

Singing Behavior of Male Henslow's Sparrows (*Ammodramus henslowii*)

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Descriptive studies of species with single-song repertoires may provide information potentially useful in understanding the factors involved in the evolution of multisong repertoires. We studied the singing behavior of Henslow's sparrows (*Ammodramus henslowii*) from April 21 to July 25, 2000 in west-central Kentucky. To examine song function and how males use single-song repertoires in intraspecific communication, we measured variation in singing rates within and among males, and compared the characteristics of songs sung in different behavioral contexts. Singing rates declined after pairing, suggesting that songs play a role in mate attraction. Male Henslow's sparrows continued singing after pairing, although at lower rates, suggesting that singing serves functions other than mate attraction. Males were observed countersinging with neighboring males and sang after chasing trespassing males from their territories, suggesting that singing also functions in territory defense. Characteristics of the songs of male Henslow's sparrows did not vary among behavioral contexts. However, we found evidence of both intra- and interindividual variation in the songs of male Henslow's sparrows, suggesting that differences between males in either fine-scale song performance or vocal performance (or both) may provide conspecifics with information about individual quality. Additional study is needed to determine the extent to which the songs of male Henslow's sparrows, and those of other songbirds with single-song repertoires, exhibit characteristics, and differences, that might serve as indicators of individual quality.

<i>Context</i>	<i>Henslow's sparrow</i>	<i>Mate attraction</i>	<i>Single-song repertoire</i>
<i>Singing</i>	<i>Song rate</i>		

The functions of passerine song may be influenced by song structure and complexity. Males with multisong repertoires may be able to communicate with conspecifics in ways that males with single-song repertoires cannot. For example, males with multisong repertoires can potentially communicate different messages, such as probability of attacking or fleeing, by changing song types or by varying the rate at which new songs are uttered (Johnson & Kermott, 1991). Ritchison (1995) noted that male common yellowthroats (*Geothlypis trichas*) have repertoires of two song types—a flight song and a

perch song—and use flight songs to warn mates of the approach of potential predators. Similarly, male great reed warblers (*Acrocephalus arundinaceus*) have two song types, with short songs used as a territorial signal and long songs to attract mates (Catchpole, 1983). The ability to communicate in such ways may have been a factor in the evolution of multisong repertoires, and may explain, in part, why males in so many species of passerines possess such repertoires (MacDougall-Shackleton, 1997).

In addition to enhanced communication, repertoire size appears to be under strong directional sexual

selection in some songbirds (Gil & Gahr, 2002). However, such selection is clearly not universal because about 30% of songbird species have single-song repertoires (Beecher & Brenowitz, 2005). One factor potentially contributing to small repertoires is that larger repertoires are costly (e.g., in terms of the volume of underlying brain mechanisms involved in song production and perception). However, evidence that repertoires are costly is limited (Gil & Gahr, 2002), and Nealen (2005) noted that synaptic densities in the song control nuclei of male zebra finches (*Taeniopygia guttata*), with one-song repertoires, and male Carolina wrens (*Thryothorus ludovicianus*), with large song repertoires, were similar. Thus, for songbirds with single-song repertoires, selection pressures likely focus on other aspects of song (Beecher & Brenowitz, 2005).

Aspects of song that might be under selection pressure include singing rates, song sharing, fine-scale song performance, and vocal performance. If singing is costly in terms of a male's energy balance, then singing rates may be positively correlated with male quality because time spent singing reduces time available for foraging. Because time and energy costs of singing are likely unrelated to repertoire size, female preferences would similarly be unrelated to repertoire size (Nowicki & Searcy, 2005). Males that share songs with neighbors may achieve greater reproductive success than those that do not (Payne & Payne, 1997), and such sharing does not require a large repertoire (Beecher & Brenowitz, 2005). Fine-scale song performance, or reduced variability among successive songs, may be an indicator of male quality used by females when selecting mates or extra-pair matings (Byers, 2007). Vocal performance may also be an indicator of quality, in that some songs might be more difficult to sing than others, and receivers might potentially use difficult songs to evaluate the singer's quality (Nowicki & Searcy, 2005, Cardoso, Awell, Ketterson, and Price, 2007).

