

Use and possible functions of large song repertoires by male Eastern Bluebirds

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ABSTRACT. Five male Eastern Bluebirds (*Sialia sialis*) were observed and songs recorded over entire breeding seasons in central Kentucky. Songs consisted of an average of 3.02 notes and the mean time between the beginning of successive songs within a bout was 7.26 s. Most songs (63.7%) given by male bluebirds were low volume, while 14.8% were moderate volume, and 21.5% were high volume. Individual male bluebirds possessed large ($\bar{x} = 59.4$) repertoires of song types, and few were shared among two or more males. Singing rates varied among breeding stages, with high rates during the pre-pairing period suggesting that song plays a role in mate attraction. However, male bluebirds also sing during interactions with conspecific males, indicating an aggressive or territorial function, to facilitate the transfer of food to incubating or brooding females, nestlings, and fledglings, and to warn mates, nestlings, or fledglings about the presence of a potential predator. Thus, as reported in an increasing number of species, singing by male bluebirds serves multiple functions.

SINOPSIS. El uso y posibles funciones de grandes repertorios de canciones en machos de *Sialia sialis*

Se observaron cinco machos de *Sialia sialis* y se grabaron sus cantos a través de toda la temporada reproductiva en el centro de Kentucky. Las canciones consisten de un promedio de 3.02 notas y el tiempo promedio entre los comienzos de canciones consecutivas en un período fué de 7.26 seg. La mayoría de los cantos de estos machos fueron de volumen bajo (63.7%), mientras que el 14.8% fueron de volumen moderado y el 21.5% de volumen alto. Los machos individuales poseían grandes repertorios de tipos de canto ($\bar{x} = 59.4$), y pocos eran compartidos por dos o más machos. Las tasas de canto variaron entre las etapas reproductivas, siendo el período pre-apareamiento el de altas tasas, sugiriendo que la canción juega un rol en atraer la pareja. Sin embargo, los machos también cantan durante interacciones con machos conspecíficos, indicando una función agresiva o territorial; para facilitar la transferencia de alimento a las hembras que incuban o crían, a los pichones o a los volantones; y para avisar las parejas, pichones, o volantones de la presencia de un depredador potencial. Por lo tanto, tal como se ha reportado para un número cada vez mayor de especies, el cantar de los machos de *Sialis sialis* tiene múltiples funciones.

Key words: Eastern Bluebird, repertoires, *Sialia sialis*, song, song function

Although singing by passerines is often assumed to function primarily in mate attraction and male-male competition, few studies have been designed to actually assess the function of song (Johnson and Kermott 1991). While few in number, such studies have revealed that singing may serve a variety of functions. For example, song may be used to 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).

Although several aspects of the behavior and ecology of Eastern Bluebirds (*Sialia sialis*) have been well studied (Gowaty and Plissner 1998; Ritchison 2000), little is known about their singing behavior. Based on extensive observation, Gowaty and Plissner (1998) suggested that male Eastern Bluebirds sing to advertise territory establishment and attract breeding females. Other authors have drawn similar conclusions (Krieg 1971; Pinkowski 1971). The objective of our study was to quantify the singing behavior of male Eastern Bluebirds and, specifically, to assess the functions of singing by male Eastern Bluebirds by examining singing rates throughout the breeding cycle and in different behavioral contexts, and determine if and how male bluebirds vary songs to convey different types of information.

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METHODS

Five male Eastern Bluebirds were observed during the breeding seasons (1 March through 31 August) of 1989 and 1993 at the Central Kentucky Wildlife Management Area (CKWMA) and at Eastern Kentucky University's Meadowbrook Farm. The CKWMA is a 680-ha area located 17 km southeast of Richmond, Madison Co., Kentucky, while Meadowbrook is a 280-ha farm located 10 km east of Richmond. Nest boxes were placed in both areas to attract mated pairs of bluebirds.

