

INTRA- AND INTERSEXUAL FUNCTIONS OF SINGING BY MALE BLUE GROSBEAKS: THE ROLE OF WITHIN-SONG VARIATION

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ABSTRACT.—Songs of individual male Blue Grosbeaks (*Passerina caerulea*) typically begin with the same combination of elements, but the sequence and number of elements in the latter portion of songs vary. We examined the possible functions of within-song variation in Blue Grosbeaks at the Blue Grass Army Depot near Richmond, Kentucky, USA from 15 April to 31 July 2007. We examined singing rates and song characteristics of second-year (SY; $n = 6$) and after-second-year (ASY; $n = 14$) males, and conducted playback experiments ($n = 15$) to identify the possible function of variation in song length. Male Blue Grosbeaks sang at highest rates prior to pairing, maintained relatively high singing rates during the post-pairing/pre-nesting and nest-building/egg-laying stages, and sang at lower rates during the incubation, nestling, and fledgling stages. These results suggest high singing rates are important in attracting mates and establishing territories, and lower singing rates may result from trade-offs associated with parental care. Males used longer songs during aggressive encounters with conspecifics and responded more aggressively to playback of longer songs. This suggests songs containing more elements signal increased aggression. Within-song variation may be an important way to vary song meaning for male Blue Grosbeaks, and perhaps other males in species with a single song type but repertoires of several different song elements. Received 13 February 2009. Accepted 17 June 2009.

Singing by male songbirds serves a variety of functions, ranging from establishing territories and attracting mates (Smith 1991) to distracting predators (Ritchison 1991), communicating with young (Beecher 1990), coordinating nest exchanges with mates (Smith 1988), and informing females about threat of predation (Johnson and Kermott 1991). The way male songbirds use song to convey different messages varies among species. Most male songbirds have repertoires of several different songs (Catchpole and Slater 1995) and may use different song types in different contexts. For example, Dark-eyed Juncos (*Junco hyemalis*) have two acoustically and structurally different song types, “short-range” songs for communicating with females and “long-range” songs for communicating with other males (Titus 1998). Similarly, many wood warblers have repertoires that include two distinct types of songs that are used in different social and environmental contexts (Spector 1991, Byers 1995).

Male songbirds in some species exhibit another level of song complexity by varying the way they sing, such as repeating or deleting certain song elements in subsequent renditions of a particular song type (Podos et al. 1992). Leitão et al. (2006) compared responses of both male and female

Common Chaffinches (*Fringilla coelebs*) to songs of equal duration that varied in number of trill phrases; they found both males and females exhibited a stronger response to songs with more phrases in the trill. Males in many other species exhibit similar within-song variation, but little is known about the role this variation may have in communication with conspecifics.

Each male Blue Grosbeak (*Passerina caerulea*) has a single song type that consists of a sequence of rapidly ascending and descending notes or elements. Songs usually begin with the same combination of elements with variation introduced by rearranging and adding elements in the second half of the song (Ingold 1993, Ballentine et al. 2003). Our objective was to examine the possible functions of this within-song variation using both observational and experimental approaches. Specifically, we examined song length (number of elements used), element repertoire, and song rate during different breeding stages and in different aggressive contexts. We also investigated potential differences in within-song variation between second-year (SY) and after-second-year (ASY) male Blue Grosbeaks, as young often sing differently than older birds, especially during their first breeding season (White and Mooney 1999).

METHODS

Study Area and Identification of Focal Males.—We studied Blue Grosbeaks from 15 April to 31 July 2007 at the Blue Grass Army Depot, 8 km south of Richmond, Madison County, Kentucky,

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USA (37° 40' N, 84° 13' W). We captured male grosbeaks ($n = 11$) and banded them with a unique combination of colored leg bands and a numbered aluminum USGS band to allow individual identification of focal birds. We were also able to identify males individually that were not captured (6 ASY and 3 SY) using territory locations, distinctive song features, and, in the case of SYs, distinctive plumage. All focal males ($n = 20$) were identified as SY or ASY based on plumage (Ingold 1993). We delineated territories by plotting the location of focal males and male-male interactions on maps of the study area.

