

# CHARACTERISTICS, USE AND POSSIBLE FUNCTIONS OF THE PERCH SONGS AND CHATTER CALLS OF MALE COMMON YELLOWTHROATS<sup>1</sup>

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*Abstract.* The vocal repertoire of male Common Yellowthroats (*Geothlypis trichas*) includes a single distinctive perch song, a flight song, and several calls, including a chatter call. To ascertain the function of perch songs and chatter calls and to determine if these vocalizations are altered to convey different information, I examined the singing and calling behavior of male yellowthroats throughout the breeding cycle and in different behavioral contexts. The singing behavior of males changed in two ways after pairing: singing rates declined, suggesting that perch songs play a role in mate attraction, and most songs were uttered with reduced volume. These low volume songs appeared to be directed at mates, perhaps serving to stimulate ovulatory cycles, elicit copulation solicitation, or provide information about potential predators. Male yellowthroats uttered regular volume songs at low rates after pairing, suggesting that their function is not limited to mate attraction. Regular volume songs uttered after pairing appeared to be used in both intrasexual and intersexual contexts. The use of chatter calls did not decline until after females began incubating, and most were directed at conspecific males in aggressive (territorial) contexts. Male yellowthroats typically uttered longer perch songs (more phrases per song) during the nest building/egg laying and incubation/nestling periods, however, the possible function of these longer songs is unknown. My results provided no other evidence that male yellowthroats convey motivational information by varying the temporal and frequency characteristics of either perch songs or chatters.

*Key words:* Perch songs; chatter calls; Common Yellowthroat; *Geothlypis trichas*; mate attraction; territory defense.

## INTRODUCTION

Despite a plethora of studies over the last several decades, our understanding of how the songs of passerines are used to communicate remains fragmentary and incomplete (Smith 1991). Singing is often assumed to function primarily in mate attraction and male-male competition, however, studies designed *a priori* to assess the function of song are surprisingly scarce (Johnson and Kermott 1991). Although few in number, such studies have revealed that singing may serve a variety of functions. For example, song may be used to attract females for extra-pair copulations (Møller 1988), coordinate nest exchanges between mates (Smith 1988), inform females that there is no immediate threat of predation (Johnson and Kermott 1991), and distract potential predators (Ritchison 1991). Singing by male passerines clearly has more kinds of functions than simply territorial advertising and mate attraction

(Smith 1991). However, discerning such functions requires detailed studies of song use throughout an entire breeding cycle because even subtle changes in singing behavior may convey information (Smith 1991).

The ways in which song is used to communicate may depend in part upon the complexity of song. For example, males with repertoires of two or more song types may be able to convey different information by uttering different song types (e.g., Baptista 1978, Gaddis 1983) or by varying the patterns of song type presentation (e.g., Kramer and Lemon 1983). Such options are not available to males in species with single song repertoires, however, such males may be able to convey different messages by altering the way in which their single song is presented. For example, male Kentucky Warblers (*Oporornis formosus*) may lower or raise the frequency range of their songs or put more energy into lower or higher frequencies to "match" other males (Morton and Young 1986). Additional detailed studies are needed to determine if males in other species with single song repertoires alter their

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songs in a similar way or in other ways to convey different information or, perhaps, whether they resort to other options, such as using non-song vocalizations in place of songs.

Song complexity may also be related to song function. For example, Catchpole (1982, 1987) suggested that intrasexual selection favors simple, stereotyped song while intersexual selection favors more complex, variable songs. Although the findings of a recent comparative analysis did not support this hypothesis (Read and Weary 1992), additional studies examining the possible relationship between song complexity and song function are clearly needed (Johnson and Kermott 1991).

Male Common Yellowthroats (*Geothlypis trichas*) possess a repertoire that includes just one primary or perch song (Wunderle 1978, 1979) that apparently functions in both territorial defense and mate attraction (Wunderle 1979). The vocal repertoire of each male yellowthroat also includes one flight song that may function as a distraction display (Ritchison 1991) and several calls, including a chatter call typically given in aggressive contexts (Hofslund 1959, Wunderle 1978). Because male yellowthroats have just one primary song, it is possible that they vary the presentation of that song to convey different types of information and, further, that non-song vocalizations may play an important role in communication with conspecifics during the breeding season. The objectives of this study were: (1) to assess the functions of the perch song and chatter call by examining singing and calling rates throughout the breeding cycle and by examining the use of perch songs and chatter calls in different behavioral contexts and (2) to determine if and how perch songs and chatter calls are altered to convey different types of information.

#### THE STUDY SPECIES

Common Yellowthroats are small (about 10–12 g) insectivorous birds that occupy moist, shrubby habitats throughout much of North America. Males typically arrive in breeding areas before females and establish territories that range in size from 0.2 to 1.0 ha (about 0.8 ha on my study area). Yellowthroats are socially monogamous but observations suggest that females willingly participate in extra-pair copulations (Hofslund 1959). Females build nests on or near the ground over a period of about 3–5 days. Incubation is by the female and averages about 12 days. Males

occasionally bring food to the incubating female. After hatching, both parents feed the young, and young remain in the nest for about eight days. Yellowthroat nests appear to suffer high rates of predation during the incubation and nestling periods. As a result, pairs may make two to four nesting attempts during a breeding season. Pairs that successfully fledge young early in the breeding season sometimes attempt to raise a second brood.