Two males were observed during the breeding season of 1989 (both at the CKWMA) and three during the breeding season of 1993 (two at the CKWMA and one at Meadowbrook). These males and their mates were captured in mist nets and banded with a numbered, aluminum band plus a unique combination of colored plastic bands. We observed and recorded each male bluebird for at least 45 min once every five days. Most observations were made between sunrise and 11:00.

During focal male observations, we recorded on tape all bouts of song, with a bout defined as a series of songs separated by intervals of less than 30 s. For each bout uttered, we noted the number of songs in the bout and the number of notes per song, with a note defined as any sound making a continuous mark on a sonagram. We also noted the date and breeding stage. The breeding period of each male was divided into seven stages: pre-pairing (the time from territory establishment through the day before pairing occurred or, later in the breeding season, the time from loss of a mate through the day before a new mate was obtained), pre-laying (from the day of pairing through the day before the first egg was laid), laying (all days on or between the days when the first and last eggs were laid), incubation (from the day after the last egg was laid through the day before hatching began), nestling (from the day eggs began hatching through the day before the young fledged), post-fledging (a 14-d period beginning on the day of fledging), and transition (from 14 d after fledging until nest building began). After a transition stage, another pre-laying stage began when a pair initiated nest building.

During observations, the location of the focal male's mate was also noted, if possible, and

categorized as close (within 5 m), medium (5–10 m away), or distant (more than 10 m away). We also noted the location of conspecifics other than the mate and, on that basis, categorized bouts of song by the focal male as either spontaneous (no conspecifics could be seen or heard) or non-spontaneous. Non-spontaneous bouts were categorized as either male interactions (apparently responding to a conspecific male) or female interactions (apparently responding to a conspecific female). Bouts were also categorized by volume, with high volume bouts audible in adjacent territories, moderate volume bouts audible throughout a territory but not in adjacent territories, and low volume bouts not audible more than 40 m from the focal male.

Recordings were made using either a Marantz cassette recorder (Model PMD 221) with a unidirectional microphone (Model V-6502, Saul Mineroff, Elmont, NY) or a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic reflector and microphone. Recordings were analyzed using a Kay Elemetrics Co. DSP Sona-Graph (Model 5500). All songs were categorized into song types. A song type was defined as a note or group of notes in which the time interval between notes was shorter than the time interval between other such notes or groups of notes, and, when used on more than one occasion, such song types were uttered in consistent form (Derrickson 1987). An attempt was made to estimate the size of each male's song type repertoire by plotting the total number of song types used versus the total number of songs uttered (Kroodsma 1982; Wunderle et al. 1992). As a measure of singing versatility, the number of different song types within each bout was multiplied by the number of transitions among song types and this product was divided by the total number of songs within the bout (Kroodsma and Verner 1978). Finally, cadence was defined as the interval from the beginning of one song to the beginning of the next song in the bout (Howes-Jones 1985).

Differences in the characteristics of songs among males, contexts, and breeding stages were examined using repeated-measures analysis of variation (Beal and Khamis 1990). When significant interactions between individuals and contexts or breeding stages were found, we analyzed data for each male separately. When sig-

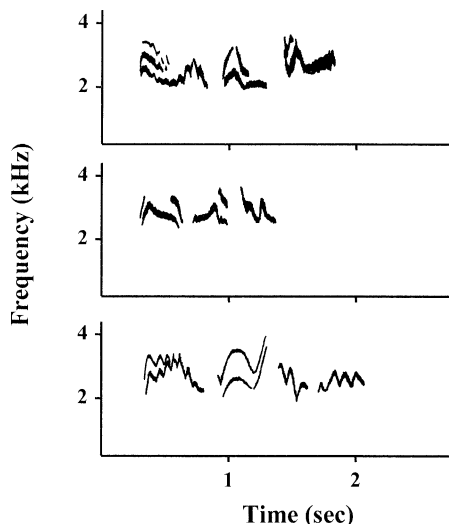


Fig. 1. Examples of songs of three male Eastern Bluebirds.

nificant effects were noted, means were estimated and compared using the Student-Newman-Keuls (SNK) procedure modified for unequal sample sizes (Ott 1993). All analyses were performed using the Statistical Analysis System (SAS 1989). All values are presented as mean \pm SD.