Male Henslow's sparrows (*Ammodramus henslowii*) have a single-song repertoire, but little is known about the structure and function of their simple "tse-zlik" songs (Herkert, Vickery, & Kroodsmas, 2002). To permit testing of the various hypotheses concerning selection pressures that might favor single-song repertoires and to better understand the function(s) of singing by males in songbirds with small repertoires, additional descriptive studies are needed. Thus, the objective of our study was to

examine the singing behavior of male Henslow's sparrows and, specifically, to examine (1) variation in singing rates of male Henslow's sparrows throughout the breeding cycle in an attempt to better understand the possible functions of singing, and (2) variation among males and behavioral contexts in the characteristics of songs to determine how males use their single song repertoires in intraspecific communication.

Methods

Study Species

Henslow's sparrows inhabit fields and meadows characterized by tall grass and standing dead vegetation (Hyde, 1939). These socially monogamous sparrows breed in loose colonies, and males arrive in breeding areas before females to establish territories (Graber, 1968). Only females build nests and incubate eggs. Both parents feed nestlings, and young fledge about 9 days after hatching (Graber, 1968). Some pairs raise two or three broods in a breeding season (Monroe, 2001). Territorial males usually sing while perched on top of grass or dead vegetation.

Study Sites and General Methods

From April 21 to July 25, 2000, male Henslow's sparrows were studied at Green River Lake State Park ($N=7$ males) (16 km south of Campbellsville, Taylor County, Kentucky) and at the Peabody Wildlife Management Area ($N=12$ males) (10 km west of Central City, Muhlenberg County, Kentucky). The two study areas are about 120 km apart. Males were captured using mist nets and fitted with a numbered aluminum band plus a unique combination of color bands to permit individual recognition. Territory boundaries were delineated by following males and observing frequently used areas and singing perches.

Recordings were made using Sony TCM-59V cassette recorders and shotgun microphones (Model ME-66, Sennheiser Electronic Corp., Old Lyme, CT; Model SMEATR55, Saul Mineroff Electronics, Elmont, NY). Each focal male was observed and recorded at least twice each week, typically from a distance of 5–10 m. Observation periods were 15–30 min in duration and during the period from sunrise through 1100 h. An observation period began when

an observer entered a focal male's territory, regardless of whether the bird's location was known. The breeding cycle was divided into five stages: prepairing (all days prior to the day pairing occurred; males were considered paired when consistently observed on territories with females), preincubation (from the day of pairing to the day before the last egg was laid), incubation (from the day the last egg was laid to the day before the first egg hatched), nestling (from the day the first egg hatched to the day before young fledged), and postfledging (from the first day young left the nest until 10 days after) (Johnson & Kermott, 1991).

Nesting stages (preincubation, incubation, and nestling) were determined by checking nests at least every 3 days. Because it was not always possible to assign a nesting stage on the day of an observation, nesting stages were sometimes determined by back-dating from the day young fledged. For back-dating, we used the duration of nest stages provided by Graber (1968), with 4 days for nest building, 11 for incubation, and 8 for the nestling period.

Nests were located by observing the behavior (such as carrying nesting material and food) of focal birds and searching likely areas for nests. If a focal bird's nest was not located, the behavior of focal males and their mates was used to assign nesting stages. For example, adults carrying nesting material were categorized as being in the preincubation period. For some observation periods, the focal bird's nesting stage was not known and those observations were not used in song rate analyses.

During each observation period, the focal male's behavior when singing was categorized as: spontaneous (no other males singing), close singing (singing by one or more conspecific males in territories adjacent to the focal male, but more than 10 m between birds), distant singing (singing by one or more conspecific males in territories not adjacent to the focal male), or direct interaction (a conspecific male located within 10 m of the focal male).