Song Recording.—Focal males were observed (with few exceptions) once a week during 20–60 min observation periods. All songs of focal males were recorded using a tape recorder (Marantz PMD-201, Kanagawa, Japan; Sony TCM-50DV, San Diego, CA, USA) and directional microphone (Sennheiser ME-88, Wennebostel, Germany). All observations and recordings were made beginning 30 min before sunrise and continuing until ~1200 hrs EST. We did not observe males on days when it was raining or when winds exceeded 25 kph. Some males disappeared during the breeding season, presumably because they either failed to attract a mate or did not manage to breed successfully. We used observational data from these males until the date they disappeared. We used ~60 hrs of recorded song to measure song rate, element repertoire, and song length.

Categorization of Breeding Stages.—We noted the date, time, and, if known, nesting stage during each observation period. Nesting stages were categorized as: (1) pre-pairing (no female present on territory), (2) post-pairing/pre-nesting (beginning the day a male obtained a mate and continuing until nest building began), (3) nest-building/egg-laying (female present, signs of nest building such as female carrying grass in beak), (4) incubation (female incubating eggs in nest), (5) nestling (male and female carrying food to young), (6) post-fledging (young out of nest, but still present in the territory), or (7) unknown. We located nests by observing the behavior of the resident pair (e.g., nest building or carrying food to nestlings) and searching likely sites within each territory. Located nests were checked at least twice weekly.

We found nests at different stages. Thus, backdating was often necessary to identify the start and duration of earlier stages. We used the

duration of nesting stages provided by Ingold (1993) with a nest building period of 3 days, an egg-laying period of either 4 or 5 days (depending on clutch size), an incubation period of 11 days, and a nestling period of 10 days.

Categorization of Aggressive Contexts.—We noted the behavior of focal males during each observation period including all movements and any interactions with conspecifics. Each song from recording sessions was categorized as: (1) spontaneous advertising (no conspecific males heard or observed), (2) long-range countersinging where a conspecific male was singing in an adjacent or distant territory ≥ 50 m distant, (3) short-range countersinging where a conspecific male was singing < 50 m distant, often with chasing or fighting behavior, and (4) post-aggressive singing, any songs heard up to 3 min after a short-range encounter. We classified focal male songs as long- and short-range countersinging up to 1 min after a conspecific was last heard singing.

Playback Experiments.—We used playback experiments to examine if males responded more aggressively to songs containing more elements. Playback experiments were conducted from 30 min after sunrise through 1100 hrs during 7 to 29 July 2007. Most male Blue Grosbeaks during this period were occupied with feeding nestlings and fledglings, and spent less time singing, but were still defending territories and responding aggressively to intruding conspecifics (CRL, pers. obs.). We used a different song for each playback experiment to avoid pseudoreplication (Kroodsma 1989). Recordings of songs were obtained from the Borror Laboratory of Bioacoustics at Ohio State University and came from different areas within the breeding range of Blue Grosbeaks. We used Raven software (Cornell Laboratory of Ornithology, Ithaca, NY, USA) to create short (3–4 elements), normal length (8–10 elements), and long (23–27 elements) songs to test the effects of song length on responses of male Blue Grosbeaks. Short songs were created by cutting songs after the third or fourth element, normal songs were left intact, and long songs were created by repeating the last six elements until the appropriate length was reached. Male Blue Grosbeaks generate long songs in a similar way. The geographic origin of songs could potentially influence response, but songs used in our experiments were generated from randomly selected songs from different locations and, there-

fore, any effect would likely have been similar for each type (short, normal, and long) of song.

