

SINGING BEHAVIOR OF MALE YELLOW-BREASTED CHATS: REPERTOIRES, RATES, REPRODUCTIVE SUCCESS, AND A COMPARISON WITH OTHER WOOD-WARBLERS

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ABSTRACT.—Previous authors have noted the unique singing behavior and apparently large song repertoires of male Yellow-breasted Chats (*Icteria virens*). We studied the singing behavior of 10 male chats in central Kentucky in an attempt to determine the size and functions of their song type repertoires and examine possible relationships among singing behavior, morphological characteristics, and reproductive success. During the 1995 breeding season, we recorded and analyzed chat songs and determined the morphological characteristics and reproductive success of focal males. Repertoire sizes varied among male chats, ranging from 46–81 song types. Larger males (as determined by tarsus length) had larger song type repertoires, and males with longer wing chords fledged more young. These relationships suggest a correlation between male quality (as determined by size and reproductive success) and repertoire size. Male chats spent less time singing after pairing, suggesting that singing plays a role in mate attraction. However, singing by male chats likely serves other functions, such as territorial defense and attracting additional mates, because males continued singing after pairing. In contrast to male wood-warblers (Parulidae), male chats have relatively large repertoires of song types and also vary the sequence of song types, the frequency of repetition of individual song types, and the length of time between consecutive song types. Such differences in singing behavior lend support to the hypothesis that chats are not parulids. Received 4 January 2002, accepted 22 August 2002.

The singing behavior of several species and genera of wood-warblers (Parulidae) have been examined, and these studies have revealed two different song systems (Spector 1992). In one system, shared by species in the genera *Protonotaria*, *Helmitheros*, *Limnithlypis*, *Seiurus*, *Oporornis*, and *Geothlypis*, males have a single primary song, plus a less commonly used extended song that includes portions of the primary song and some additional notes (Spector 1992). In the second system, shared by species in the genera *Vermivora*, *Parula*, *Dendroica*, *Mniotilta*, *Setophaga*, and *Wilsonia*, males have two distinct groups of songs; one group seemingly used primarily in intersexual contexts, and another used in intrasexual contexts (Spector 1992). While the singing behavior of most male parulids fits into one of these two song systems, the song systems of several species of parulids, including Yellow-breasted Chats (*Icteria virens*), have yet to be examined.

Based on anecdotal reports, some authors have suggested that the singing behavior of

Yellow-breasted Chats may be unique among wood-warblers. For example, Morse (1989) noted that male chats may have repertoires of more than 100 songs. In describing the singing behavior of chats, Chapman (1917:267) reported that “the voice of this bird is flexible to an almost unlimited degree. It has no notes suggesting its place among the warblers.” Bent (1953:593) stated that the chat’s “. . . vocabulary is so extensive and varied that . . . it does not need to learn much from others.”

The objective of our study was to examine the singing behavior of male Yellow-breasted Chats. Specifically, we wished to (1) determine the size of their song repertoires and how males used those repertoires, (2) determine possible functions of singing by examining singing rates throughout the breeding cycle and in different behavioral contexts, and (3) examine possible correlations among male singing behavior, morphological characteristics, and reproductive success.

METHODS

We studied Yellow-breasted Chats from 28 April through 19 August, 1995, at the Central Kentucky Wildlife Management Area located 17 km southeast of Richmond, Madison County, Kentucky (37° 37' N, 84° 12' W). This area consisted of fence rows, thickets,

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and small woodlots separated by cultivated and old fields. We captured chats in mist nets either by playing back chat songs or by placing nets in areas used by chats. We banded captured chats with a numbered aluminum band and a unique combination of colored plastic bands. We also measured wing chord and tarsus length.

We observed each focal male ($n = 10$) at least once every two weeks. Most observations were 1 h in duration and were conducted from sunrise to 11:00 EST. During focal male observations, we recorded all bouts of song using either a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone or a Marantz cassette recorder with a Mineroff directional shotgun microphone. We also spent several hours per week looking for nests. Once located, nests were checked at least twice weekly to determine stage and outcome. Because chats are multibrooded, we used the number of young fledged during the entire breeding season as a measure of reproductive success.