#### METHODS

Seven male Common Yellowthroats located on contiguous territories were observed from 21 April through 15 August 1987 at the Central Kentucky Wildlife Management Area, located 17 km SSE of Richmond, Madison County, Kentucky. Yellowthroat territories were located in open, brushy areas with occasional small trees. Males were captured in mist nets and individually marked with colored leg bands and plastic tape attached to the tail (Ritchison 1984). I recorded and observed the yellowthroats almost daily. Typically, I followed one male each day for about 2–3 hr. Although most of these focal male observations were during the period from sunrise to 10:00, some observations were also made from 18:00 to sunset. Territory boundaries were delineated by following males and by noting the location of interactions with neighboring males. In addition to these focal male observations, I spent several hours per week looking for nests and checking the status of nests.

During the focal male observations, I recorded on tape all bouts of song. For each bout uttered, I noted the number of songs in the bout and the number of phrases per song (see definitions below). I also noted the date and nesting stage. The breeding period of each male was divided into five stages: pre-pairing, pre-nesting, nest building/egg laying, incubation/nestling, and post-nesting. The post-nesting period began when young fledged (left the nest). If a pair fledged young from a nest and initiated another nest, the post-nesting period ended seven days after young fledged and was followed by a pre-nesting period. If, later in the season, a pair fledged young or lost a nest to predation and did not initiate another nest, the post-nesting period continued until the male left the territory. If a pair lost a nest to predation during the incubation/nestling period and subsequently initiated another nest, the

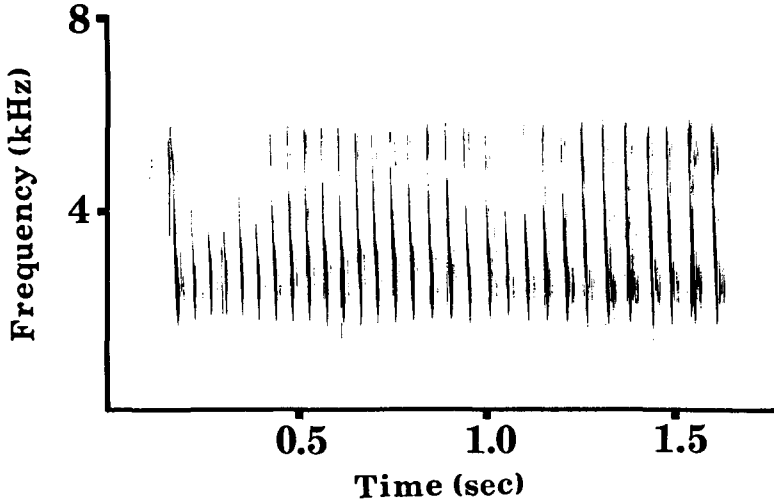


FIGURE 1. The chatter call of a male Common Yellowthroat.

pre-nesting period began the day after the nest was lost.

I further noted whether or not conspecific males were singing and, if possible, the location of the conspecific(s). On that basis, I categorized bouts based on four possible situations: spontaneous song (no other males singing), distant singing (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), close singing (perch songs being uttered by one or more conspecific males with territories contiguous to that of the focal male), and interacting (males within 10 m of each other either preceding or following a chase). I also noted the location of males relative to females (i.e., whether or not a female was within 5 m). Finally, the volume of each song was noted. Wunderle (1979) suggested that variation in the volume of yellowthroat songs may provide motivational information. Thus, I categorized yellowthroat songs (and bouts) as either regular volume or low volume. Regular volume songs could, in my opinion, be heard by conspecifics in adjacent territories while low volume songs could not.

I also attempted to record on tape all chatters. The chatter vocalization is made up of a series of rapidly uttered notes having a rattling-chattering quality (Wunderle 1978; Fig. 1). For each chatter uttered by a focal male I noted the date, nesting stage, type of interaction with conspecific

males and, if possible, the location of the male relative to conspecifics (both male and female). I also noted the interval since the last song or chatter by a conspecific male. Finally, I noted the number of notes in the chatter and the duration of the chatter.

Recordings were made using a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic reflector and microphone. Sonagrams of songs and chatters were produced with Kay Elemetric Corporation Sonographs (Model 6061A for songs and Model 5500 for chatters). For the songs, duration and frequency measurements were made directly from the sonagrams. Mean frequency was defined as the mean of nine measures of frequency (or eight for one male) taken from the third phrase of a song (see Fig. 2). The number of phrases per song and intersong interval were determined for all songs while interphrase intervals were determined for every fifth song and mean frequency for every tenth song. For chatters, measurements were made using the sonagraph.

All analyses were performed using the Statistical Analysis System (SAS Institute 1989). The General Linear Model (GLM) procedure was used to examine variation in song characteristics and singing behavior among individuals and among contexts. All analyses of variance were done on rank-transformed data and then followed by a Student-Newman-Keuls test to detect any difference among means. Because I analyzed songs

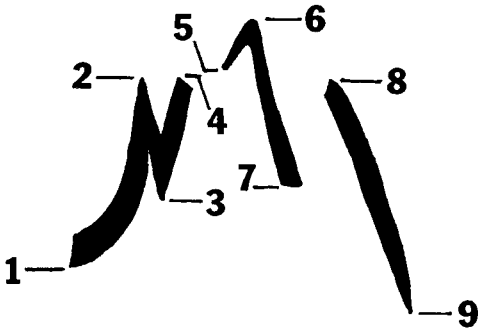


FIGURE 2. Frequency measurements taken from the third phrase of Common Yellowthroat songs.

