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A CONTEXTUAL ANALYSIS OF SINGING BEHAVIOR IN MALE TUFTED TITMICE

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Abstract.—Recent studies have revealed that singing by male passerines may serve a variety of functions, including, but not limited to, mate attraction and territory defense. Examination of singing rates throughout the breeding season, and the contexts in which Tufted Titmice (*Parus bicolor*) were observed singing, suggest that male song may be used to establish and maintain territories, coordinate activities at the nest and with fledged young, and tutor fledged young. Male titmice also appeared to alter the characteristics of songs to enhance communication with conspecifics. Titmice uttered shorter songs at higher rates and sang with greater versatility when near conspecific males, possibly providing information about the probability of interacting. There were few correlations between particular song types and specific breeding stages or behavioral contexts. However, male titmice often matched song types when countersinging with neighboring males. By permitting changes in singing versatility and the matching of a neighbor's song type, song type repertoires may enhance communication between conspecific males.

UN ANÁLISIS CONTEXTUAL DE LA CONDUCTA DE CANTO DE MACHOS DE *PARUS BICOLOR*

Sinopsis—Estudios recientes han revelado que la canción de los machos paserinos puede servir una variedad de funciones incluyendo, pero no limitada a, atraer parejas y defender territorios. El examen de las tasas de canto a través de la temporada reproductiva y del contexto en que machos de *Parus bicolor* se hallaron cantando sugiere que la canción de los machos puede servir para establecer territorios, coordinar actividades en el nido y con jóvenes volantones, y educar jóvenes volantones. Los individuos también parecen alterar las características de las canciónes para mejorar la comunicación con los conspecíficos. Los *Parus* presentaron canciones cortas a tasas mayores y cantaron con mayor versatilidad cerca de machos conspecíficos, posiblemente proveyendo información sobre la probabilidad de interactuar. Hubieron pocas correlaciones entre tipos particulares de canción y etapas reproductivas o contextos de conducta específicos. Sin embargo, los machos de *Parus* a menudo imitaban tipos de cantos cuando contracantaban con machos cercanos. Al permitir cambios en la versatilidad del canto y el igualar el tipo de canto de los vecinos, los repertorios de tipos de canto pueden mejorar la comunicación entre machos conspecíficos.

Among many passerines, males have repertoires of two or more song types (Read and Weary 1992). In some species, particular song types convey particular messages. For example, males may use one song type for intersexual communication and another for intrasexual communication (e.g., Smith 1959). Certain song types may also communicate increased tendencies to interact (Jarvi et al. 1980, Nelson and Croner 1991). In other species, song types apparently do not convey particular messages and, in such species, repertoires may serve a variety of functions. For example, speaker replacement experiments have revealed that a repertoire of songs may be more effective than a single song in preventing

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trespassing by conspecific males (Krebs 1978, Yasukawa 1981). Repertoires may also enable males to more effectively match song types (Capp 1992), and permit them to direct a message to a specific conspecific. Repertoires may also play an important role in mate attraction. In some species, females appear to prefer males with larger repertoires (Horn et al. 1993, Searcy 1988).

Among those passerines with multiple song types is the Tufted Titmouse (*Parus bicolor*). Male titmice have repertoires of 8–15 song types and previous investigators have suggested that some song types, or groups of song types, may be associated with particular contexts (Gaddis 1983, Schroeder and Wiley 1983a). However, associations between song types and context were imperfect (Gaddis 1983, Schroeder and Wiley 1983a), and not all song types were associated with particular contexts (Gaddis 1983). Such results suggest that Tufted Titmice use their repertoires, or at least some songs in their repertoires, for purposes other than conveying specific messages. One objective of our study was to re-examine the relationship between song types and context in Tufted Titmice in an attempt to further understand the functions of titmouse song repertoires. More generally, we sought to determine the functions of singing by male Tufted Titmice by monitoring changes in singing behavior throughout the breeding season and in different behavioral contexts.

METHODS

Six male Tufted Titmice were observed from 10 Mar.–31 Aug. 1993 at the Central Kentucky Wildlife Management Area, 17 km SSE of Richmond, Madison County, Kentucky (37°40′N, 84°10′W). Males were individually marked with colored leg bands and plastic tape attached to the tail (Ritchison 1984). We recorded and observed titmice almost daily. Typically, each of us recorded one male each day for 1–2 h. All focal male observations were made during the period from 0.5 h before sunrise until 4 h after sunrise. Territories were delineated by following males and noting the location of interactions with neighboring males.