We analyzed recordings using a Kay Electronic DSP SonaGraph (Model 5500). For each observation we determined the number of song types, new song types, singing rate (total number of song types given/duration of observation period), and the percentage of time spent singing (calculated by determining the total duration of all song bouts given during an observation period, dividing by the duration of the period, and multiplying by 100%). We also determined the extent to which song types were shared among seven male chats.

We defined a song type as either a single sound or a series of sounds where the interval between sounds was less than the time interval between successive song types. Song types were categorized based on differences in structure (appearance in a sonagram), duration, rate of delivery, and frequency at maximum amplitude. Chats consistently sang particular song types. For each male, all song types were identified and classified in a numeric directory (Derrickson 1987). Examples of four song types are provided in Fig. 1. When singing, male chats vary the sequence of four types and the length of time between consecutive song types. Thus, a song bout was defined as a series of song types in which the

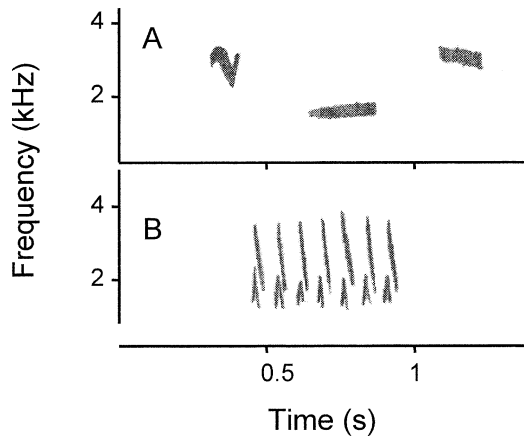


FIG. 1. Sonagrams of four song types given by male Yellow-breasted Chats (*Icteria virens*) in Madison County, Kentucky. (A) An example of three song types consisting of continuous sounds. (B) An example of a song type consisting of a series of sounds. Recorded by Natalie Dussourd, May 1995.

interval between song types was <15 s. Song types separated by >15 s were considered part of separate bouts.

To examine possible temporal variation in singing behavior, we divided the breeding season into six periods: pre-pairing, postpairing/prenesting, incubation, nestling, postfledging, and internesting (between nesting attempts). For pairs whose last nesting attempt of the season was unsuccessful, additional stages included either postnesting after losing a nest with eggs or postnesting after losing a nest with nestlings.

We determined song type repertoires for seven males, while 10 males were used for analyses of possible correlations between morphology and singing rates. We estimated the size of song type repertoires by plotting the cumulative number of new song types over the cumulative number of songs in a particular individual's repertoire and fitting a curve to the plot using the model $y = 1/x^2$. This model was used because it produced a higher r^2 value than several alternative models [$y = 1/x$, $y = e^{-x}$, and $y = \arctan(x)$]. The cumulative number of new song types at the asymptote of the curve was used as that individual's total song type repertoire. This model explained 92% of the total variance in the data, however, the residuals were not normally distributed ($P = 0.0001$). This was cor-

rected when the second and third observation periods of male LB1 were excluded from the analysis ($P = 0.106$). Male LB1 was the first bird on the study site and, because few other males had arrived on the study area, we observed him three times over a 2-day period. Because most other observation periods were separated by approximately two weeks, the inclusion of these observations apparently affected the normality of the residuals.

We calculated Pearson correlation coefficients for all predictor variables. To determine if there were differences among either breeding stages or males in singing rate and percentage of time spent singing, we used the general linear model repeated measures procedure. If significant differences were found, we used Tukey's studentized range test to determine which breeding stages or males differed. All statistical procedures were performed using the Statistical Analysis Systems (SAS) package (SAS Institute, Inc. 1989).