and calls recorded from the same seven males over several months, repeated measures analysis of variance was used. Repeated measures analysis provides a test for interactions (Beal and Khamis 1990), and I examined male by breeding stage and male by context interactions for several variables. I assumed that for variation in the characteristics of songs to convey information, most or all males would vary songs in the same way. For example, if changing the number of phrases in songs conveys certain information (e.g., shorter songs appear to indicate an increased likelihood of interacting in some species), then most or all males would be expected to change their songs in the same way in similar contexts. A significant male by context interaction indicated that the songs of different males varied in different ways or, perhaps for some males, did not vary at all. Thus, when significant interactions were found, I analyzed data from each male to determine if any trends were apparent (e.g., to determine if most males exhibited similar patterns of variation and the significant interaction was due to just one or two males). All values are presented as means  $\pm$  standard errors.

I use the terminology of Borror (1967) and Wunderle (1979) to describe the vocalizations 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 (Figs. 2 and 3). All phrases given by yellowthroats in my study consisted of three notes (Fig. 3). However, males often terminated songs with partial phrases (see top song in Fig. 3). When determining the number of phrases per song, partial phrases were assigned values of  $\frac{1}{3}$  if only one of the three notes was given or  $\frac{2}{3}$  if two of the notes were given.

So, for example, the top song in Figure 3 consisted of three and  $\frac{2}{3}$  phrases. I defined a song bout as a series of songs separated in time from each other by intervals of 60 sec or less.

## RESULTS

### DESCRIPTION OF PERCH SONGS

The songs of the seven male Common Yellowthroats consisted of an average of  $3.60 \pm 0.007$  ( $n = 8,093$ ) phrases per song. The mean interval between phrases within songs was  $0.048 \pm 0.00014$  sec ( $n = 2,157$ ) while the mean interval between songs within a bout was  $14.48 \pm 0.09$  sec ( $n = 7,953$ ). The mean frequency of the third phrase was  $4,439 \pm 28$  Hz ( $n = 924$ ).

The perch songs of the seven males exhibited significant individual variation (repeated measures ANOVA,  $P < 0.01$  for all variables) in the number of phrases per song, interphrase interval, and frequency. Males also exhibited individual differences in note and phrase morphology (Fig. 3).

### EFFECT OF BREEDING STAGE ON USE AND CHARACTERISTICS OF PERCH SONGS

The number of songs per hour of observation varied significantly with breeding stage ( $F = 12.61$ ,  $P < 0.0001$ ), with singing rates significantly higher during the pre-pairing period (SNK test; Fig. 4). Singing rates were highest during the pre-pairing period for all seven males, with no significant interaction between individual and breeding stage ( $F = 0.72$ ,  $P = 0.765$ ). The number of bouts per hour also varied with breeding stage ( $F = 9.0$ ,  $P = 0.0004$ ), with no significant interaction ( $F = 0.69$ ,  $P = 0.794$ ). Males uttered significantly more bouts per hour during the pre-pairing and post-nesting periods (SNK test).

The number of phrases per song varied significantly with breeding stage ( $F = 3.45$ ,  $P = 0.033$ ), with the fewest phrases per song during the pre-pairing period and the most phrases per song during the nest building/egg laying period. Although there was a significant interaction between bird and breeding stage ( $F = 34.21$ ,  $P < 0.0001$ ), most males (five of seven) uttered shorter songs (fewer phrases per song) during the pre-pairing period. In addition, five of seven males uttered longer songs during either or both the nest building/egg laying and the incubation/nestling periods. Differences in intersong intervals also varied significantly ( $F = 3.87$ ,  $P = 0.022$ ),