During focal male observations, we recorded on tape all bouts of song. For each bout, we noted the date and the nesting stage. The breeding period was divided into five stages: pre-nesting, nest building/egg-laying (female fertile period), incubation, nestling, and post-fledging. Because all but one pair of titmice nested in inaccessible cavities, the timing of the fertile, incubation, and nestling periods was estimated by observing the behavior of adults (e.g., when adults began feeding nestlings) and, in some cases, by backdating from the day of fledging. For backdating, the nestling period was assumed to be 17 days and the incubation period 13 days (Brackbill 1970). All pairs of titmice in our study produced one brood and none of the pairs re-nested.

We categorized the location of conspecific males and females (if known) as distant (>25 m apart), intermediate (5–25 m apart), or close (within 5 m). In addition, we noted whether or not conspecific males were singing and, if so, the song type being used. On that basis, we categorized focal male bouts into three singing contexts: spontaneous singing (no other males singing), countersinging and not matching (a conspecific male singing and not using the same song type), and countersinging and matching (a conspecific male singing and using the same song type). During the incubation, nestling, and post-fledging periods, we also noted the location of focal males relative to their nest or fledged young. Finally, we subjectively categorized the volume of bouts as normal (could be heard throughout a male's territory and into adjacent territories), intermediate (could not be heard in adjacent territories), or low (could not be heard more than about 10 m from the focal male).

Recordings were made using a Marantz cassette recorder (Model PMD221 or PMD430) with a directional microphone (Saul Mineroff SME V-6502) or a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone. Sonograms of songs were produced with a Kay Elemetric Corporation Sonograph (Model 5500). For each song, we determined the song type, number of syllables per song, and the time since the preceding song (intersong interval). Songs were categorized into song types based on the structure of syllables (Schroeder and Wiley 1983a). All song types were discrete (i.e., no intermediate types) and were uttered consistently over time. For each observation period, we determined the number of songs and the number of bouts (with a bout defined as a series of songs separated in time from each other by intervals of 60 s or less). For each bout, we determined the number of songs, number of song types, and the total versatility (the product of total song types in the bout times the number of transitions among song types in the same bout; Kroodsma and Verner 1978). This value was divided by the total number of songs in a bout to allow comparison of bouts of different sizes.

All analyses were performed using the Statistical Analysis System (SAS Institute 1989). G-tests were used to examine possible non-random use of song types among breeding stages and contexts. The General Linear Model (GLM) procedure was used to examine variation in song characteristics and singing behavior among individuals and among contexts. Analysis of variance was performed on rank-transformed data (equivalent to Kruskal-Wallis tests; SAS Institute 1989) and then followed by a Student-Newman-Keuls test to detect differences among means. Because we analyzed songs recorded from the same six males over several months, repeated measures analysis was used. This analysis provides a test for interactions (Beal and Khamis 1990), and we examined male by breeding stage and male by context interactions for several variables. We assumed that for variation in the characteristics of songs to convey information, most or all males would vary songs in the same way (Ritchison 1995). All values are presented as means ± 1 SE.

RESULTS

Sharing of song types.—The mean number of song types in the repertoires of male titmice (n = 6) in our study was 12.3 (range = 10–13). Overall, the six males used 23 song types, with five shared by all six males