RESULTS

The estimated size of the song type repertoires of seven male chats ranged from 46–81 song types, with a mean of 62.2 ± 5.0 SE. Sharing of song types was common, with 50% of all song types shared by at least two males (41% among males in contiguous territories). Overall, male chats ($n = 10$) sang at a mean rate of 145.9 ± 20.4 SE song types/h and the mean time spent singing was $20.3\% \pm 3.1$ SE ($n = 7$). Singing (song bout) rates did not vary significantly among breeding stages ($F_{6,19} = 1.54$, $P = 0.22$), however, time spent singing did vary among breeding stages ($F_{6,19} = 5.87$, $P = 0.001$; Fig. 2). Males sang more during the pre-pairing period than during the incubation, postfledging, internesting, and posteggs lost periods (Tukey's test; $P < 0.05$). Male chats also spent more time singing during the postpairing/prenesting period than during the postfledging period ($P < 0.05$).

The mean singing bout consisted of 4.2 ± 0.2 SE song types, with no significant difference in the number of song types per bout among breeding stages ($F_{5,9} = 2.96$, $P = 0.071$). Neither singing (song type) rates ($F_{6,19} = 0.29$, $P = 0.93$) nor time spent singing ($F_{6,19} = 0.28$, $P = 0.94$) varied significantly among the seven male chats. Similarly, we found no

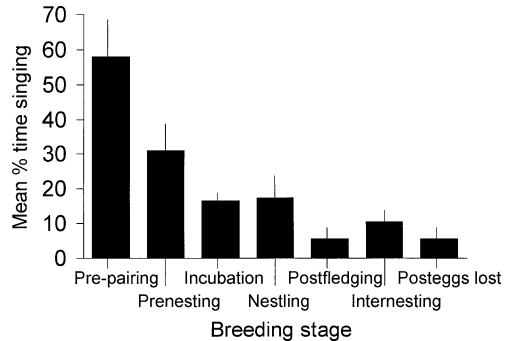


FIG. 2. Percentage of time spent singing by seven male Yellow-breasted Chats (*Icteria virens*) in Madison County, Kentucky, during different stages of the 1995 breeding season. Recorded by Natalie Dussourd.

significant variation among males in mean bout length ($F_{6,9} = 2.49$, $P = 0.11$).

We found few significant correlations between morphological characteristics and either singing behavior or reproductive success. However, male chats with longer wing chords fledged more young ($r^2 = 0.87$, $P = 0.010$). In addition, males with longer tarsi had larger song repertoires ($r^2 = 0.82$, $P = 0.023$).

DISCUSSION

The song type repertoires of seven male Yellow-breasted Chats in our study ranged from 46 to 81 types, and the positive correlation between tarsus length and song type repertoire size suggests that sexual selection may have played a role in the evolution of chat song repertoires. Females may be able to choose males that provide superior resources based on male repertoire sizes, which may reflect the age of males. In support of this hypothesis, we found that male chats with longer tarsi had larger song repertoires. Tarsus length may be a reliable indicator of male quality and size (older males are larger than younger ones; Lampe and Espmark 1994). The correlation between these two characteristics in chats may indicate that larger (and, thus, older and more experienced) males have larger repertoires and may be able to provide females and young with superior resources.

Sharing of song types.—Sharing of song types among male chats in our study was common. Such sharing may permit matched countersinging, with one male singing a particular song type and another male responding

with the same song type (Krebs et al. 1981). Matched countersinging may play a role in territorial interactions and in conveying dominance status (Krebs et al. 1981, Kroodsmma 1979). A related suggestion is that matching is a "keep out" signal directed at a specific intruder (Armstrong 1973).

Singing rates.—In many passerines, male singing rates decline after pairing (Wasserman 1977, Gottlander 1987), suggesting that singing functions primarily to attract females. Although the singing rates of male chats in our study did not decline after pairing, the time spent singing did. This decline in time spent singing after pairing suggests that singing by male chats serves to attract mates. The continued singing by males after pairing, however, also suggests additional functions, including territorial defense. Male chats respond aggressively to playback of the songs of conspecific males (Ritchison 1988) and display flights accompanied by song occur during territorial disputes (Eckerle and Thompson 2001), suggesting that singing serves to maintain territory boundaries (Eckerle and Thompson 2001). Singing by male chats also may serve to attract additional mates. Although predominantly socially monogamous, the mating system of chats ranges from monogamy to successive monogamy to polygyny (Thompson and Nolan 1973). Males may, therefore, continue singing to attract a second female (McDonald 1989). One male chat in our study was polygynous (with two females), and this male also had the largest song repertoire of all focal males and was the first to arrive on our study site.