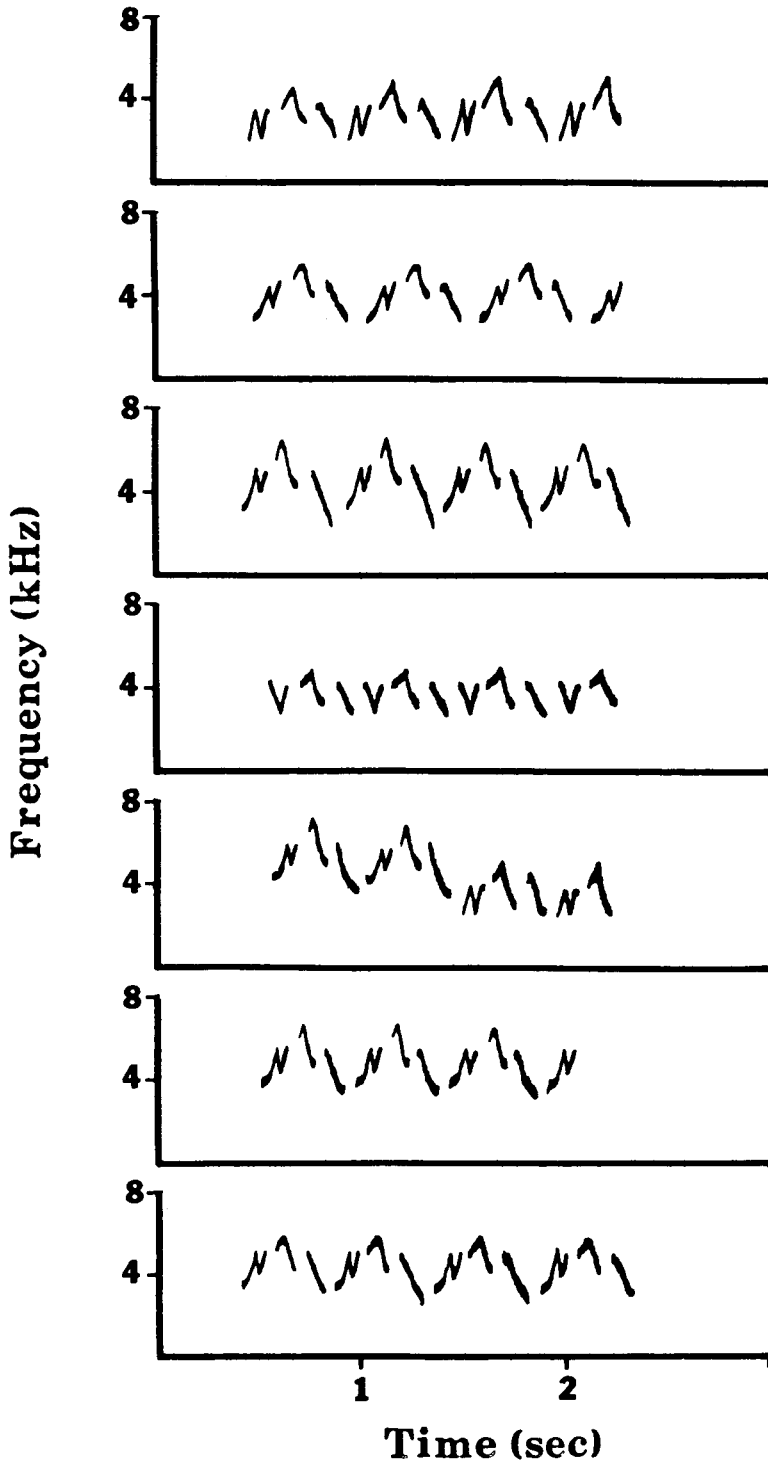


FIGURE 3. The perch songs of seven male Common Yellowthroats.

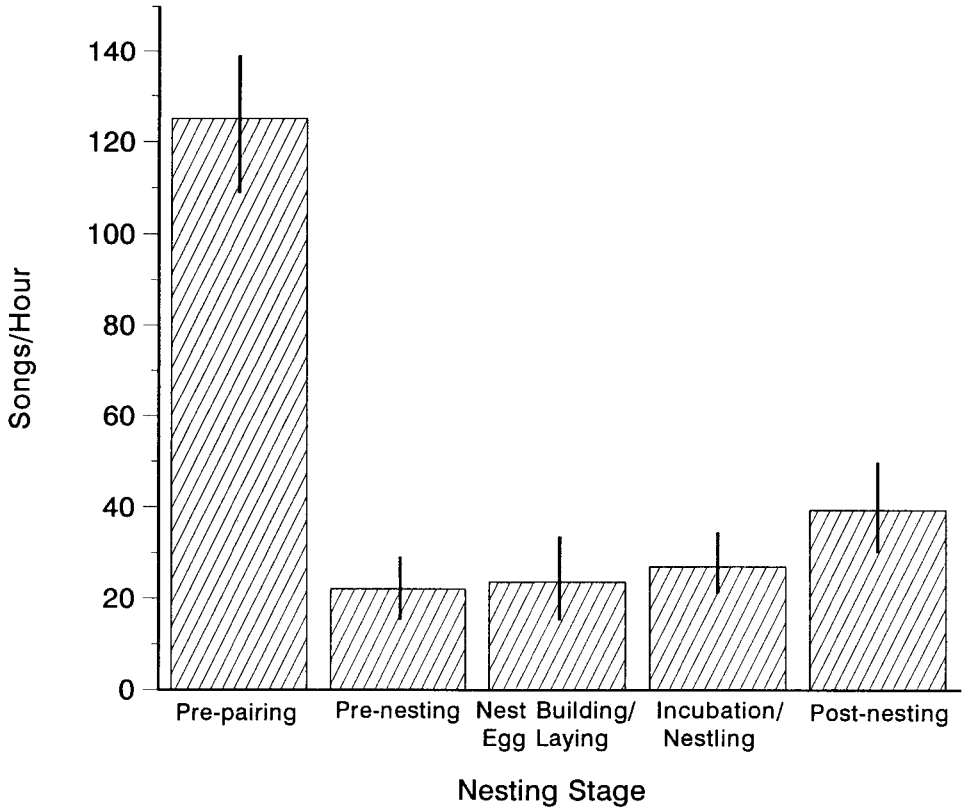


FIGURE 4. The mean number of perch songs ( $\pm$  SE) per hour of observation during the breeding season.

however, there was a significant interaction ( $F = 18.17$ ,  $P < 0.0001$ ) with no consistent trends in the relationship between intersong interval and nest stage among the seven males. Neither mean frequency ( $F = 0.32$ ,  $P = 0.81$ ) nor interphrase interval ( $F = 1.46$ ,  $P = 0.26$ ) varied significantly with breeding stage and, although there were significant interactions for both variables, no consistent trends were found. Finally, the height of perches used by males when giving perch songs did not vary significantly with breeding stage ( $F = 0.17$ ,  $P = 0.95$ ).