RESULTS

The songs of the five male Eastern Bluebirds consisted of an average of 3.02 ± 1.70 notes ($N = 4238$), and all songs were uttered at frequencies between 2 and 4 kilohertz (Fig. 1). The mean time between the beginning of successive songs within a bout was 7.26 ± 6.09 s ($N = 3669$). Most songs given by male bluebirds were low volume (2487 of 3904 or 63.7%), while 14.8% (579 of 3904) were moderate volume, and 21.5% (838 of 3904) were high volume.

The mean number of song types in the repertoires of the five male bluebirds was 59.4 ± 17.4 , ranging from 40 to 81. However, plots of the cumulative number of normal song types versus the total number of songs uttered indicated that the males continued to add new song types throughout the study and none of the plots approached an asymptote. Thus, additional sampling would have undoubtedly re-

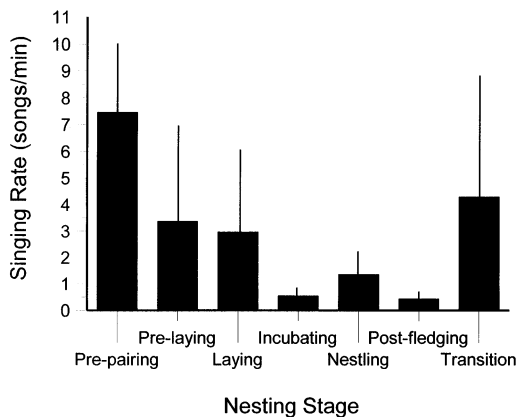


Fig. 2. Variation among nesting stages in the singing rates of male Eastern Bluebirds.

vealed additional song types in the repertoires of all five males.

Each male's song type repertoire was largely unique, with only six of 309 song types shared among two or more males. In addition, most song types were used infrequently, with 63.9% used only during a single day's observations.

Effect of nesting stage. Singing rates varied among nesting stages ($F_{6,17} = 9.23$, $P < 0.0001$; Fig. 2), with rates highest during the pre-pairing stage ($P < 0.05$, SNK test). In addition, singing rates during the pre-laying, laying, and transition stages were lower than during pre-pairing, but higher than during the incubation, nestling, and post-fledging stages ($P < 0.05$, SNK test). All five males exhibited similar variation in singing rates among nesting stages, with no significant interaction between individual and nesting stage ($P = 0.23$).

For all songs combined, the mean number of notes per song did not vary among nesting stages ($F_{6,17} = 0.42$, $P = 0.86$). Cadence did vary among nesting stages ($F_{6,17} = 3.44$, $P = 0.021$), with a faster cadence ($P < 0.05$, SNK test) during the pre-pairing, pre-laying, and laying stages and a slower cadence during the post-fledging stage ($P < 0.05$, SNK). Although there was a significant interaction between individual and nesting stage ($P < 0.0001$), most males uttered songs with a faster cadence during the pre-laying stage (four of five males) and a slower cadence during the nestling stage (all five males). In addition, a relatively slow cadence was typical during the incubation stage (three of four males) and during the post-fledging stage (three

of three males). Cadences during the transitional stage were variable, with no consistent trend apparent. Sample sizes were insufficient to permit comparison among males for the pre-pairing (one male) and laying (three males, but most songs uttered by just one male) stages.

Singing versatility varied significantly among nesting stages ($F_{6,17} = 3.55$, $P = 0.021$), with no significant interaction between individual and nesting stage ($P = 0.09$). Post-hoc analysis revealed greater versatility during the pre-pairing, pre-laying, and laying stages ($P < 0.05$, SNK) and less versatility during the incubation, nestling, and post-fledging stages ($P < 0.05$, SNK). Versatility during the transition stage was intermediate to, and significantly different from ($P < 0.05$, SNK), that during the other stages.