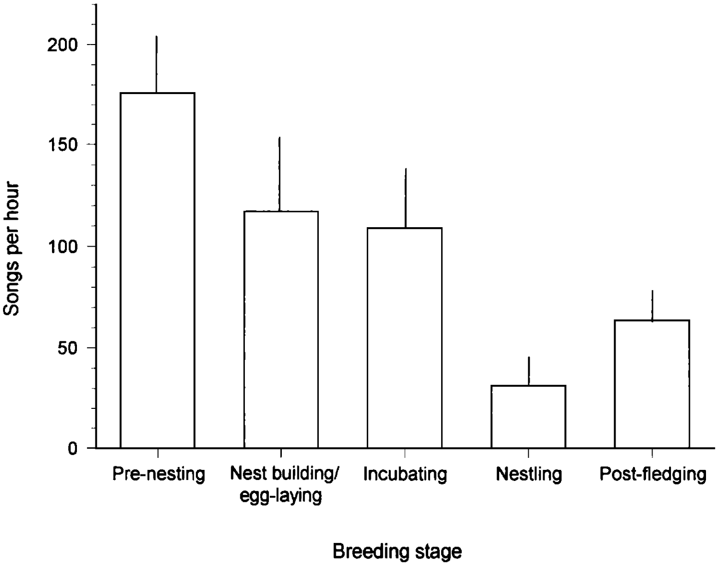

FIGURE 1. Singing rates of male Tufted Titmice during the five breeding stages.

and eight shared by five males. Neighboring males (n = 4) shared an average of 66% of their song types, while non-neighboring males (n = 9) shared an average of 45%. Three males had one unique song type each and one male had two unique song types.

Effect of breeding stage.—Singing rates varied significantly among breeding stages ($F_{4,20}$ = 6.56, P = 0.0025), with rates higher during the pre-nesting, nest building/egg-laying, and incubation periods (Fig. 1). There was no significant interaction between individual and breeding stage (P = 0.54). Neither the number of notes per song ($F_{4,20}$ = 0.59, P = 0.67) nor intersong interval ($F_{4,20}$ = 2.71, P = 0.07) varied among breeding stages.

Song volume varied with breeding stage (χ^2 = 75.3, df = 8, $P <$ 0.0001). The use of intermediate and low volume songs increased during the nestling and post-fledging stages, with about 40% of the bouts uttered during these stages consisting of intermediate or low volume songs (Fig. 2). In contrast, 20% or less of the bouts uttered during the pre-nesting, fertile, and incubation stages consisted of intermediate or low volume songs (Fig. 2).

Total versatility varied among breeding stages ($F_{4,20}$ = 6.68, P = 0.0014), with no significant interaction between individual and breeding stage (P = 0.34). Versatility was highest during the post-fledging period and lowest during the nest building/egg-laying period (Fig. 3).

Effect of Intra- and Intersexual Context.—Songs consisted of fewer syllables ($F_{2,8}$ = 6.21, P = 0.024) when conspecific males were close (SNK

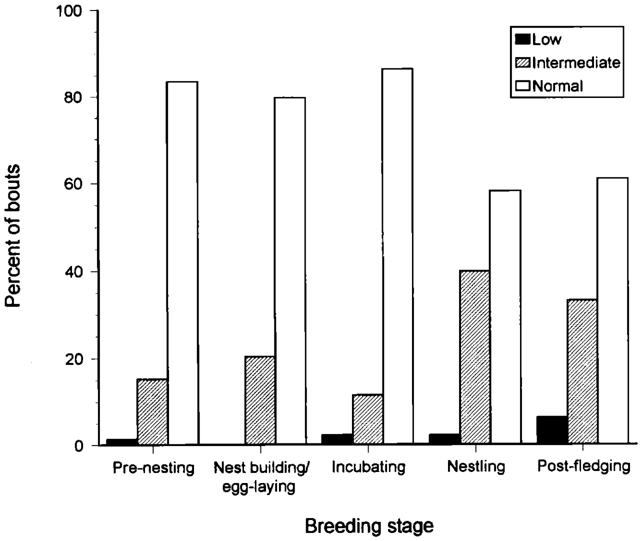

FIGURE 2. Volume of songs uttered by male Tufted Titmice during the five breeding stages.

test, $P < 0.05$). There was a significant interaction between individual and distance ($P = 0.0001$), however, three of four males sang shorter songs when close to conspecific males. The number of syllables per song did not vary with distance from mates ($F_{2,10} = 3.1$, $P = 0.089$), distance from

