EFFECTS OF BREEDING STAGE AND BEHAVIORAL CONTEXT ON SINGING BEHAVIOR OF MALE INDIGO BUNTINGS

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ABSTRACT.—We studied the effects of breeding stage and behavioral context on the singing behavior of male Indigo Buntings (Passerina cyanea; n = 15) during the 2004 breeding season in Madison County, Kentucky, USA, to better understand how males with a single-song repertoire vary the characteristics of their song to convey different information. Playback experiments were conducted in 2005 in territories of focal males (n = 14) to further examine the possible effect of male-male interactions on singing behavior. We analyzed 10,919 songs of 15 male Indigo Buntings with songs consisting of a series of figures that were usually paired (i.e., phrases). Mean song duration was 2.30 ± 0.13 (SE) sec (range = 1.44–3.40 sec) with males varying song duration by varying the number of figures and phrases in each song. Singing rates varied significantly (P < 0.0001) among breeding stages and were highest prior to pairing, suggesting singing has a role in mate attraction. Singing rates also differed (P = 0.013) during playback experiments with rates higher during playback and post-playback periods (\bar{x} = 4.4 songs/min) than during the pre-playback period (\bar{x} = 2.9 songs/min). These results suggest that singing also has a role in territory defense. Songs of male buntings tended to be shorter prior to pairing and were generally longer in duration after pairing. Playback experiments revealed that bunting songs were longer (P = 0.03) during and after playback (\bar{x} = 2.6 sec) than during the pre-playback period (\bar{x} = 2.0 sec). These results suggest male Indigo Buntings vary singing rates and song duration to convey different information, appearing to use shorter songs uttered at high rates to attract mates and longer songs to convey aggression during male-male interactions. Received 21 December 2009. Accepted 3 June 2010.

Males of most species of passerines have multilong repertoires (MacDougal-Shackleton 1997). These repertoires may be important in male-male interactions (song matching; Stoddard et al. 1992), preventing habituation (Krebs et al. 1978, Yasukawa 1981), providing information about motivational state (Falls 1969), and repelling intruders (Krebs et al. 1978, Yasukawa 1981). Song repertoires may also have intersexual functions. For example, female Atlantic Canaries (Serinus canaria) exhibit more nest building behavior when subjected to playback of larger repertoires (Kroodsma 1976).

Males of some species, such as Ovenbirds (Seiurus aurocapilla; Weary and Lemon 1988) and Henslow’s Sparrows (Ammodramus henslowii; Leftwich and Ritchison 2008), have a single song type. Males with single-song repertoires could potentially use singing to convey different information, but may do so by altering the characteristics of their single song (Morton and Young 1986, Leftwich and Ritchison 2008). However, few investigators have examined how male songbirds with single-song repertoires vary their singing behavior or the characteristics of their songs during the breeding season and in different behavioral contexts.

Male Indigo Buntings (Passerina cyanea) have a repertoire of one song type or theme (Payne 2006), and little is known about how their singing behavior varies during the breeding season and in different social contexts (Thompson 1972, Shiozvit 1975). We examined the effects of breeding stage and behavioral context on their singing rates and singing behavior to better understand (1) the possible functions of singing by male Indigo Buntings, and (2) how males with a single-song repertoire might vary their singing behavior to convey different information.

METHODS

We studied Indigo Buntings from 26 April to 20 August 2004 and 19 May to 5 June 2005 at the Central Kentucky Wildlife Management Area, 17 km southeast of Richmond, Madison County, Kentucky, USA. Male buntings were observed and recorded in 2004, and playback experiments were conducted in 2005. The study area consisted primarily of wooded edges, scattered trees, and fields in early stages of succession. Male buntings were captured using playback of conspecific songs to lure them into mist nets. Captured buntings were banded with a U.S. Geological Survey aluminum band plus a unique combination of three colored plastic bands to aid in individual recognition. Male age (second-year [SY] or after-second-year [ASY]) was assigned using plumage differences (Pyle 1997, Payne 2006).