To examine variation in singing rates throughout the breeding cycle, the number of songs heard during each recording session (songs/minute) was noted. In addition, songs ($N=412$) of male Henslow's sparrows ($N=17$) were analyzed using a DSP SonaGraph (Model 5500; Kay Elemetrics Corp., Lincoln Park, NJ) to examine possible variation in song characteristics among individual males, behavioral contexts, and nesting stages. Characteristics of songs

measured (all by C.L. using on-screen cursors) included song duration (seconds), dominant frequency, and the number of phrases. A phrase was defined as a group of notes for which the interphrase interval was greater than the interval between notes within a phrase and a note was defined as a sound that produced a continuous line on a sonagram (Fig. 1).

Possible differences in singing rates among nesting stages and in the characteristics of songs among behavioral contexts and nesting stages were examined using repeated measures analysis of variance (SAS Institute, 1999). One-way analysis of variance (ANOVA) was used to examine variation in song characteristics among males, and Student-Newman-Keuls (SNK) post hoc tests assessed which means differed. Because the number of songs recorded from different individuals varied (range: 5–51; SD: 24), descriptive statistics were calculated using mean values for each individual. Such analysis eliminates bias that might result from pooling different sized samples (Leger & Didrichsons, 1994). Values are presented as means \pm 1 SE.

Results

Each male Henslow's sparrow in our study ($N=17$) had a repertoire of one song type. The mean duration of songs was 0.286 ± 0.005 s (range: 0.26–0.34 s; $N=17$ males), and the mean number of phrases per song was 5.12 ± 0.09 (range: 4.61–5.70; $N=17$ males). The mean dominant frequency was 5.20 ± 0.17 kHz ($N=17$ males), with a range of 4.19–6.74 kHz.

Song characteristics sometimes varied within songs of individual males. For example, examination of the songs ($N=51$) of one male revealed that the number of phrases per song varied between four and five, and the phrase with the highest power also varied among songs. Similar variation in the number of phrases per song and the phrase with the dominant frequency was noted in the songs of 10 of the 17 males observed.

Similarities in song and phrase morphology were apparent among males (Fig. 1). Songs of most male Henslow's sparrows ($N=15$ of 17) shared a series of five phrases, with two phrases at a higher frequency than the remaining three phrases (Fig. 1). However, we found temporal and morphological variation in these phrases among males. For example, the last two phrases in the song of male 2B were higher in