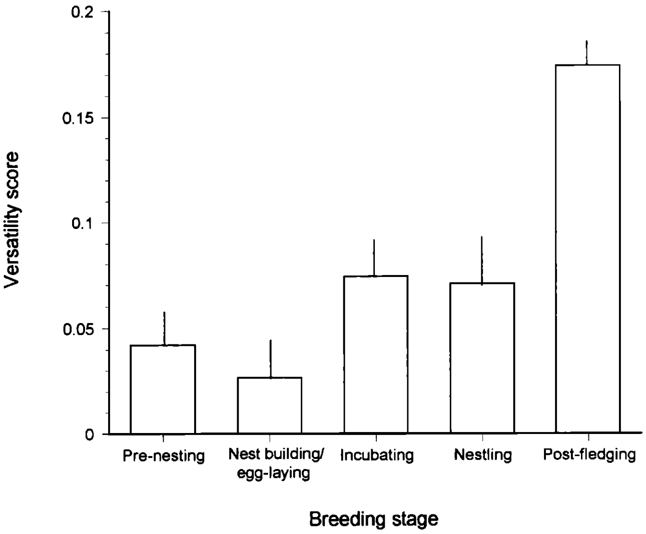

FIGURE 3. Singing versatility of male Tufted Titmice during the five breeding stages.

fledged young ($F_{2,6}$ = 0.31, P = 0.74), or singing context ($F_{2,10}$ = 1.01, P = 0.42).

Intersong intervals varied with a male's distance from conspecific males ($F_{2,8}$ = 6.62, P = 0.02), with shorter intervals (SNK test, $P < 0.05$) during close encounters. There was a significant interaction between individual and distance from conspecific males (P = 0.0001). However, intersong intervals were shorter during close encounters for four males (and the other two males were not observed in close encounters). Intersong intervals did not vary with singing context ($F_{2,10}$ = 0.24, P = 0.79), distance from fledged young ($F_{2,6}$ = 0.28, P = 0.76), or distance from mate ($F_{2,10}$ = 0.04, P = 0.96).

Males uttered more low and intermediate volume songs when singing spontaneously (χ^2 = 34.5, df = 4, $P < 0.0001$). Distance from conspecific males had no effect on volume (χ^2 = 3.9, df = 4, P = 0.42), with more normal volume songs uttered at all distances. Males uttered more low and intermediate volume songs when either a mate (χ^2 = 11.3, df = 4, P = 0.023) or fledged young (χ^2 = 28.9, df = 4, $P < 0.0001$) were within 25 m.

Males sang with greater versatility when conspecific males were within 25 m ($F_{2,6}$ = 6.01, P = 0.037). In contrast, singing versatility did not change with singing context ($F_{2,10}$ = 1.86, P = 0.21), distance from mates ($F_{2,9}$ = 1.21, P = 0.34), or distance from fledged young ($F_{2,6}$ = 0.58, P = 0.58).

Use of song types with breeding stage.—Song type use varied significantly among breeding stages for five of six males (χ^2 tests, $P < 0.001$). However, different males did not use the same song types during particular breeding stages.

Use of song types among behavioral contexts.—Song type use did not vary with distance from conspecific males for five males (χ^2 tests, $P > 0.05$) but did vary significantly for one male (P = 0.047). One male was never observed within 25 m of a conspecific male.

For four males, the use of song types did not vary with distance from mates (χ^2 tests, $P > 0.1$). In contrast, the use of song types did vary with distance from mates for two males ($P < 0.001$). Each of these males used two song types (different song types for each male) more when within 25 m of his mate.

Five males were observed near their young during the post-fledging period, and the use of song types by four of these males did not vary significantly with distance from their young (χ^2 tests, $P > 0.05$). One male used two song types most often when within 25 m of his young (P = 0.045).

Song type use did not vary significantly with singing context for four males (χ^2 tests, $P > 0.2$). For two males, the use of song types did vary with singing context ($P < 0.04$), with these males using one and two song types, respectively, most frequently when countersinging.

DISCUSSION

Male titmice sang at higher rates during the pre-nesting, nest building/egg-laying, and incubation periods. Because male titmice in central Kentucky establish territories from March through late April (pre-nesting period), frequent singing during this time suggests that song plays a role in this process. Other species also sing at high rates during territory establishment (Catchpole 1982, Haftorn 1993). The period of territory establishment often coincides with or overlaps the period of mate attraction and, in several species, singing rates decline dramatically after pairing (e.g., Hanski and Laurila 1993, Ritchison 1995). In such species it may be difficult to determine if singing is important in territory establishment or mate attraction or both. Tufted Titmice appear to form pairs during the winter and early spring (Brawn and Samson 1983), often before males begin singing. Such timing suggests that singing during the pre-nesting period is used primarily to establish territories.