The volume of songs varied significantly with nesting stage ( $\chi^2 = 241.1$ ,  $df = 4$ ,  $P < 0.0001$ ;  $n = 563$  bouts). Prior to pairing, most bouts (202 of 216 or 93.5%) consisted of regular volume songs (Fig. 5). After pairing, bouts of low volume songs were uttered more frequently than bouts of regular volume songs (244 of 347 bouts or 70.3%; Fig. 5). The use of low volume songs peaked during the nest building/egg laying period, with 84.2% of all bouts of song (59 of 70)

uttered during this period being low volume (Fig. 5).

#### EFFECT OF INTRA- AND INTERSEXUAL CONTEXT ON THE USE AND CHARACTERISTICS OF PERCH SONGS

Most bouts of perch songs were uttered either as spontaneous song (308/601 bouts or 51.2%) or during close singing (202 bouts or 33.6%). Relatively few songs were uttered during distant singing (63 bouts or 10.5%) or direct interactions (28 bouts or 4.7%).

Mean frequency, interphrase intervals, and intersong intervals did not vary significantly (repeated measures ANOVAs,  $P > 0.55$ ) among intrasexual contexts. The number of phrases per song did vary significantly ( $F = 4.99$ ,  $P = 0.012$ ) with intrasexual context, with spontaneous songs being longest. However, this effect was apparently due to the tendency of males to sing longer songs during the nest building/egg-laying and incubation/nestling periods. That is, most spon-

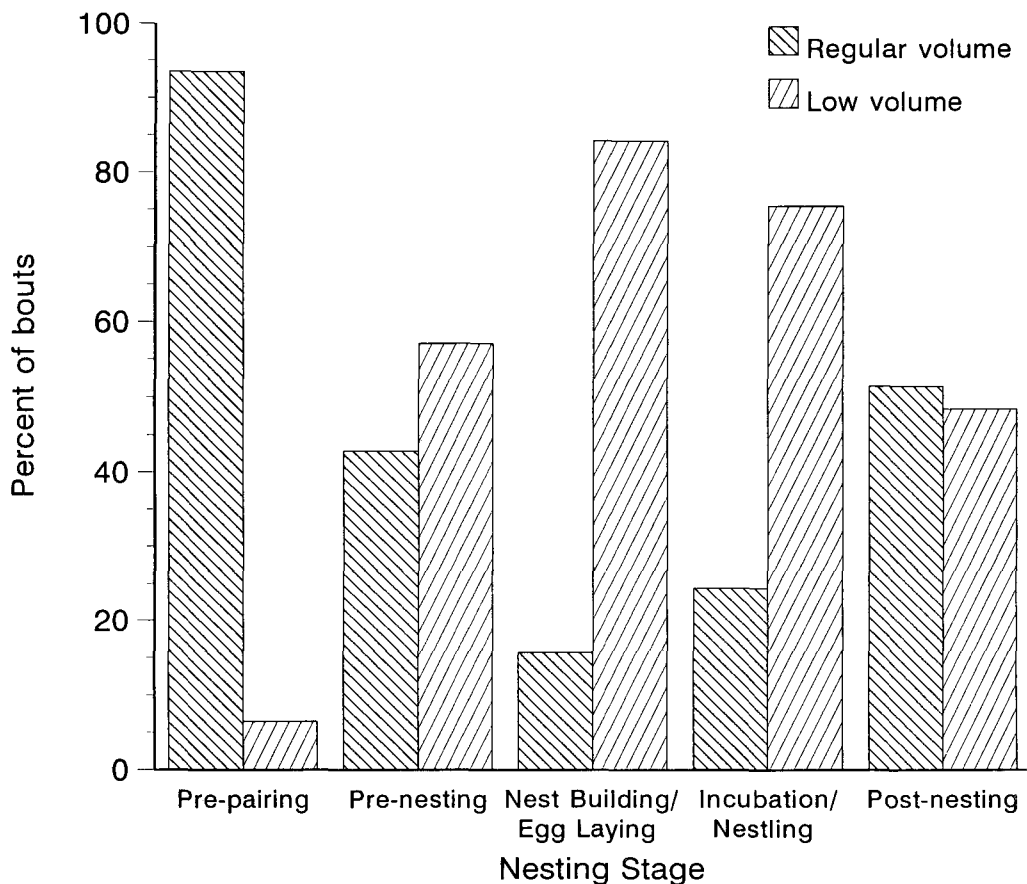


FIGURE 5. Percent use of regular and low volume songs by male Common Yellowthroats during the breeding season.

taneous singing (187 of 308 bouts or 60.7%) occurred during these periods and, as a result, spontaneous songs had more phrases per song. When the pre- and post-pairing periods were examined separately, analysis revealed no significant relationship between the number of phrases per song and intrasexual context either before pairing (pre-pairing period;  $F = 0.97$ ,  $P = 0.43$ ) or after pairing (all breeding stages except pre-pairing;  $F = 0.95$ ,  $P = 0.44$ ). Finally, the location of females had no significant effect (repeated measures ANOVA,  $P > 0.2$  for all variables) on the characteristics of songs (phrases per song, interphrase interval, mean frequency, and inter-song interval).

The volume of songs varied significantly with intrasexual context ( $\chi^2 = 128.2$ ,  $df = 3$ ,  $P < 0.0001$ ). For all breeding stages combined, male yellowthroats typically used regular volume songs

when conspecific males were singing (close or distant) or while interacting (Fig. 6). However, many of the close singing observations (119 of 202 or 58.9%) and all of the interactions ( $n = 28$ ) occurred during the pre-pairing period. After pairing, most bouts of song were low volume, including 77.1% (206 of 267) of bouts classified as spontaneous, 55.4% (46 of 83) of the bouts classified as close singing, and 57.1% (20 of 35) of the bouts classified as distant singing.