We placed flagging at 5, 10, 15, and 20-m intervals radiating out in the four cardinal directions from where we placed the playback speaker several days before each playback experiment to permit better estimates of the distance of focal birds from the speaker. We broadcast songs from within each focal bird's territory. We placed the speaker 35 m from known nest sites and at least 35 m inside a bird's territorial boundary when nest location was not known. We chose playback locations in part for habitat characteristics with the speaker placed in an open area with a mix of grasses, shrubs, and trees within 20 m to provide possible perches for focal males. Songs were played using a directional speaker (Model SME-AFS, Saul Mineroff Electronics, Elmont, NY, USA) placed on a 0.38-m high platform and connected to a portable cassette player. We played songs during all playback experiments at a volume approximately twice that of a typical Blue Grosbeak song to facilitate detection.

Each male Blue Grosbeak in the playback experiments ($n = 15$) was tested with short, normal length, and long songs. Each test consisted of a 3-min pre-playback silent period as a control, a 3-min bout of song with 10-sec pauses between each song, and a 3-min post-playback silent period. We maintained the same pause length between songs (whether short, normal length or long), because song rate can be an important signal of aggression in some bird species (e.g., Hyman 2003). Therefore, there were more short songs, slightly fewer normal length songs, and still fewer long songs during the 3-min playback period. We cannot exclude the possibility that male Blue Grosbeaks may have been responding to the number of songs in a playback period, or the amount of song relative to the amount of silence, rather than to song length.

We noted the location of the focal male every 15 sec during each period (pre-playback, playback, and post-playback). This allowed us to estimate mean distance of the male from the playback speaker during each period, as well as closest approach to the speaker. We also noted the number of flights, number of chip calls, and number of songs, and all vocal responses from focal males were tape-recorded. We randomly assigned the order of the three playback experiments in each territory and separated tests by at

least 2 days. Males on adjacent territories were not tested on the same day.

Song Analysis.—We analyzed recorded Blue Grosbeak songs from observations and playback experiments using Raven software. We counted the number of elements and number of unique elements in each song when song quality permitted. "Elements" were defined following Ballentine et al. (2003) as the smallest independent units produced by each male separated by periods of silence >50 msec, and typically made up of single notes.

We noted all element types used by the focal male in each observation period to ascertain if previously undetected element types had been used. We were generally able to identify most of a male's element repertoire after a single observation period; subsequent observations typically added few "new" elements to a male's repertoire. We assumed we had sampled a male's complete element repertoire when a plot of total elements in a male's repertoire versus observation period reached an asymptote. Four ASY males were excluded from analysis because we had too few observation periods to completely sample their element repertoires.

Statistical Analysis.—We observed focal individuals repeatedly during the breeding season. Possible variation in singing rates of male Blue Grosbeaks among breeding stages and characteristics of songs among breeding stages and different behavioral contexts were examined using repeated measures analysis of variance. Each individual was included as an independent random variable in a mixed-model analysis. Responses of males to playback of songs of different length were also compared using repeated measures analysis of variance. Variables were checked for normality and homoscedasticity prior to these analyses, and transformed when necessary. We used a Wilcoxon test to compare the mean element repertoires of ASY and SY males. All analyses were conducted using the Statistical Analysis System (SAS Institute 1999). Values are presented as means \pm SE.

RESULTS

Element Repertoire Size.—ASY male Blue Grosbeaks had larger element repertoires than SY males ($Z = 2.2$, $P = 0.032$). The mean number of elements in the repertoires of male Blue Grosbeaks was 19.9 ± 0.6 (range = 15–22)