Titmice in our study sang at relatively high rates during the nest building/egg-laying (fertile) and incubation periods, with most songs being normal volume. Singing during these periods may serve multiple functions, e.g., maintaining territory boundaries, stimulating a female's reproductive cycle (e.g., Logan 1983), or soliciting copulations (Johnson and Kermott 1991). Møller (1991) suggested that male song during a mate's fertile period may be a form of mate guarding. Such guarding may be important for male titmice because, although not yet reported for Tufted Titmice, extra-pair copulations have been reported in other parids (e.g., Kempenaers et al. 1992, Smith 1988).

Male titmice sang at low rates (and typically with low volume) during the nestling period (see also Ritchison 1988, 1995). One function of singing during this period may be to coordinate feeding activity. We sometimes observed male titmice sing low volume songs when approaching nests with food. Similarly, male House Wrens (*Troglodytes aedon*) sing when approaching nests, and this probably facilitates the rapid transfer of food (Johnson and Kermott 1991).

Male titmice continued to sing at relatively low rates during the postfledging period, and this singing probably serves at least two functions. First, song may inform young that a male is approaching with food and, second, males may be tutoring young. Of 47 species of parids, six exhibit some vocal learning (Kroodsma 1982). Tufted Titmice are known to learn songs, and song learning appears to begin before young disperse from family flocks (Schroeder and Wiley 1983a). In support of the tutoring hypothesis, we observed young titmice singing immediately after a male parent sang, sometimes using the same song type. Schroeder and Wiley (1983a) reported that song types used by both parents and neighbors were recognizable in the repertoires of young titmice within four weeks of fledging. By singing with greater versatility, male titmice may expose young to more song types. The apparent tutoring of young prior to dispersal has been reported in other species (Greig-Smith 1982, Hiett and Catchpole 1982).

Except for changes in volume, the characteristics of songs used by male titmice varied little among breeding stages. However, song characteristics did vary with intra- and intersexual context. Male titmice uttered shorter songs when near conspecific males and females. Similar singing behavior has been reported in other species (e.g., Radesater and Jakobsson 1988, Ritchison 1995). Changing the characteristics of songs, e.g., shorter songs, may transmit information about a singer's motivational state, and may communicate the probability of interaction (Falls 1969).

Male titmice also sang with greater versatility when near conspecific males (see also Kramer et al. 1985, Simpson 1985). Falls and D'Agincourt (1982) proposed that song type switching by male Eastern Meadowlarks indicates a willingness to interact. Kramer et al. (1985) suggested that song type switching by male Song Sparrows also serves as a graded signal in agonistic communication. Thus, rapid song type switching by male Tufted Titmice may serve the same function as shorter, more rapidly uttered songs, i.e., indicating an increased likelihood of interacting.

Male titmice typically used normal volume songs when countersinging with males in adjacent territories and intermediate and low volume songs during spontaneous singing and when mates or young were nearby. Using normal volume songs for countersinging would ensure that neighboring males would hear the songs. The use of intermediate and low volume songs during spontaneous singing indicates that songs were directed at a nearby mate or fledged young, and supports the hypothesis that singing by male titmice serves functions other than territory defense.

We found few significant correlations between song types and contexts, and all song types were used in more than one context. Similar use of particular song types in multiple contexts has been reported for Bridled, Plain, and Tufted Titmice by Gaddis (1983), Johnson (1987), and Schroeder and Wiley (1983b), respectively. Even imperfect associations between song types and context might allow conspecifics to make some predictions about a titmouse's behavior on the basis of the song type it sings (Schroeder and Wiley 1983b). However, such singing behavior also suggests that the song type repertoires of male titmice serve other functions.

Song repertoires may be important in intrasexual communication. Male titmice often match song types when countersinging with neighboring males. Matching may direct a message to a specific individual (McGregor et al. 1992) and serve as a "keep out" signal (Bremond in Armstrong 1973). Krebs et al. (1981) suggested that matched countersinging indicates a higher probability of escalating an encounter. Because a large repertoire would improve the chances of being able to match a neighbor's song type, one advantage of a large repertoire is that it might improve a male's ability to efficiently communicate with neighboring males.

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