 Territory boundaries were delineated by monitoring movements of focal males and noting
locations of interactions with conspecifics. Focal individuals were observed and recorded 2–3 times per week during observation periods of 20–30 min. All observations were conducted during the period from just after sunrise to 1100 hrs (EDT) when singing rates of Indigo Buntings are relatively constant (Thompson 1972). Inclement weather may influence singing behavior so buntings were not observed when it was raining. The date, time, and focal bird’s identity were noted on tape prior to each session. Recordings were made using a Sony (TCM-50DV) cassette recorder with a Sennheiser shotgun microphone (Model ME 88), typically at a distance of 10–30 m from focal males.

All songs of focal males were recorded during each observation period and the breeding stage was noted. Songs were categorized during each observation, as: (1) spontaneous advertising (no conspecific males heard or observed), (2) long-range interaction, where a conspecific male was singing in an adjacent or distant territory ≥50 m away, and (3) short-range interaction, where a conspecific male was singing <50 m away. Focal male songs were classified as long- and short-range up to 1 min after a conspecific was last heard singing.

We divided the breeding season into six stages: (1) pre-pairing (no female present on male’s territory), (2) nest building (period of nest construction by the female), (3) egg-laying (from the day the first egg was laid to the day the penultimate egg of a clutch was laid), (4) incubation (from the day the last egg was laid to the day before first egg hatched), (5) nestling (from the day the first egg hatched to the day before young fledged), and (6) post-fledging (from the day the young leave the nest to the time when fledglings leave male’s territory). Female buntings frequently produce two broods during the breeding season and often began new nests several days after young from a previous nest fledged. Thus, the post-fledging period ended when a female began building a new nest.

An attempt was made to locate and monitor all nests in the territories of focal males to identify breeding stages. Nests were located by observing movements of females during nest building and nestling provisioning, and by searching likely nest sites in focal territories. Nests were found at several stages and we, at times, backdated to ascertain the dates of breeding stages. We used the following durations for backdating: 8 (first nest of the season) or 2 (later nests) days for nest building, 1 day for each egg in a clutch for egg laying, 12 days for incubation, and 9 days for the nestling period (Bradley 1948, Payne 2006).

Playback experiments were conducted in 2005 in territories of focal males (n = 14) to further examine the possible effect of male-male interaction on the singing behavior of male Indigo Buntings. All songs used for the playback experiments were taken from commercially-available recordings (Common Birds and Their Songs, Houghton Mifflin Company; More Birding by Ear—Eastern/Central, Houghton Mifflin Company, Boston, MA, USA). Three tapes, each with songs of a different male, were used in the experiments (Tape 1 means: song length = 1.8 sec, number of figures = 4.3, number of phrases = 5.3; Tape 2 means: song length = 2.9 sec, number of figures = 12.5, number of phrases = 7.5; Tape 3 means: song length = 2.8 sec, number of figures = 14.7, number of phrases = 9.3; definitions of figure and phrase are below). Tapes 1, 2, and 3 had three, four, and three different versions of each male’s song, respectively. Male buntings on all three tapes sang at a rate of four songs/min. Recordings of males singing at higher rates would have increased the probability of the songs of focal males overlapping those on the recordings, making subsequent song analysis more difficult. A speaker was placed near the center of the focal male’s territory to simulate singing by an intruding male during each experiment. Each experiment consisted of a 3-min pre-playback period and a 6-min playback/post-playback period (with songs played back for 3 min and observations continuing for an additional 3 min after playback ended).

All songs recorded during each observation period were analyzed. Characteristics of songs measured included song duration, number of figures (“a sound which produces a single, complete, and distinct impression uninterrupted by silence greater than two centiseconds”; Shiovitz 1975:133), and the number of phrases (“a subdivision of a song based upon recognizable groups of sequential figures”; Shiovitz 1975:133; Fig. 1). In addition, we noted if songs had “squeaky” notes added or were uttered at higher than normal volume during the playback experiments. High-frequency “squeaky” notes are occasionally inserted between phrases in songs of male Indigo Buntings during territorial disputes (Emlen 1972, Thompson 1972, Margo-
liash et al. 1994). Song volume was subjectively categorized as either normal or high volume. We attempted to maintain a constant distance from focal males during playback experiments to permit better estimation of song volume. Recordings of the songs of focal males were subsequently analyzed using sound-analysis software (Raven Version 1.2.1, Cornell Laboratory of Ornithology, Ithaca, NY, USA).

