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Conveying information with one song type: changes in dawn song performance correspond to different female breeding stages

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Many bird species participate in dawn singing, a behaviour categorized by intensive singing at dawn; however, many of these species deliver only one song type at dawn. While there are many proximate and ultimate hypotheses for why birds sing at dawn, little is known about whether males are able to vary one simple song to convey different information. We used autonomous acoustic recorders to record dawn songs of field sparrows and quantified three parameters of singing performance: 1) bout length, 2) song rate, and 3) song complexity. We found that males sang the longest dawn bouts during their mate’s fertile period, the highest song rates during the post-fertile period, and the most complex songs during the pre-fertile period. The change in dawn singing behaviour with their mate’s breeding stage suggest the purpose of dawn song may be context dependent. Our results demonstrate that male field sparrows, while only having a single song type sung at dawn, may convey information for both intra- and intersexual purposes. While it is generally assumed that dawn song has a specific function, the variability in the duration, rate, and complexity of dawn song in field sparrows suggests that they are conveying different information and that dawn song likely has multiple functions.

Keywords: field sparrow; birdsong; dawn song; female fertility; song performance; song type

Introduction

Dawn singing in birds is characterized by a pronounced bout of singing activity, which often occurs 30–60 minutes before sunrise (Catchpole and Slater 2008). During this time, most birds will initially sing at exceptionally high rates, but as sunrise approaches, singing decreases in intensity, eventually ending completely with the commencement of their daily activities (Kroodsma 1971; Hutchinson et al. 1993; Liu and Kroodsma 2007). Despite the prevalence of dawn singing in birds and the numerous studies on this behaviour, the explanation for this distinct singing behaviour remains unclear (Staicer et al. 1996).

Several hypotheses describing the function and evolution of dawn singing have been proposed by Staicer et al. (1996). These hypotheses include proximate explanations, such as environmental (enhanced acoustic communication transmission and low predation risk) and intrinsic factors (hormone stimulation and circadian rhythms), and ultimate explanations related to social functions (i.e. intra- and intersexual functions). In most species, dawn song is considered primarily an intrasexual signal used in territory establishment/defence (Amrhein and Erne 2006; Liu and Kroodsma 2007) and mediating

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social relationships among male competitors via counter-singing (Foote et al. 2008; Sethi et al. 2011). In some species, however, dawn signing appears to have direct (i.e. used by male singers as a mate guarding strategy) (Mace 1987; Möller 1991; Welling et al. 1995), and indirect intersexual functions (i.e. allowing females to assess a male’s quality) (Otter et al. 1997; Gammon 2004; Poesel et al. 2006). Dawn singing may therefore be directed toward both males and females, and its expression may vary depending on the social context in which it is used (Kroodsma et al. 1989; Rodrigues 1996; Burt and Vehrencamp 2005).

Dawn singing behaviour can vary greatly among species; some species are highly vocal, whereas others vocalize infrequently or not at all (Berg et al. 2006). Among the species that sing at dawn, those with large repertoires deliver song types interchangeably (Kroodsma et al. 1989; Weary et al. 1991; Greig and Pruett-Jones 2008), or incorporate syllables rarely heard at other times of the day (Staicer et al. 2006). These qualitative and quantitative changes in their use of song appear to effectively convey non-redundant information (Lohr et al. 2013). In contrast, species with small repertoires, such as wood-warblers or emberizine sparrows that often possess two acoustically distinct song types (Nelson and Croner 1991; Weary et al. 1994; Price and Crawford 2013), use only one song at dawn, while the other song is sung during the day (Spector 1992). In these ‘small-repertoire’ species, it is unclear how single songs may convey information across different contexts of intra- and/or intersexual nature (Searcy et al. 2000).