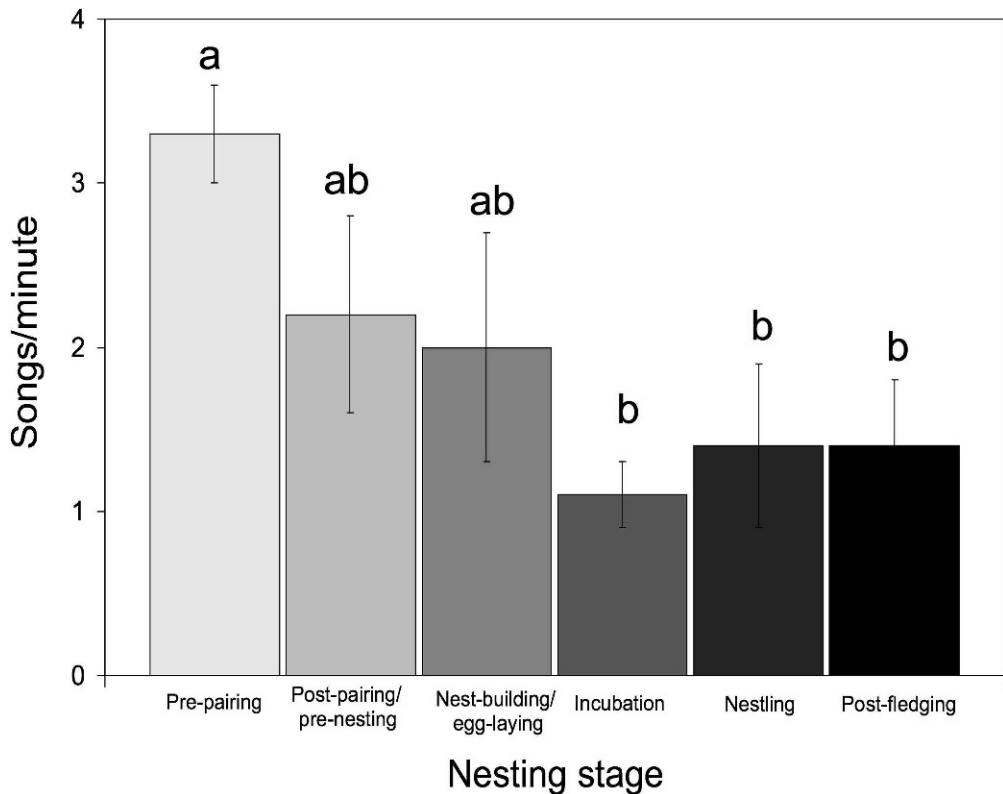


FIG. 1. Singing rates (mean \pm SE) of male Blue Grosbeaks ($n = 20$) varied among nesting stages. Bars with the same letter above them indicate similarity between groups ($\alpha = 0.05$).

for ASY males ($n = 10$) and 16.2 ± 1.2 (range = 13–21) for SY males ($n = 6$).

Song Variation at Different Breeding Stages.—Singing rates varied among nesting stages ($F_{5,19} = 7.7$, $P = 0.003$) with males singing at the highest rates during the pre-pairing period (Fig. 1). Singing rates decreased after pairing and were lowest during the incubation stage. We found no interaction between individual and nesting stage ($P = 0.79$); all males exhibited the same trends regardless of age class. A *post-hoc* test revealed that singing rates during pre-pairing were significantly higher (Tukey's test; $P < 0.05$) than during the incubation, nestling, and fledgling stages. The mean number of elements per song did not differ among nesting stages for either SY ($F_{1,1} = 0.9$, $P = 0.52$) or ASY ($F_{4,7} = 2.9$, $P = 0.32$) males.

Song Variation in Different Aggressive Contexts.—Most male Blue Grosbeak songs recorded were uttered spontaneously (5,685 songs, 85%; n

= 20 males). Fewer songs were uttered during countersinging with a distant neighbor (652 songs, 10%; $n = 19$ males), close-range singing (182 songs, 3%; $n = 12$ males), and post-aggressive singing (138 songs, 2%; $n = 10$ males). The mean number of elements per song varied among intrasexual contexts ($F_{3,33} = 144.9$, $P < 0.001$; Fig. 2) and between SY and ASY males ($F_{1,19} = 83.3$, $P < 0.001$). There was a significant interaction between age and intrasexual context ($F = 14.9$, $P < 0.001$). The number of elements per song for ASY males increased in increasingly aggressive contexts ($F_{3,25} = 8.3$, $P < 0.001$) with a mean of 12.7 ± 0.1 during spontaneous singing, 14.6 ± 0.2 during long-range countersinging, 19.0 ± 0.7 during short-range countersinging, and 15.9 ± 0.3 during post-aggression singing. The mean number of elements per song for SY males did not differ among intrasexual contexts ($F_{3,8} = 1.4$, $P = 0.32$).