Possible variation in characteristics of songs of male Indigo Buntings with male age, breeding stage, and behavioral context were examined using repeated measures analysis of variance with Student-Newman-Keuls (SNK) post-hoc tests to examine possible differences among means. All analyses were conducted using the Statistical Analysis System (SAS Institute 1999). All values are presented as mean ± standard error. Mean values were calculated using the means for each focal male to avoid bias due to different sample sizes.

RESULTS

We found no differences in characteristics of songs of SY and ASY male Indigo Buntings (song duration, number of figures, and number of phrases; all $P \geq 0.17$). Thus, songs of all males (SY and ASY) were combined for subsequent analyses.

All male Indigo Buntings ($n = 15$) in our study had a repertoire of a single song type. Mean song duration was $2.30 \pm 0.13$ sec and the mean number of figures per song was $9.95 \pm 0.51$. The mean number of phrases per song was $6.15 \pm 0.46$.

Songs of male buntings exhibited both intra-(Fig. 2) and inter-individual (Fig. 3) variation. Each male had a typical song that included a series of figures (phrases), usually paired, and usually uttered in the same order. The number of figures in each phrase occasionally varied, and figures (phrases) typically used later in songs were often omitted (Fig. 2).

Songs of some males (5 of 15, 33%) were unique and shared few or no song figures with other males. Males in adjacent territories typically shared some and, at times, all of the figures used in their songs and formed song neighborhoods where males used either the same or similar song figures (10 of 15, 67%; Fig. 4). One SY male in our study altered his song shortly after arriving in the study area (Fig. 5).

Effects of Breeding Stage and Natural Interactions on Singing Behavior.—Singing rates (songs/min) of male Indigo Buntings varied significantly among breeding stages ($F_{5,45} = 15.1$, $P < 0.001$) with rates highest during the pre-pairing stage (SNK test, $P < 0.05$; Fig. 6). Singing rates during the other breeding stages (nest-building, egg-laying, incubation, nestling, and post-fledging) did not differ (SNK test, $P > 0.05$; Fig. 6).

FIG. 1. Spectrograph of a typical song of a male Indigo Bunting showing the terminology used.
FIG. 2. Spectrographs illustrating the typical variation that exists in the single song of a male Indigo Bunting.
FIG. 3. Spectrographs illustrating the typical variation among songs of different male Indigo Buntings.
FIG. 4. Spectrographs illustrating the close matching of songs of several neighboring male Indigo Buntings in a song neighborhood.
Differences in the mean duration of songs uttered by male Indigo Buntings during different breeding stages approached significance ($F_{5,31} = 2.2, P = 0.075$) with longer songs during the nest-building period (Fig. 7). Songs were shorter in duration during post-fledging and pre-pairing periods than during other breeding stages (Fig. 7).

Differences among breeding stages in the mean number of figures ($F_{5,31} = 2.1, P = 0.099$) and phrases ($F_{5,31} = 2.1, P = 0.094$) per song also approached significance with more figures and phrases per song during nest-building and egg-laying stages and fewer during post-fledging and pre-pairing stages (Fig. 8). None of the characteristics of songs of male buntings, including duration and number of figures and phrases per song differed among behavioral contexts (short-range interaction, long-range interaction, or spontaneous singing; $P \geq 0.24$).

Effects of Song Playback on Singing Behavior.—We compared singing behavior of male Indigo Buntings prior to presentation of the stimulus (pre-playback period) to that during and after presentation of the stimulus (playback and post-playback periods combined). Singing rates (songs/min) differed ($F_{1,10} = 8.3, P = 0.013$) between periods with higher rates during the

FIG. 5. Spectrographs of two songs uttered by a second-year (SY) Indigo Bunting male illustrating song switching. The first song was used immediately after arrival on his territory. Several days later, the second song incorporated figures and phrases from those of a neighboring male.