One way a single song could convey different information is by varying the duration, rate, and complexity of the song. Studies have shown that changes in song performance, i.e. bout length, song rate, or song complexity play an important role in intra- and/or intersexual interactions (Ballentine et al. 2003; Ballentine 2009). For instance, studies have shown that bout length can be an honest advertisement of individual quality, as it reflects a male’s energetic condition (Cuthill and Macdonald 1990; Otter et al. 1997). Song rates can also be indicative of phenotypic and genetic quality due to its positive relationship with larger tarsi and genetic paternity (Murphy et al. 2008; Grunst and Grunst 2014). Similarly, song complexity has been suggested to be related to larger brains (Catchpole 1996), lower parasite loads (Buchanan et al. 1999; Pfaff et al. 2007), and better adrenocortical stress responses that regulate energy balance (Grunst and Grunst 2014). It is possible, therefore, that species that deliver a single song during dawn use song performance as a way to convey information; however, little is known about the variation in dawn song and how that variation may vary with context (e.g. the fertile status of their female).

We used autonomous acoustic recorders to examine the performance of the complex song (i.e. dawn song) in field sparrows (*Spizella pusilla*) during dawn and over the course of their mate’s breeding stages: pre-fertile, fertile, and post-fertile periods. Field sparrows sing only one song type at dawn, the ‘complex’ song, which is heard almost exclusively during dawn interactions and is thought to be used primarily in male–male counter-singing interactions (Nelson and Croner 1991) (Figure 1). Field sparrows also have a ‘simple’ song (Figure 1) that is delivered during the day and appears to primarily serve in mate attraction (Nelson and Croner 1991). We focused on investigating the following three characteristics of the complex song at dawn: 1) bout length (overall duration of dawn song), 2) song rate (maximum number of songs sung per minute), and 3) song complexity (defined through principle component analysis by using the number and types of syllables and song length) (Cardoso and Mota 2007). These characteristics were selected because, in some species, despite the song type they use, they often play a role in inter- and intra-sexual communication (Poesel et al. 2006; Murphy et al. 2008;
Grava et al. (2009). The dawn singing behaviour of field sparrows (which is similar to many other passerines) makes it an ideal species for examining how characteristics of dawn song (i.e. duration, rate, and complexity) may vary with social context (i.e. mate’s breeding stage).

Methods

Study area

This study was conducted between May 1st and August 15th of 2012–2014 at Kennekuk Cove Park, Vermilion County, IL, USA (40° 11.5' N, 87° 42.9' W). The vegetation of Kennekuk Cove Park is a mosaic of grassland patches surrounded by oak-hickory forest.

Acoustic sampling

This study was part of a larger project that mapped the territories of approximately 60 breeding male field sparrows each year from 2012–2014. Field sparrows are relatively common at this site, where they are migratory and multi-brooded (Celis-Murillo 2015). Territorial males were distributed across 12 grassland patches of varying sizes (3–9 ha). All male and female field sparrows were captured using mist-nets and marked with aluminium and coloured-plastic bands. Sex and age (when possible) were recorded for each individual. Of the 60 breeding males studied each year, we randomly selected four paired individual males to continuously record over the course of the breeding season. A total of 12 males were recorded from 2012 to 2014 using four Stereo Autonomous Acoustic Recording Units (SM2® – Wildlife Acoustics, Inc., Concord, MA). SM2 recorders were placed at the centre of a male’s territory from 1 May to 15 August and recorded daily and continuously from 04:00 am to 07:00 am. This schedule was selected to specifically capture periods of dawn singing activity and to account for twilight time variation occurring across the season. The termination of dawn song was
abrupt, and easily distinguished from the commencement of daytime singing. Post-hoc investigation of the data suggested that dawn singing (complex song) started up to 60 min before sunrise and stopped 5–10 min before sunrise. Field recordings always encompassed the dawn singing period and were made in stereo at 16 bits and 44.1 KHz and stored weekly in the laboratory. For each male and his mate, we monitored breeding activity every three days and determined the onset of each breeding stage (nest building, laying of eggs, and incubation of eggs). Breeding activity was later combined into more conservative fertility periods. Pre-fertile period was defined as the time when the male is courting the female and the female is building the nest, fertile period when the female is laying eggs, and post-fertile period when the female is incubating eggs or attending nestlings.