Effect of conspecific interactions and distance from mate. Focal males uttered 2729 songs during observations when we knew the location of their mates. Most songs (43.3%) were given when males were more than 10 m from mates (distant), while 18.7% were uttered at medium distance (5–10 m away), and 38.0% were uttered at close range (within 5 m). In addition, most songs (90% of 4148 songs) were given spontaneously, while 7.9% were given during male interactions and 2.1% during female interactions.

The number of notes per song did not vary with distance from mates ($F_{2,7} = 0.47$, $P = 0.65$) or with other conspecific contexts ($F_{3,4} = 0.64$, $P = 0.62$). Similarly, cadence did not vary either with distance from mate ($F_{2,6} = 1.26$, $P = 0.35$) or with conspecific context ($F_{3,4} = 2.25$, $P = 0.22$).

Although no attempt was made to quantify singing behavior in the vicinity of nests or fledged young, male bluebirds sometimes sang when near nests and fledged young. Most singing near the nest occurred during the pre-laying ($N = 621$ songs by five males within 5 m and 188 songs by four males within 5–10 m), laying ($N = 11$ songs by three males within 5 m and 196 songs by one male within 5 to 10 m), and nestling ($N = 99$ songs by five males within 5 m and 56 songs by 5 males within five to 10 m) stages. Fewer songs were uttered within 10 m of fledglings ($N = 236$ by four males) and most of these were given during the transitional ($N = 114$ songs by three males) and pre-laying ($N = 56$ songs by two males) stages.

DISCUSSION

Several features of the singing behavior of male Eastern Bluebirds suggest that song functions in intersexual communication. First, singing rates varied with nesting stage, with rates lowest during those stages when males would have fewer interactions with their mates (incubation, nestling, and post-fledging). Although based on only one male, singing rates were highest during the pre-pairing stage. This male was paired when first observed early in the study but subsequently lost his mate during the post-fledging stage of their nesting attempt. After losing his mate, this male's singing rates increased significantly and remained high until he also disappeared. Pinkowski (1971) also reported that singing rates of Eastern Bluebirds varied with pairing status, with males uttering as many as 20 songs per minute prior to arrival of their mates. With the arrival of the females, singing rates declined considerably (5 to 10 songs per minute; Pinkowski 1971). Saunders (in Bent 1949) noted that while male bluebirds sang at high rates during courtship and nest building, little singing occurred after incubation began. Other investigators have reported increased singing rates in response to the loss of a mate in other species (Wasserman 1977; Johnson 1983; Cuthill and Hindmarsh 1985), or reduced singing rates by males after pairing (Powlesland 1983; Lampe and Espmark 1987; Bjorklund et al. 1989; Ritchison 1995).

In addition to increasing singing rates, the unpaired male bluebird in our study sang with greater versatility and high volume. The increase in singing versatility suggests that the complex song repertoires of male bluebirds may serve primarily an intersexual function. Overall, this change in singing behavior provides strong circumstantial evidence that singing by male Eastern Bluebirds, and, specifically, highly versatile singing, plays a role in mate attraction.

Although singing rates were lower after pairing, male bluebirds continued to sing during the pre-laying, laying, and transitional stages. In addition, singing versatility remained relatively high and most songs were low volume. The use of low-volume songs suggests that at least some of this singing was directed at mates. During these stages, female bluebirds are either preparing to nest (or re-nest) or are actually producing a clutch (and, therefore, would be fertile). John-

son and Kermott (1991) reported frequent use of low-volume 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. Using low-volume songs at this time 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). Extra-pair copulations have been reported in Eastern Bluebirds (Gowaty and Karlin 1984) and may account for between 8% and 35% of nestlings (Gowaty and Bridges 1991). Thus, if male bluebirds must sing 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.