FIG. 6. Mean singing rates ($\pm SE$) of male Indigo Buntings during different breeding stages.

FIG. 7. The mean duration of songs ($\pm SE$) uttered by male Indigo Buntings during different breeding stages.
playback and post-playback periods (\(\bar{x} = 4.4 \pm 0.4\) songs/min) than during the pre-playback period (\(\bar{x} = 2.9 \pm 0.6\) songs/min). The characteristics of songs also differed between periods with longer songs (\(F_{1,10} = 6.4, P = 0.03\)) that included more figures (\(F_{1,10} = 6.6, P = 0.028\)) and phrases (\(F_{1,10} = 5.0, P = 0.049\)) uttered during and after playback than before. Male buntings also uttered a significantly higher percentage (\(F_{1,10} = 6.3, P = 0.026\)) of high-volume songs during the post-presentation period (\(\bar{x}\) duration = 2.6 ± 1.0 sec; \(\bar{x}\) number of figures = 11.4 ± 0.1; \(\bar{x}\) number of phrases = 6.8 ± 0.2) than prior to playback (\(\bar{x}\) duration = 2.0 ± 0.1 sec; \(\bar{x}\) number of figures = 8.8 ± 0.4; \(\bar{x}\) number of phrases = 5.5 ± 0.2). Male buntings also uttered a significantly higher percentage (\(F_{1,10} = 3.7\)) than the pre-presentation period (none uttered). Comparison of pre- and post-presentation periods revealed no difference in use of songs including high-frequency ‘squeaky’ notes (\(F_{1,10} = 0.02, P = 0.9\)).

**DISCUSSION**

**Song Matching.**—All male Indigo Buntings in our study had a repertoire of one song type. Songs of some male buntings were unique, as also noted by previous investigators (Thompson 1970, Payne et al. 1988). Most males with adjacent territories in our study shared some, if not all, of the figures in their songs with conspecifics, and formed song neighborhoods where males in adjacent territories used the same or similar song figures. Song neighborhoods have been reported in other populations of Indigo Buntings (Thompson 1970, Payne and Westneat 1988). Song neighborhoods may develop because incorporating figures used by resident males into their songs may be beneficial for young male buntings with SY males that song match more likely to successfully acquire and defend a territory, acquire a mate, and fledge young (Payne 1982, 1983).

**Song Function.**—Our results indicate singing by male Indigo Buntings functions in mate attraction with singing rates declining significantly after pairing. Thompson (1972) also reported male Indigo Buntings sang more songs per bout and more bouts/hr when unmated. Previous studies suggest male singing rates represent a performance-related trait under positive sexual selection (Gil and Gahr 2002) that can influence mate choice and timing of mate acquisition (Alatalo et al. 1990, Hoi-Leitner et al. 1995). Otter et al. (1997) reported that singing rates represented accurate signals of male quality in Black-capped Chickadees (Poecile atricapillus). Singing rates of male buntings and males of other species of songbirds (e.g., Albrecht and Oring 1995, Ritchison 1995, Balsby 2000) decline after pairing. Thus, high singing rates prior to pairing may provide females with information concerning male status (paired or not) and their quality.

Male Indigo Buntings in our study continued singing after pairing, but at lower rates. Singing by male buntings, both before and after pairing, as for males of many species of songbirds (e.g., Krebs et al. 1978, Nowicki et al. 1998), is likely important in territorial defense. Male Indigo Buntings typically arrive in breeding areas ~1–2 weeks before females (Payne 2006; GR, pers. obs.) and establish breeding territories. During this period, and throughout our study, males were at times observed counter-singing with neighboring males and chasing conspecifics near territory boundaries while singing; males responded to playback by increasing their singing rates. These observations indicate that singing by male Indigo Buntings has an important role in establishing and defending territories.