Playback Experiments.—Male Blue Grosbeaks ($n = 15$) during the playback and post-playback

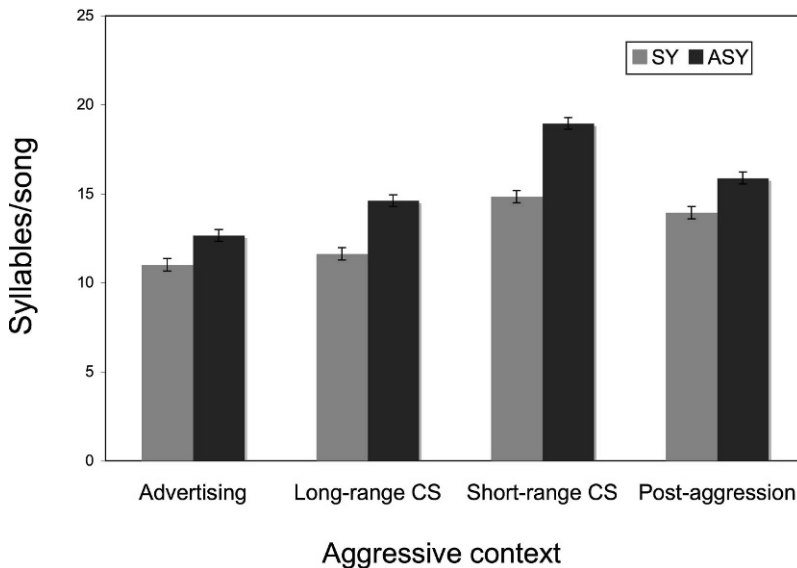


FIG. 2. The number of elements (mean \pm SE) in songs of male Blue Grosbeaks ($n = 20$) increased in increasingly aggressive contexts.

periods approached the speaker significantly more in response to long songs than in response to short and normal length songs. The mean distance of males from the speaker was also significantly closer during playback of long songs (Tables 1, 2). Focal males during the post-playback period also sang more songs in response to playback of long songs than to playback of short and normal length songs (Table 2).

DISCUSSION

Song Rate.—Male Blue Grosbeaks sang at the highest rates before pairing, maintained relatively high singing rates during the post-pairing/pre-nesting and nest-building/egg-laying stages, and sang at lower rates during incubation, nestling, and fledgling stages. This pattern is similar to that reported for several other species, including Great Reed Warblers (*Acrocephalus arundinaceus*) (Catchpole 1973),

TABLE 1. Responses (mean \pm SE) of male Blue Grosbeaks ($n = 15$) during playback at the Blue Grass Army Depot, Madison County, Kentucky, July 2007^a.

| | Short songs | Normal length songs | Long songs | Statistics |
|---|---------------------------------|---------------------------------|----------------------------------|-----------------------------|
| Distance of closest approach to speaker (m) | 25.1 \pm 5.7 ($n = 10$) | 33.9 \pm 3.8 ($n = 14$) | 15.3 \pm 4.2 ($n = 12$) | $F_{2,19} = 5.8, P = 0.011$ |
| Number of flights | 1.4 \pm 0.4 ($n = 14$) | 1.4 \pm 0.6 ($n = 15$) | 2.0 \pm 0.5 ($n = 14$) | $F_{2,26} = 0.51, P = 0.61$ |
| Number of 'chip' calls | 3.9 \pm 1.9 ($n = 14$) | 9.8 \pm 6.3 ($n = 15$) | 4.7 \pm 3.6 ($n = 14$) | $F_{2,26} = 1.0, P = 0.38$ |
| Number of songs | 2.6 \pm 1.2 ($n = 14$) | 2.3 \pm 0.6 ($n = 15$) | 3.1 \pm 1.1 ($n = 14$) | $F_{2,26} = 0.2, P = 0.86$ |
| Number of elements/song | 13.5 \pm 1.2 ($n = 4$) | 10.5 \pm 0.5 ($n = 2$) | 16.0 \pm 2.1 ($n = 6$) | $F_{2,1} = 0.03, P = 0.97$ |
| Time spent <50 m from speaker (sec) | 87.0 \pm 17.7 ($n = 10$) | 83.6 \pm 19.6 ($n = 14$) | 103.8 \pm 16.9 ($n = 12$) | $F_{2,19} = 0.2, P = 0.86$ |
| Distance from speaker (m) | 26.4 \pm 4.5 ($n = 9$) | 31.4 \pm 3.0 ($n = 11$) | 15.0 \pm 2.9 ($n = 11$) | $F_{2,14} = 5.8, P = 0.015$ |