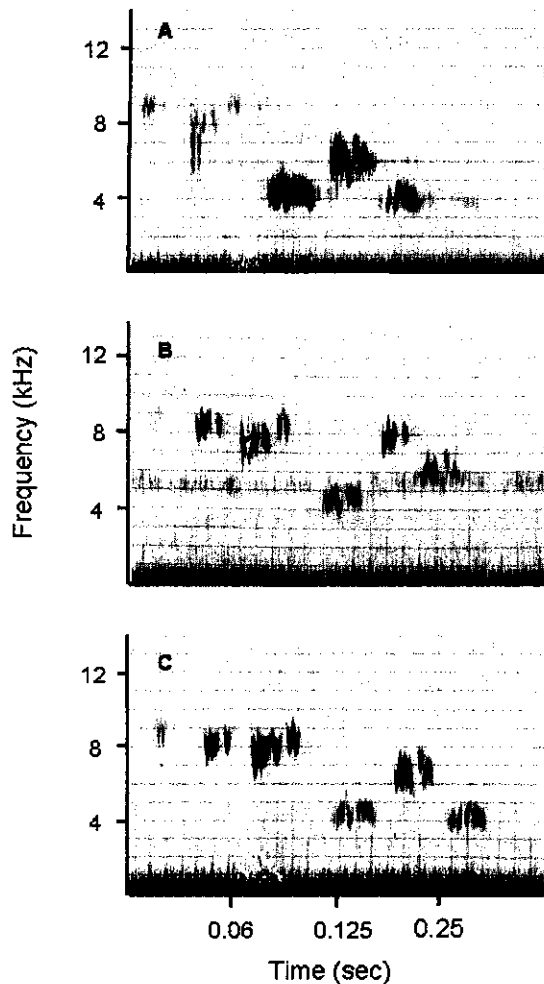


Figure 1. The songs of three male Henslow's sparrows illustrating similarities in song and phrase morphology and the components of songs. Song A consists of five phrases, whereas songs B and C consist of six phrases. For song B, notice that the last phrase is at a higher frequency than in songs A and C and, in addition, the penultimate phrase exhibits less frequency modulation than the same phrases in songs A and C.

frequency than the same two phrases in the song of males 2A and 2C, respectively, and the interval between phrases four and five (within the five shared phrases) in the song of male 2B was greater than that of the same interval in the song of males 2A. Song morphology also differed among males because the songs of some males included either one or two phrases prior to the five common phrases. No songs included phrases after the five common phrases.

Singing rates varied significantly among nesting stages [$F(4, 34) = 6.3$, $p = 0.007$], with rates higher during the prepairing stage than the preincubation, nestling, and postfledgling stages (Tukey's test, $p < 0.05$) (Fig. 2). Singing rates during the prepairing and incubation stages did not differ (Tukey's test, $p > 0.05$). We found no significant interaction between bird and nesting stage ($F = 1.3$, $p = 0.17$).

Sample sizes were too small to examine possible variation in song characteristics among nesting stages, with only one male observed and recorded during all five nesting stages. Therefore, the preincubation, incubation, nestling, and postfledgling stages were combined and the characteristics of songs recorded during these stages (i.e., nesting) were compared to those recorded during the prepairing (or prenesting) stage. Mean song duration did not differ between the prenesting and nesting stages [$F(1, 7) = 2.52$, $p = 0.16$]. Similarly, we found no difference between prenesting and nesting stages in either the dominant frequency or the mean number of phrases per song.

Characteristics of the songs of male Henslow's sparrows did not vary among close, distant, or spontaneous contexts (repeated measures ANOVA, $p > 0.07$ for all variables). However, among individual males, song duration [$F(16, 395) = 34.2$, $p < 0.0001$], dominant frequency [$F(16, 395) = 16.1$, $p < 0.0001$], and number of phrases per song [$F(16, 395) = 15.2$, $p < 0.0001$] differed significantly.

Discussion

All male Henslow's sparrows in our study had a repertoire of one song type, and the songs of most males shared the same series of five phrases. Thus, one potential advantage of a single-song repertoire is that it enhances song sharing that, in turn, facilitates communication with neighbors and enhances reproductive success (Beecher, Campbell, & Nordby, 2000; Payne & Payne, 1997). In support of this hypothesis, the song of one male Henslow's sparrow in our study did not include the five phrases shared by other males and this atypical song sounded, to us, more like the "buzzy" song of a grasshopper sparrow (*Ammodramus savannarum*). The male singing this atypical song never paired and apparently abandoned his territory in mid-June (Leftwich, 2003).

Although our sample size is small, we found evidence of both intra- and interindividual variation in

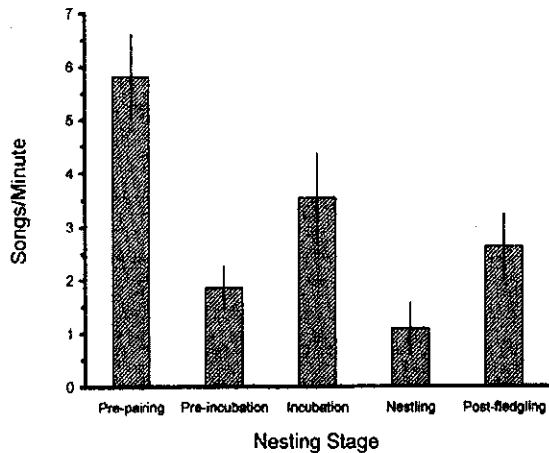


Figure 2. Singing rates of male Henslow's sparrows during the breeding season.