#### DESCRIPTION OF CHATTER CALLS

The chatter call of male yellowthroats consisted of a series of short duration, broad frequency notes (Fig. 1). Chatters consisted of an average of  $22.06 \pm 0.93$  notes ( $n = 104$ ) uttered at a mean rate of  $20.40 \pm 0.40$  notes/sec ( $n = 104$ ). The mean duration of chatters was  $1.10 \pm 0.05$  sec ( $n = 104$ ). Chatters were generally given sin-

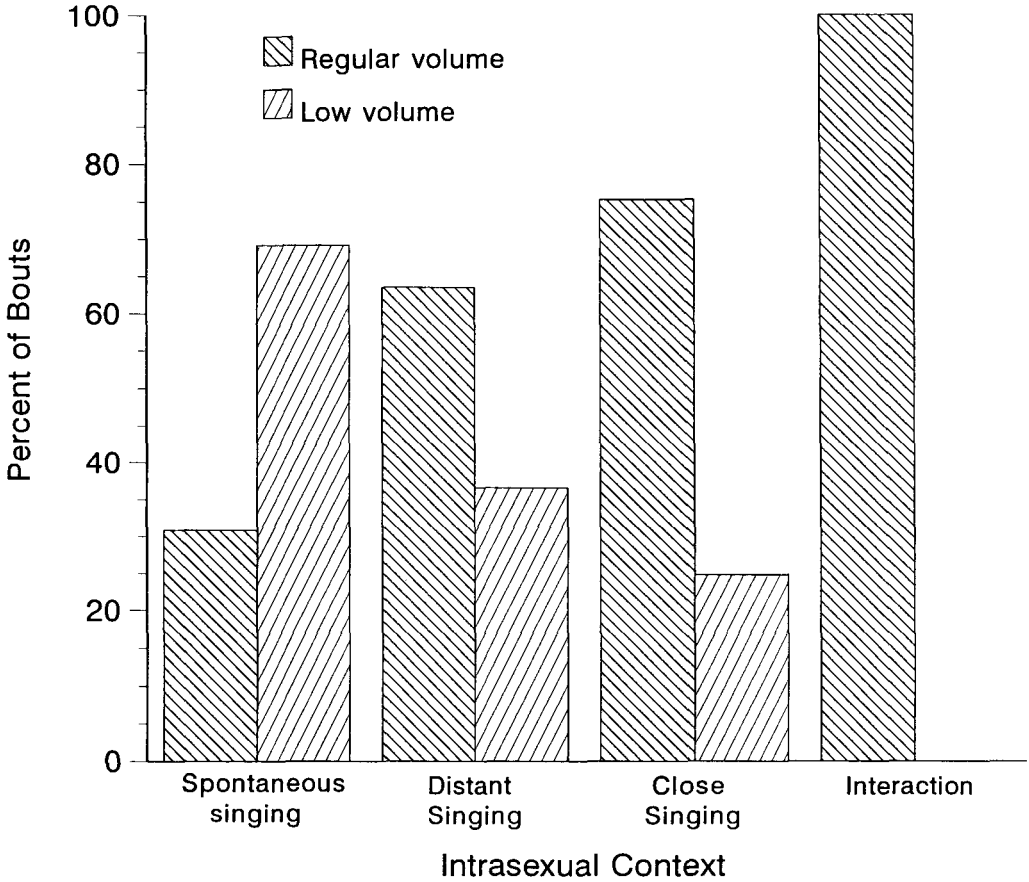


FIGURE 6. Percent use of regular and low volume songs by male Common Yellowthroats among different intrasexual contexts.

gly. For observation periods during which at least two chatters were given, the mean interval between chatters was  $11.86 \pm 1.46$  min ( $n = 204$ ). Chatters were typically not uttered during bouts of song, with a mean interval between chatters and the last song of  $20.9 \pm 2.0$  min ( $n = 194$ ). Male yellowthroats often uttered chatters shortly after ( $\bar{x} = 15.2 \pm 2.5$  sec;  $n = 128$ ) a conspecific male vocalized (usually a song). The mean distance between male yellowthroats uttering chatters and the nearest known conspecific male was  $24.9 \pm 1.2$  m ( $n = 119$ ).

#### EFFECT OF BREEDING STAGE AND INTRASEXUAL CONTEXT ON USE AND CHARACTERISTICS OF CHATTER CALLS

The number of chatters per hour varied significantly with breeding stage ( $F = 3.5$ ,  $P = 0.028$ ), with males giving significantly fewer chatters during the post-nesting period (SNK test; Fig. 7).

Chatters were typically uttered either when neighboring males (i.e., males with territories contiguous with the focal male's) were singing (109/217 or 50.2%) or during interactions (70/217 or 32.3%), with few given when only distant males (i.e., males more than one territory removed from the focal male) were singing (20/217 or 9.2%) or when no male yellowthroats could be heard singing (18/217 or 8.3%).

The number of notes in chatter calls did not vary significantly with intrasexual context ( $F = 0.98$ ,  $P = 0.45$ ). Similarly, the rate at which notes were uttered in chatter calls (notes/sec) did not vary significantly with intrasexual context ( $F = 1.37$ ,  $P = 0.31$ ).