Singing rates during the incubation, nestling, and post-fledging stages were significantly lower than during other nesting stages. During these stages, male bluebirds are involved in bringing food to the nest (for their mate and young) or to fledged young (Bent 1949; Krieg 1971; Zeleny 1976; Gowaty and Droge 1990; B. Huntsman and G. Ritchison, pers. obs.). Such activity may have contributed to the relatively low rates of singing. Similarly low singing rates by males engaged in feeding nestlings have been reported in Northern Cardinals (*Cardinalis cardinalis*; Ritchison 1988), Common Yellowthroats (*Geothlypis trichas*; Ritchison 1995), and Tufted Titmice (*Parus bicolor*; Duguay and Ritchison 1998). In addition, most songs uttered during these stages were low volume, suggesting that they were directed at conspecifics within the territory.

One possible function of singing by male bluebirds during the incubation and nestling stages may be to coordinate feeding activities at the nest. Males sometimes uttered songs near nest boxes before approaching to feed mates (four of 11 observed feedings). Such songs might prepare a mate or nestlings for the male's visit and, perhaps, reduce the time that a male needs to spend at the nest. Johnson and Kermott (1991) also reported that male House Wrens sang when approaching the nest and suggested that such singing probably signals the female that the male is about to come to the nest cavity with food. Such behavior would

probably facilitate the rapid transfer of food (Johnson and Kermott 1991).

Male bluebirds in our study sometimes sang before approaching the nest box during the nestling stage (20 of 37 observations). Such singing may serve to facilitate the transfer of food. However, this did not always appear to be the case. On several occasions, males flew to within 10 m of a nest box, uttered several songs, flew to the box entrance but did not deliver prey, then flew away from the box and uttered more songs before finally delivering the food to the nestlings. Such behavior suggests that another possible function of singing during the nestling period is to teach nestlings to associate singing with food. After the young fledge, family units typically range long distances from the nest (up to 500 m) while foraging. Fledglings familiar with the songs of their parents might be better able to remain in contact. Duguay (1995) suggested that singing by male Tufted Titmice during the post-fledging stage served a similar function.

Our results indicate that singing by male bluebirds also plays a role in intrasexual, or territorial, communication. Similarly, Pinkowski (1971:22) suggested that singing by male bluebirds was used for "territory proclamation." Male bluebirds sang during interactions with conspecific males and, in addition, it is likely that at least some of the singing categorized as spontaneous could be heard by conspecific males and could serve an intrasexual function. Other investigators have also found that male bluebirds sing during interactions with conspecific males (Pinkowski 1971; Gowaty 1981) and, in addition, males typically respond to the playback of conspecific songs in their territory by singing (Plissner and Gowaty 1995; B. Huntsman and G. Ritchison, pers. obs.). Our observations, and those of others, also indicate that male bluebirds do not rely entirely on song during intrasexual encounters. Aggressive interactions between male bluebirds may also involve the use of "chuck" or staccato calls or even attacks (Pinkowski 1971; Gowaty 1981).

In addition to the possible functions of song already noted, Pinkowski (1971) suggested that singing by Eastern Bluebirds may be used for "distress communication." He observed that "bluebirds frequently break into full song when they are disturbed" and that this behavior "occurred most often when we were checking the

nesting box of a breeding pair which had eggs or young." Other investigators have also reported that both male and female Eastern Bluebirds utter "predator or alarm songs" in the presence of nest predators (Morton et al. 1978; Gowaty and Plissner 1998). Although we did not quantify such behavior, male (and female) bluebirds sometimes sang when we approached and checked nest boxes. Such singing may serve to warn a mate or nestlings that a potential predator was nearby or, as with the flight songs of male Common Yellowthroats (Ritchison 1991), may serve to distract potential predators.

Our results indicate that singing by male Eastern Bluebirds serves multiple functions. Smith (1991) pointed out that singing serves more functions than is generally recognized. This study, along with other studies (Johnson and Kermott 1991; Ritchison 1995), supports this conclusion. Although these studies have provided important insight into some functions of song, detailed observations of the natural patterns of song use and behavior in a large number of species are needed to completely reveal the diversity of functions that song may serve (Johnson and Kermott 1991).

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