Chats in our study population did engage in extrapair copulations (Mays 2001). Thus, singing by male chats also might function to solicit extrapair copulations from neighboring females. Singing also may represent a form of mate guarding. For example, male Yellowhammers (*Emberiza citrinella*) announce the fertility status of their mate via song. Males that sang at higher rates experienced fewer territorial intrusions by neighboring males than those that sang at lower rates (Møller 1991). Because male and female chats do apparently solicit extrapair copulations, males may sing to prevent territorial intrusions by neighboring males attempting to copulate with their females.

Singing behavior, morphology, and reproductive success.—Male chats with longer wing chords fledged more young, and males with longer tarsi had larger song repertoires. Measures of body size, such as wing chord and tarsus length, may be good indicators of male quality (Lampe and Espmark 1994). Larger males would have smaller constraints placed on temperature and energy requirements (Morse 1989). A larger individual also may be more likely to win territorial disputes (McGregor et al. 1981, Searcy and Andersson 1986) and thus maintain a better territory. Female reproductive success is affected by territory quality in many passerines (Searcy 1982, Searcy et al. 1985). The significant correlations between tarsus length and repertoire size and between wing chord and number of fledglings suggests that male chats of higher quality may have larger repertoire sizes and fledge more young. Thus, females may use singing ability as an indicator of male quality. Similarly, blacker (and thus older and more experienced) male Pied Flycatchers (*Ficedula hypoleuca*) have longer wings (Slagsvold and Lifjeld 1988), more complex songs (Lampe and Espmark 1994), and survive better (Slagsvold and Lifjeld 1988). Several studies of other species, however, have revealed no such correlations between singing behavior and male quality (Lambrechts and Dhondt 1986, Bijmens 1988, McGregor 1988).

Comparison with other wood-warblers.—The singing behavior of male Yellow-breasted Chats in our study differed from that described previously for wood-warblers (Spector 1992). Male chats, in contrast to male wood-warblers, possess relatively large repertoires of highly variable song types (this study; Eckerle and Thompson 2001). Also, in contrast to male wood-warblers, male chats vary the sequence of song types, the frequency of repetition of individual song types, and the length of time between consecutive song types (Eckerle and Thompson 2001; ND and GR pers. obs.). Finally, male chats, in contrast to wood-warblers, may incorporate the songs and calls of other species into their repertoires (Kroodsmma and Baylis 1982). Because singing behavior can suggest relationships among taxa (Spector 1992), such differences between Yellow-breasted Chats and other wood-warblers suggest possible phylogenetic differences. The

taxonomic placement of chats has generated considerable controversy (Eckerle and Thompson 2001). Recent work, however, suggests that several genera traditionally assigned to the Parulidae, including *Icteria*, probably are more closely allied to other nine-primaried oscine families (Lovette and Bermingham 2002). Specifically, mtDNA-based and *c-mos* reconstructions suggest that Yellow-breasted Chats may be allied to a group of icterids, particularly *Dolichonyx* (Lovette and Bermingham 2002). Similarly, Klicka et al. (2000), based on analysis of mitochondrial cytochrome-b and NADH dehydrogenase subunit 2 genes, reported that *Icteria* grouped with either *Dolichonyx* or *Sturnella*. Thus, our results support a growing body of evidence that Yellow-breasted Chats are not allied to the Parulidae.

ACKNOWLEDGMENTS

We thank P. Costello for help in determining the model for estimating song type repertoire size, and three anonymous reviewers for many helpful comments. Financial support for our work was provided by Kentucky NSF EPSCoR and the Eastern Kentucky Univ. Research Committee.

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