^a Not all males responded or were observed during each period of each playback experiment (sample sizes in parentheses).

TABLE 2. Responses (mean \pm SE) of male Blue Grosbeaks ($n = 15$) during the post-playback period at the Blue Grass Army Depot, Madison County, Kentucky, July 2007^a.

| | Short songs | Normal length songs | Long songs | Statistics |
|---|----------------------------------|----------------------------------|----------------------------------|-----------------------------|
| Distance of closest approach to speaker (m) | 33.2 \pm 5.1 ($n = 13$) | 30.1 \pm 3.7 ($n = 14$) | 15.1 \pm 3.8 ($n = 14$) | $F_{2,24} = 7.5, P = 0.003$ |
| Number of flights | 0.6 \pm 0.2 ($n = 14$) | 0.9 \pm 0.2 ($n = 15$) | 1.0 \pm 0.3 ($n = 14$) | $F_{2,26} = 0.4, P = 0.65$ |
| Number of 'chip' calls | 1.9 \pm 1.2 ($n = 14$) | 11.1 \pm 6.0 ($n = 15$) | 10.5 \pm 6.8 ($n = 14$) | $F_{2,26} = 1.4, P = 0.27$ |
| Number of songs | 5.6 \pm 1.5 ($n = 14$) | 3.1 \pm 1.0 ($n = 15$) | 8.4 \pm 1.4 ($n = 14$) | $F_{2,26} = 4.4, P = 0.023$ |
| Number of elements/song | 13.4 \pm 1.8 ($n = 7$) | 19.5 \pm 7.5 ($n = 4$) | 16.5 \pm 2.0 ($n = 10$) | $F_{2,7} = 1.9, P = 0.22$ |
| Time spent <50 m from speaker (sec) | 108.5 \pm 22.5 ($n = 13$) | 113.0 \pm 20.1 ($n = 15$) | 153.2 \pm 15.6 ($n = 14$) | $F_{2,25} = 2.0, P = 0.16$ |
| Distance from speaker (m) | 29.9 \pm 5.2 ($n = 10$) | 26.5 \pm 1.9 ($n = 11$) | 15.0 \pm 2.4 ($n = 13$) | $F_{2,17} = 5.8, P = 0.012$ |

^a Not all males responded or were observed during each period of each playback experiment (sample sizes in parentheses).

Marsh Warblers (*A. palustris*) (Kelsey 1989), Northern Mockingbirds (*Mimus polyglottos*) (Logan 1983), and Eastern Bluebirds (*Sialia sialis*) (Huntsman and Ritchison 2002). Several investigators have suggested high singing rates are important for attracting females (Krebs et al. 1981, Cuthill and Hindmarsh 1985, Huntsman and Ritchison 2002), perhaps because a high singing rate makes it easier for unpaired females to find males.

Singing rates may also represent an honest signal of male quality (Vehrencamp 2000). Singing requires complex patterns of muscular contraction (Suthers et al. 1999), but there is little evidence that a high singing rate represents a significant energetic expense (Gil and Gahr 2002). High singing rates could be costly and an honest signal of quality if males have to trade off between time spent singing and time spent foraging. For example, Thomas et al. (2003) found that male European Robins (*Erithacus rubecula*) gained less mass when they sang more. High singing rates may, therefore, indicate that a male is good at foraging, or possesses a high-quality territory with ample food resources (Radesater et al. 1987, Radesater and Jakobsson 1989, Alatalo et al. 1990).