#### DISCUSSION

Each male Common Yellowthroat in this study utilized just one type of perch song, with dis-



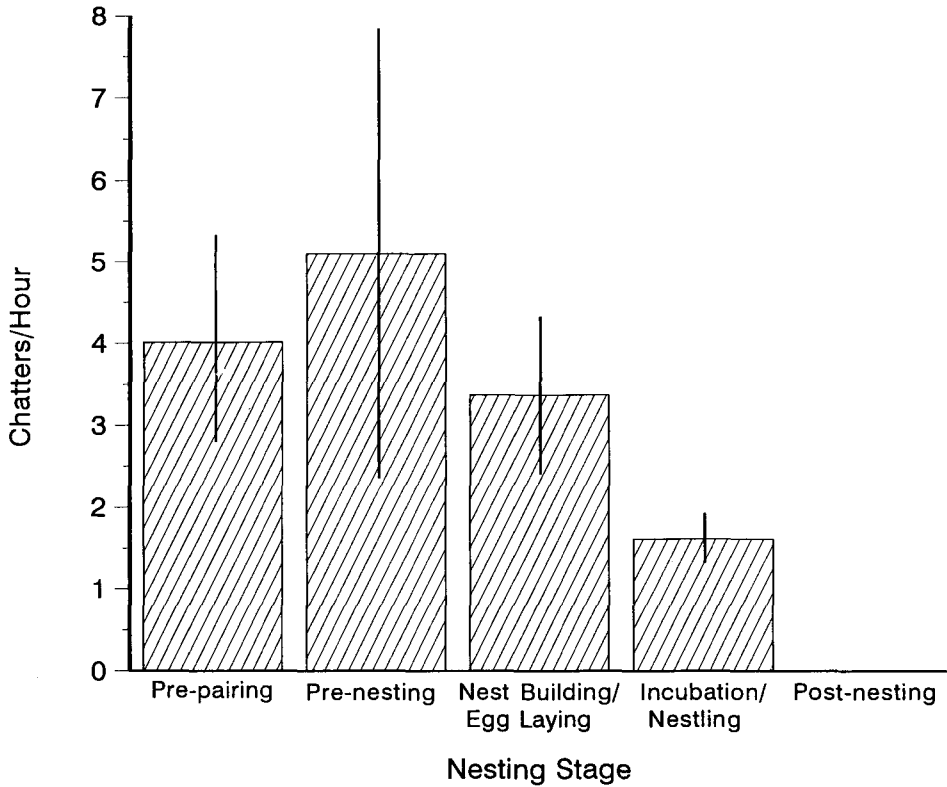


FIGURE 7. The mean number of chatter calls per hour ( $\pm$  SE) during the breeding season.

tinctive note and phrase types. Similar individual variation in the perch songs of male yellowthroats has been reported previously (Borror 1967, Wunderle 1978). The perch songs of male yellowthroats also exhibited significant individual variation in several temporal and frequency characteristics. Thus, the perch songs of male yellowthroats are individually distinct. This variation permits male yellowthroats to discriminate between the songs of neighboring and non-neighboring males and also apparently allows female yellowthroats to recognize their mates by song alone (Wunderle 1978).

The singing behavior of male yellowthroats in my study changed in two ways after pairing: singing rates declined and most bouts of song were low volume. Wunderle (1979) also noted that unmated male yellowthroats had higher singing rates than mated males and Kowalski (1983:141) reported that male yellowthroats gave fewer perch songs, "later in the season." Reduced singing rates by males after pairing have been reported in other species of birds (e.g., Powlesland 1983, Lampe

and Espmark 1987, Björklund et al. 1989), including several wood-warblers (e.g., Nolan 1978, Lein 1981, Hayes et al. 1986, Spector 1992). Although such indirect evidence is not conclusive (Kroodsma and Byers 1991), a significant reduction in male singing rates after pairing does provide strong circumstantial evidence that singing plays a role in mate attraction. Thus, male yellowthroats do appear to use their relatively short, stereotyped songs to attract females. This result does not support the hypothesis that intersexual selection favors complex songs (Catchpole 1982, 1987) but does support the hypothesis that male-male competition and female choice do not necessarily impose antagonistic selective pressures on song (Read and Weary 1992).

In some species, singing may stop completely after pairing (Catchpole 1973). Although rates were much reduced, male yellowthroats continued to sing after pairing. However, most bouts of song were low volume, particularly during the nest building/egg laying and incubation/nestling periods. Wunderle (1979: 995) reported that male

yellowthroats gave low volume songs when “foraging near the female, after territorial conflicts, and sporadically during the heat of the day.” I found that most bouts of low volume songs uttered by male yellowthroats after pairing were spontaneous (i.e., no conspecific males were singing). Such results suggest that many low volume songs were not directed at neighboring males. Johnson and Kermott (1991) reported frequent use of low volume songs (“whisper songs”) by male House Wrens (*Troglodytes aedon*) during the late pre-laying and early laying period and suggested that such songs may be used to stimulate ovulatory cycles of females and to elicit copulation solicitation. Using low volume songs at this time in these contexts may be beneficial because such songs would make it more difficult for an intruding male, intent on copulating with the fertile female, to pinpoint the location of the singing male and his mate (Johnson and Kermott 1991). The use of low volume songs by male yellowthroats peaked during the nest building/egg laying period, the period during which females would be fertile. Further, Hofslund (1959) found that female yellowthroats will engage in extra-pair copulations and sometimes appear to solicit such copulations. Thus, if male yellowthroats must continue singing after pairing to stimulate females or to solicit copulation, the use of low volume songs may be a strategy to reduce the likelihood of extra-pair copulations.