the songs of male Henslow's sparrows. Such variation suggests that differences between males in either fine-scale song performance or vocal performance (or both) may provide conspecifics with information about individual quality. Although the songs of Henslow's sparrows are among the shortest in duration of any songbird, our analysis revealed that their songs exhibited short interphrase intervals, phrases with rapid frequency modulation, and phrases that also varied in amplitude (with the initial phrases lower in volume and typically not even apparent to human listeners; hence, the incorrect references to their "tse-zlik" song, or two-phrase song rather than five-phrase song). Although short in duration, producing songs with such characteristics may be physiologically demanding. Similarly, Cardoso et al. (2007) found that songs of male dark-eyed juncos (*Junco hyemalis*) with short intervals between syllables and uttered with greater amplitude were apparently difficult to sing, and that juncos may be able to infer a male's quality by how well songs are performed. Additional study is needed, but the manner in which male Henslow's sparrows utter their short, but surprisingly complex, songs may, in support of the nutritional stress hypothesis (Nowicki, Peters, & Podos, 1998) and in lieu of a multisong repertoire, provide conspecifics with important information about male quality.

Singing rates of male Henslow's sparrows in our study declined significantly after pairing. Studies of several other species of passerines have also

revealed that singing rates decline after pairing. For example, Balsby (2000) found that singing rates of male whitethroats (*Sylvia communis*) declined after pairing and concluded that singing functioned primarily to attract females. Similarly, Ritchison (1995) found that singing rates of male common yellowthroats (*Geothlypis trichas*) declined after pairing and suggested that such results provided evidence that singing functions in mate attraction. Although not conclusive, a significant decrease in singing rates after pairing does provide strong circumstantial evidence that male song is used to attract females (Kroodsma & Byers, 1991). Thus, it seems likely that male Henslow's sparrows sing to attract females.

Continued singing by male Henslow's sparrows after pairing, although at lower rates, suggests functions other than mate attraction. Male Henslow's sparrows in our study often sang when neighboring males were singing. In addition, male Henslow's sparrows observed trespassing into adjacent territories were, upon discovery, immediately chased from neighboring territories by the resident male and, shortly thereafter, one or both males began to sing (Leftwich & Ritchison, unpublished observation). Such observations suggest that singing by male Henslow's sparrows functions in territory defense.

Singing by male Henslow's sparrows after pairing may also serve other functions. For example, singing may attract females for extra-pair copulations (perhaps a possible reason for the higher singing rates during the incubation period) or, during the nestling stage, serve to alert a female or nestlings to a possible nest visit (Johnson & Kermott, 1991; Ritchison, 1995). Singing during the postfledging period may permit communication with fledglings, and may be important in the song learning process of young males (Greig-Smith, 1982).

Songs of passerines exhibit much variation in duration (0.27–52.0 s; Read & Weary, 1992), with those of male Henslow's sparrows among the shortest reported. Short songs may be advantageous for male Henslow's sparrows because territories are small (0.3–0.7 ha; Burhans, 2002) and, in suitable habitat, densities of territorial males can be high. With numerous males nearby, short duration songs, with more "non-singing" time, may permit better monitoring of the singing and locations of other males. Such monitoring may be important for male

Henslow's sparrows because females do engage in extra-pair copulations (Graber, 1968).

In summary, our results suggest that singing by male Henslow's sparrows functions in both inter- and intrasexual communication. Their short, but surprisingly complex, songs may provide conspecifics with important information about male quality. In addition, the decline in singing rates after pairing and the use of song by males during territorial conflicts suggest that song functions in both mate attraction and territory defense. However, we found no evidence that male Henslow's sparrows vary the temporal or frequency characteristics of their songs to convey information to conspecifics.

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