Singing rates of male Blue Grosbeaks in our study remained relatively high after pairing before and during the period when females were fertile (the post-pairing/pre-nesting and nest-building/egg-laying stages). Ballentine et al. (2003) also found that singing rates of male Blue Grosbeaks were higher during than after their mates' fertile period. These results suggest singing may be used

to stimulate females, either in terms of reproductive physiology, reproductive behavior, or both, as reported in other species (Nowicki and Searcy 2004). These results are also consistent with the fertility announcement hypothesis (Møller 1991) with males singing at higher rates to announce their mate's fertility and simultaneously advertise their ability to guard her.

Singing rates of male Blue Grosbeaks decreased after pairing, but males continued to sing during incubation, nestling, and fledgling stages. Blue Grosbeaks exhibit biparental care (Ingold 1993), and males may have to trade off during nestling and fledgling stages between time spent provisioning young and time spent singing. Investigators have found decreased singing rates after egg laying in several species, including Redwings (*Turdus iliacus*) (Lampe and Espmark 1987), Sedge (*Acrocephalus schoenobaenus*) and Eurasian Reed (*A. scirpaceus*) warblers (Catchpole 1973), and Northern Mockingbirds (Logan 1983). Male Blue Grosbeaks may sing primarily for territory defense during these later stages of the breeding cycle, and, perhaps, to communicate with mates and fledged young, as reported for other species (Ritchison 1983, Lind et al. 1996).

Song Length.—We found no variation in the mean number of elements per song during different breeding stages, but male Blue Grosbeaks used longer songs with more elements in more aggressive contexts and also responded more aggressively to playback of longer songs. Balsby and Dabelsteen (2001) reported male Common Whitethroats (*Sylvia communis*) re-

sponded more strongly to playback of longer songs than shorter songs, regardless of whether long songs were composed of a small repertoire of repeating elements or a larger repertoire with fewer repeats. McGregor and Horn (1992) reported a significant positive correlation between song length (the number of repeated phrases) and strength of response to playback by male Great Tits (*Parus major*).

Longer songs could function as a signal of increased aggression through a deliberate attempt to overlap the songs of a rival. Song overlapping is an important agonistic signal in a number of bird species, including Great Tits (McGregor et al. 1992), European Robins (Dabelsteen et al. 1997), and Common Nightingales (*Luscinia megarhynchos*) (Naguib 1999), and is used not just by singing males but also by eavesdropping females and other males to assess male quality and motivation (Peake et al. 2001, Mennill et al. 2002).

Differences Between SY and ASY Males.—ASY male Blue Grosbeaks generally had larger element repertoires and sang longer songs than SY males. Similar differences in the singing behavior of second year and older males have been reported for a number of other species (Eens et al. 1992, Espmark and Lampe 1993, O'Loughlen and Rothstein 1993, Cucco and Malacarne 1999). An increase in size of song repertoires with age is a widespread phenomenon (McGregor and Krebs 1989), although most studies have focused on species with multiple song repertoires rather than element repertoires.

The shorter songs of SY male Blue Grosbeaks may represent a mechanism for avoiding aggression. Older male (ASY) Blue Grosbeaks use longer songs in aggressive contexts to signal an increased likelihood of interacting. Therefore, the shorter songs of SY males, both when singing spontaneously and during interactions with conspecific males, may be less likely to elicit aggressive responses.

ACKNOWLEDGMENTS

We thank Charles Elliott, Robert Frederick, Nicholas Santangelo, and two anonymous reviewers for helpful suggestions on this manuscript. We also thank Doug Mott, Ian Horn, Michelle Carder, Sarah Martin, Jason Courter, and Louise Peppe for help with fieldwork, and the Borror Laboratory of Bioacoustics at Ohio State University for access to their library of Blue Grosbeak recordings. Financial support was provided by the Kentucky Academy of Science and the Kentucky Society of Natural History.

Additional funding and equipment was provided by Eastern Kentucky University.

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