**Song measurements and analysis**

Despite collecting song recordings on a total of 12 individuals across the years, due to the quality of some recordings (low signal-to-noise ratio), we were only able to successfully quantify dawn singing performance for nine individual males, with one individual from 2012, four individuals from 2013, and four from 2014. We attempted to normalize our measurements for amplitude differences using $-24$ or $-16$ db thresholds following Podos (1997) and Zollinger et al. (2012). However, due to overlaps between songs from focal males and neighbouring males or the low quality of recordings, we measured dawn song characteristics via visual inspection using a spectrographic view in Audacity® 4.0. The difficulty of identifying our focal male in the recordings for an entire bout also contributed to our low sample size. We measured the following bioacoustics characteristics of dawn song: 1) dawn bout length, defined as the length of the entire bout of singing at dawn. Dawn bout length was determined as the time between the first complex song heard in the morning to the last complex song or when males stopped delivering complex songs for at least 3 min (Foote et al. 2008), 2) peak song rate, defined as the maximum observed rate (songs per minute) at which ten songs were delivered in succession, and 3) Song complexity, defined through a principal component analysis of song length, number of syllables, and syllable types within a song (Cardoso and Mota 2007) (Figure 1). For song complexity, we measured for every fifth songs, within a randomly selected section, until a total of 10 songs were evaluated. The first principal component factor explained 79% of the variation in song complexity, and therefore was taken as the song complexity score (eigenvalue = 2.36). For each of the nine individual males, measurements of dawn singing performance were obtained from four to six dawn bouts spread over the course of the breeding stages (4–6 observations per bird) ($n = 46$). The distribution of all dawn song characteristics did not deviate from normality (Kolmogorov–Smirnov test, $n = 46, 0.06 < P < 0.16$). We used general linear mixed models (PROC MIXED procedure, SAS® 9.3) to test the effect of breeding stage on each of the three characteristics of the dawn song. Dawn bout length, song rate, and song complexity were analysed separately and treated as response variables and breeding stages as independent variables. Male bird identity was treated as a random effect. We conducted a Bonferroni correction test to examine the differences among breeding stages. We also examined potential correlations among response variables using Pearson’s correlation test (PROC CORR procedure, SAS® 9.3). Due to our limited sample size, we could not account for the different years in our models. However, similar studies examining dawn vocal behaviour across breeding stages did not find any significant differences among years (Bruni and Foote 2014).
Results

Dawn bout length varied significantly with the breeding stage ($F = 3.59$, $df = 35$, $n = 46$, $P = 0.0382$) (Figure 2). Male field sparrows sang for significantly longer periods during their mate’s fertile period than during their mate’s post-fertile period ($P = 0.03$), while bout length did not significantly differ between pre-fertile and fertile periods ($P = 0.23$) and pre-fertile and post-fertile periods ($P = 0.86$). Peak song rate also varied significantly with breeding stage ($F = 3.79$, $df = 35$, $n = 46$, $P = 0.03$) (Figure 3). Male field sparrows sang at greater song rates during the post-fertile period than during the pre-fertile period ($P = 0.04$), while song rate among post-fertile and fertile periods ($P = 0.12$) (Figure 3) and pre-fertile and fertile periods were not different ($P = 1.00$). Song complexity varied across all three breeding stages ($F = 45.53$, $df = 35$, $n = 46$, $P < 0.01$) (Figure 4), with song complexity being greatest during the pre-fertile period, and greater than fertile

Figure 2. Dawn bout length (mean minutes ± SE) of male field sparrows over three breeding stages. 46 observations for dawn bout length ($n = 46$) were obtained from 9 individual males recorded in the years 2012–2014 in Kennekuk Cove Park, Vermilion County, IL.

Figure 3. Peak song rate (mean song rate ± SE) of male field sparrows over the three breeding stages. 46 observations for peak song rate ($n = 46$) were obtained from 9 individual males recorded in the years 2012–2014 in Kennekuk Cove Park, Vermilion County, IL.
and post-fertile periods ($P < 0.01$) and song complexity being significantly greater during fertile periods than post-fertile periods ($P < 0.01$). We also found a negative correlation between peak song rate and song complexity (Pearson’s correlation coefficient $= -0.64$, $n = 46$, $P < 0.01$).

