, I found that male yellowthroats did not direct their flight songs toward me. Further, whereas mobbing calls are often given repetitively, the flight songs of male yellowthroats were always given singly. The flight songs of yellowthroats may serve to warn conspecifics about the presence of a potential predator. Although I found no significant differences in use of flight songs before and after pairing, previous workers have reported that flight songs may be uttered more frequently after pairing (Hofslund 1959, Kowalski 1983). This suggests that the "warning" may be directed to a mate located elsewhere in the territory. Because of the characteristics of flight songs, males uttering these songs advertise both their location and identity. Thus, females know if their mate uttered the song and, therefore, if the predator is in or near their territory. Although easily locatable, flight songs do not appear to provide information concerning the specific location of a predator because, as just noted, such songs are usually not directed toward or uttered over the predator. Rather, the easily located flight song may serve as a distraction display, directing the attention of the predator to the male and giving the mate opportunity to slip away (Hofslund 1959). Perhaps enhancing this distraction, most flight songs in this study were initiated by male yellowthroats located more than 20 m from females (or a nest) and males were usually further away from a female (or a nest) at the end of a flight song than at the beginning. Such displays may be particularly important when a female is on the nest and, perhaps, more vulnerable. After the young fledge, females are probably less vulnerable. Further, during the post-fledging period males and females typically remain together with the young (pers. obs.). This reduced vulnerability and close presence of the female may explain the decline in use of flight songs noted after fledging of the young.

Individual male yellowthroats uttered flight songs at significantly different rates. Hofslund (1959) reported similar observations. The reasons for such variation are unclear. It is possible, however, that flight songs are uttered by males when a potential predator approaches to within a certain distance of a female (or nest). Thus, differences in rates among male yellowthroats may simply have been due to the frequency with which I approached within that distance.

ACKNOWLEDGMENTS

I would like to thank Tammy Ritchison for assistance in the field and D. A. Spector and J. M. Wunderle for very helpful comments. Financial assistance was provided by Eastern Kentucky University.

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