Singing rates of male Indigo Buntings in our study were lowest during the fertile periods of their mates (nest-building and egg-laying periods) and remained relatively low during the incubation, nestling, and post-fledging periods. Some investigators have suggested singing may be important for stimulating female reproductive cycles (Hinde and Steel 1976) or guarding mates (Møller 1988). Singing by male Indigo Buntings does not appear to serve these functions because singing rates in our study were lowest during female fertile periods. Males of most songbird species do not sing or sing at low rates during the fertile periods of their mates (Gil et al. 1999).
Song Characteristics.—Songs of male Indigo Buntings in our study tended to be shorter prior to pairing and were generally longer in duration after pairing. In addition, bunting songs were significantly longer during and after playback than during the pre-playback period. These results suggest male Indigo Buntings may use shorter songs to attract females, and longer songs to convey aggression during male-male interactions. Although females in some species appear to prefer males that sing longer songs (e.g., White-throated Sparrows, Zonotrichia albicollis; Wasserman and Ciglino 1991), females in other species prefer males that sing at faster rates (e.g., European Pied Flycatcher, Ficedula hypoleuca; Gottlander 1987, Alatalo et al. 1990). If mate choice decisions by female Indigo Buntings are influenced by singing rates, then one possible explanation for the tendency of males to sing shorter songs prior to pairing is that such songs allow males to sing at higher rates (i.e., more songs per unit time). In addition, however, given that longer songs appear to convey an increased tendency for aggression, male buntings may also sing shorter songs prior to pairing to signal their non-aggressive intentions to potential mates. Similarly, Staicer (1996) suggested that male Adelaide’s Warblers (Dendroica adelaidae) may use songs with characteristics that convey less aggression (‘appeasing songs’) during interactions with females.

Male buntings in our study often added additional phrases to their songs during encounters with other males, both in response to playback and when chasing conspecifics. Emlen (1972) noted that buntings used ‘lengthened’ songs during agonistic encounters, and Saunders (1929:48) witnessed ‘male Indigo Buntings chasing each other about from tree to tree, and both of them singing prolonged songs in flight.’ In addition, Shiovitz (1975) found that playback of long variations of songs elicited stronger responses by male buntings than shorter variations. Shiovitz (1975) also suggested the first few figures of the songs of male buntings likely functioned as a ‘sign on’ in gaining the attention of conspecifics, whereas the remainder of the song seemed to convey aggression. Thus, male Indigo Buntings appear to increase song duration to convey aggression, and perhaps the likelihood of interacting, during intrasexual encounters. Males of other species also appear to use longer songs to convey an increased likelihood of aggression during intrasexual encounters (e.g., McGregor and Horn 1992, Balsby and Dabelsteen 2001, Leitao et al. 2006, Lattin and Ritchison 2009).

We found male Indigo Buntings at times added ‘squeaky notes’ to songs and sang with increased volume during male-male interactions. Thompson (1972) also indicated male Indigo Buntings inserted high-frequency (about 9 kHz), ‘squeaky’ notes into songs when an intruding male was present in a territory. Emlen (1972) noted that male buntings at times added high-pitched ‘squeak’ notes when responding aggressively to playback of conspecific songs. These results suggest male buntings alter the characteristics of their single song to convey an increased likelihood of aggression, i.e., singing longer, louder songs that at times include ‘squeaky’ notes. In further support of this hypothesis, male buntings in our study at times inserted high-frequency ‘squeaky notes’ into songs during territorial chases with conspecifics and uttered songs at higher than normal volume when countersinging at territory boundaries (MDB and GR, pers. obs.). Changes in characteristics of songs during intrasexual encounters have also been reported in other species of songbirds. For example, male Barn Swallows (Hirundo rustica) emphasize ‘rattles’ in their songs during aggressive encounters, indicating that ‘rattles’ are an important component of competitive interactions between males (Galeotti et al. 1997). Similarly, American Pipits (Anthus rubescens) incorporate ‘snarr’ notes, a rasping element with a broad frequency range, into their songs during territorial disputes (Rehsteiner et al. 1998).

Our results suggest the single song type of male Indigo Buntings serves several functions, including mate attraction and territory defense. In addition, male buntings vary song rates and song duration during the breeding season and in different behavioral contexts, appearing to use shorter songs uttered at high rates to attract mates and longer songs to convey aggression during male-male interactions.

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