Although the use of low volume songs peaked during the nest building/egg laying periods, male yellowthroats also uttered low volume songs during the incubation/nestling and post-nesting periods. The function of these songs is unclear, however, as noted above, some may have been directed at mates. Similarly, Johnson and Kermott (1991) suggested that most singing by male House Wrens after pairing was directed at mates and, further, that most songs may provide information to mates concerning the presence or absence of potential predators. Singing by male House Wrens during the nestling period may also signal a brooding female that the male is about to come to the nest (Johnson and Kermott 1991). Singing by male yellowthroats during the nesting period could serve similar functions.

Although, in my judgement, low volume songs could not be heard in adjacent territories, it is certainly possible that neighboring males located near territory boundaries sometimes heard such songs. After pairing, most bouts of song uttered

by male yellowthroats when neighboring males were singing (close singing) were low volume. These songs may have been directed at mates, however, as suggested by Wunderle (1979), low volume songs could also be directed at conspecific males to convey information concerning the probability of attacking or fleeing.

Male yellowthroats continued to utter regular volume songs at low rates after pairing. In addition, the use of chatter calls by male yellowthroats increased after pairing, then declined after their mates initiated incubation. The use of regular volume songs after pairing suggests that the function of these songs is not limited to mate attraction. One such function appears to be territorial defense. In support of this hypothesis, I found that male yellowthroats often used regular volume songs when conspecific males were singing. In addition, male yellowthroats respond to the playback of conspecific songs by uttering regular volume songs (Wunderle 1978, pers. observ.). Thus, it appears that regular volume songs are important in intrasexual contexts (i.e., territory defense) as well as in intersexual contexts (i.e., attracting mates). Regular volume songs uttered after pairing may also serve other functions. For example, males sometimes uttered regular volume songs when no conspecifics were singing. These songs could serve a variety of functions, such as informing neighboring females of a male's availability for extra-pair copulations (Møller 1988) or, perhaps in conjunction with low volume songs, physiologically stimulating a mate prior to and during the initiation of another nest (Logan 1983, Morton et al. 1985).

Chatter calls also appeared to be important in intrasexual communication. I found that over 80% of the chatter calls given by male yellowthroats were uttered either during close singing (i.e., a neighboring male singing) or during interactions. Further, male yellowthroats typically give chatter calls in response to playback of conspecific song (Wunderle 1978, pers. observ.) or when another male enters the territory (Hofslund 1959, pers. observ.). Wunderle (1978) also found that both songs and chatter calls appear to play a role in territorial defense, noting that male yellowthroats responding to a conspecific male singing near a territory boundary typically increased singing rates then uttered several chatter calls. The use of chatter calls by male yellowthroats during interactions (this study) and prior to actually approaching and chasing intruders (pers.

observ., Wunderle 1978) indicates that these calls advertise an increased probability of initiating aggression.

Although singing rates declined immediately after pairing, the use of chatter calls by male yellowthroats did not decline until females initiated incubation. If, as just suggested, chatter calls advertise an increased probability of aggression, such results indicate that male yellowthroats exhibit similar levels of aggression (territorial defense) until females initiate incubation. Early in the season (pre-pairing), male yellowthroats may use chatter calls when establishing territories. Although territorial boundaries soon become well-defined (Kowalski 1983, pers. observ.), male yellowthroats continued to utter chatter calls during the pre-nesting and nest building/egg laying periods. Female yellowthroats would probably be fertile during these periods. Thus, male yellowthroats may maintain relatively high levels of territory defense (and continue to utter chatters) in an attempt to reduce trespassing (and extra-pair copulations) by neighboring males. Once females began incubation (and were no longer fertile), the use of chatter calls (and levels of aggression) declined.

Most characteristics (temporal and frequency) of yellowthroat perch songs did not vary significantly with either breeding stage or context. However, most male yellowthroats uttered longer songs (more phrases per song) during the nest building/egg-laying and incubation/nestling periods. The reasons for this are unclear. Singing by males during a female's fertile period may have an important stimulatory effect (Hinde and Steel 1976, Morton et al. 1985, Guyomarc'h and Guyomarc'h 1989) and, although male yellowthroats sang at relatively low rates when mates were fertile, longer songs could be more effective in stimulating a mate's ovulatory cycles or eliciting copulation. In addition, if, as suggested above, singing by male yellowthroats during the incubation/nestling period serves to inform females on the nest about the location of potential predators or the location and intentions of the male, then longer songs may help ensure transmission of the signal (especially when such songs are low volume songs). Although I found no clear relationship between song length and intrasexual context, Wunderle (1979) previously suggested that male yellowthroats might vary song length to convey motivational information to conspecific males and noted that males sometimes gave

"incomplete" songs during the playback of conspecific song.

Although the use of longer songs by male yellowthroats might play some role in intersexual communication, my results provide no other evidence that male yellowthroats convey motivational information by varying the temporal and frequency characteristics of their perch songs. One reason for this may be the substantial inter-individual variation in the frequency and temporal characteristics of yellowthroat songs (Borror 1967, Wunderle 1979). Wunderle (1979) examined numerous characteristics (morphological, syntactical, frequency, and temporal) of the songs of yellowthroats and hypothesized that only two components (notes per song and song length) might provide motivational information. He suggested that other components of songs might be important in species and individual recognition.

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