**Discussion**

The duration, rate, and complexity of field sparrows’ complex song at dawn changes across their mates’ breeding stages. Males during the pre-fertile and fertile stages, a time when pairs are forming pair bonds, sang for longer periods (longer bouts) and used songs that were more complex than during the post-fertile stage. Once their mate was no longer fertile, males began singing at higher rates, possibly for territorial defence or to attract extra-pair mates. Our result highlight how a species that has one song type that is used at dawn can vary the duration, rate, and complexity of its song to potentially convey different information.

Male field sparrows increased their dawn bout length during the pre-fertile and fertile periods, suggesting that bout length could potentially have a role in intersexual communication. Singing for long periods requires more time and energy (Grava et al. 2009; but see Oberweger and Goller 2001), especially since songbirds do not feed at night and should thus be in a condition of energy deficit early in the morning (Hutchinson 2002). Consequently, increasing the duration of dawn bout at the expense of foraging opportunities may only be beneficial in a limited number of scenarios, such as the period when they are attracting a female and developing a pair bond. Because females are likely continually assessing the quality of males even after paring (Mace 1987), there may be a close relationship between singing as a courtship display during the pre-fertile period and as a mate guarding strategy during the fertile period. Increased singing activity during the fertile period might be directed toward other males and function as a mate guarding to deter potential intruders seeking extra-pair copulations (Møller 1991).
As might be expected, song complexity was negatively correlated with song rate. This was due to the inclusion of the song length variable in the song complexity analysis, and males with greater song complexity must have lower variability in song rate. Of the three song performance measures analysed, the most striking differences were found in song complexity, with songs being most complex in the pre-fertile period and least complex in the post fertile period. The pre-fertile (nest-building) period is an energetically and temporally expensive activity for both males and females (Mainwaring and Hartley 2013). Male field sparrows may utilize song complexity as a secondary, relatively inexpensive cue to attract and stimulate females, when singing longer bouts or at higher rates is more costly (Thomas and Cuthill 2002; Franz and Goller 2003). In other species, females exposed to more complex songs built nests faster and laid more eggs than those exposed to simpler songs (Kroodsma 1976; Okanoya 2012). Increased song complexity may also stimulate a physiological response in females to invest greater concentrations of testosterone in their eggs during the fertile period, as females could be assessing their mates’ quality and fine-tuning reproductive investment after a pair bond is already formed (Gil et al. 2004). Furthermore, the costs of greater song complexity may be a trade-off against other song characteristics, which would explain the decreased trend in song complexity over the course of the breeding stages. Mate guarding or territory defence may become progressively more important than mate stimulation after the pre-fertile period, and other forms of signalling such as singing for greater lengths of time or at higher rates might be more efficient in those situations.

In contrast to bout length and song complexity, males sang at the fastest rates during the post-fertile period. Increased song rates might be directed toward other males and likely functions in territorial defence. In other multi-brooded species, territory defence remains important throughout the breeding season (Kunc et al. 2005; Bruni and Foote 2014); because success in mate guarding and territory defence cannot be maximized simultaneously (Slagsvold et al. 1994), males might only increase their investment in territory defence through greater song rates when their mate is no longer fertile. Alternatively, males may also increase their song rates during the post-fertile period to attract extra-pair mates (Gil et al. 1999; Sexton et al. 2007); males may preferably endeavour to attract extra-pair mates when their females are no longer fertile (Møller 1991). Thus, as various trade-offs may be associated with dawn song performance throughout the breeding stages, individual males may utilize different singing strategies when attracting mates and defending territories or acquiring extra-pair mates.

Male field sparrows may only have a single song type at dawn, but they can change the duration, rate, and complexity of this song in ways that suggest that they are related to the fertile stage of their females. The use of song performance (duration, rate, and complexity of complex songs) may allow field sparrows to convey different information when needed. Specific dawn song characteristics might provide information on different aspects of male quality, with some characteristics potentially having a role in male–female communication (bout length and song complexity) and others in male–male communication (song rate). While other studies have shown that species that have large repertoires use their multiple song types interchangeably to convey information (Trillo and Vehrencamp 2005; Lohr et al. 2013), this study provides evidence that field sparrows, through changes in song performance, could potentially convey information even with a single song type. Future studies should experimentally test response patterns of males and females in the field to different complex song performances and under different social contexts.
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