



Nocturnal songs in a diurnal passerine: attracting mates or repelling intruders?



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We addressed the role of nocturnal singing in the diurnal field sparrow, *Spizella pusilla*. We were particularly interested in whether nocturnal song is used to repel intruders (intrasexual function) and/or to attract females seeking extrapair copulations (intersexual function). First, we used autonomous acoustic recording units (ARUs) and an automated detection and classification system to examine the associations of singing behaviour of mated field sparrows with social factors (fertility stage, presence of neighbour song and presence of intruder song). Second, using an automated radiotelemetry system (ARTS), autonomous acoustic recording units (ARUs) and automated playback systems, we conducted a nocturnal playback experiment to explore how mated male and female field sparrows respond to nocturnal songs at night and across prefertile, fertile and postfertile stages. We found that neighbours and intruder males tended to sing complex songs on the same nights when focal males sang. While not all focal males sang at night, all male birds (resident males, neighbours and intruders) that sang tended to sing according to the fertility periods of the resident male's female. Our playback experiment demonstrated that, although field sparrows usually slept and were inactive at night, they moved in response to nocturnal field sparrow songs more than to control stimuli (other species vocalizations). Interestingly, we found that males did not respond by singing or countersinging to field sparrow nocturnal songs (simulated intrusions). We also demonstrated that male activity responses were similar during the prefertile and postfertile stages, while females responded more during the prefertile and fertile stages than during the postfertile stage. Consequently, the nocturnal song in the field sparrow appears to play a role in extrapair mate attraction (intersexual function) more than in repelling intruders (intrasexual function). While nocturnal singing is an infrequent behaviour of most diurnal birds, it may be important in the mating system of these birds. © 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Nocturnal vocalizations are typically considered a characteristic exclusive to nocturnal birds. Nevertheless, recent evidence has shown that many diurnal birds also sing at night (Barclay, Leonard, & Friesen, 1985; Loughheed & Handford, 1989; Perrault, Lobert, Ehnes, & Foote, 2013). Studies suggest that singing at night may serve similar functions as diurnal song, such as attracting females (Amrhein, Korner, & Naguib, 2002; Roth, Sprau, Schmidt, Naguib, & Amrhein, 2009; Tyler & Green, 1996) and/or repelling intruder males (Luschi & del Seppia, 1996; Naguib, 1999). Although these

explanations are reasonable, they are based on a small subset of diurnal species with regular and well-developed nocturnal singing habits (corncrake, *Crex crex*: Tyler & Green, 1996; nightingale, *Luscinia megarhynchos*: Amrhein et al., 2002) and do not consider the many diurnal species that sing occasionally or rarely at night.

In a review of nocturnal singing in North American diurnal birds, La (2012) reported that out of 126 species included in the analysis, 52% were classified as regular nocturnal singers (singing 'frequently' and 'continuously'), 27% as occasional singers (sing infrequently) and 20% as rare singers (species that 'can' or 'may' sing at night). For the species that regularly sing at night, nocturnal singing might provide information regarding their location, identity, and potentially individual quality, supporting the hypotheses of mate attraction and/or repulsion of male intruders. However, for the species

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that only sing occasionally or rarely at night, the function of nocturnal songs remains unknown. These rare vocalizations may be ineffective at repelling intruders or attracting mates. A more parsimonious explanation for these rare nocturnal vocalizations may be an individual's reaction to a disturbance event, such as nest predation (as seen in some species; jays, *Aphelocoma coerulescens*: Carter, Legare, Breininger, & Oddy, 2007; peahens, *Pavo cristatus*: Yorzinski & Platt, 2012) or environmental factors, such as moonlight (York, Young, & Radford, 2014). However, recent work has demonstrated seasonal variation in the occurrence of nocturnal songs in the field sparrow, *Spizella pusilla*, a species that rarely sings at night (Celis-Murillo, Stodola, Pappadopoli, Burton, & Ward, 2016), potentially indicating a role of nocturnal singing in reproductive activities.

Although considered a relatively infrequent behaviour, nocturnal movements in search of extrapair mates have been documented in males and females of many species (e.g. Chiver, Stutchbury, & Morton, 2008; Pedersen, Dunn, & Whittingham, 2006). Studies of birds' nocturnal behaviour have shown that female nocturnal movements often coincide with night-time singing by males (e.g. Naguib, Altenkamp, & Griebmann, 2001), suggesting that nocturnal songs of territorial males may be used to attract extrapair females actively foraging and seeking extrapair copulations (intersexual function). Nocturnal singing may function to attract an extrapair female while the cover of darkness allows the female to leave her social mate's territory undetected, especially as females that are detected leaving a social mate's territory are often retaliated against (e.g. withholding parental care of young: Weatherhead, Montgomerie, Gibbs, & Boag, 1994; Westneat, 1988). In addition, if males are moving at night in search of extrapair females, rare nocturnal songs may serve as a means for territory holders to engage intruders and possibly dissuade them from being in their territory, an intrasexual function (Arcese, 1987). Furthermore, rare nocturnal songs may also let male intruders inform females about their presence and that they are seeking extrapair copulations, a mate attraction function during extrapair interactions.

The aim of our study was to address the functional role of nocturnal song in species that sing at night occasionally or rarely, particularly in the context of acquiring extrapair mates. We used the field sparrow as our study species because they sing during daylight hours and, despite spending most of the night sleeping and inactive (Slay, Ellison, Ribic, Smith, & Schmitz, 2012), they occasionally sing at night. Field sparrows sing two song types; 'complex' songs primarily serve an intrasexual function and they are sung almost exclusively at dawn, while 'simple' songs primarily serve an intersexual function and they are sung throughout the day (Nelson & Croner, 1991; Fig. 1). During the night, however, both songs are sung and appear to have strong seasonal patterns; simple songs reach their peak occurrence early in the season, coinciding with the arrival of females at the breeding site, whereas complex songs are most common later in the season, coinciding with the nest-building and egg-laying stages of most females (Celis-Murillo et al., 2016). Field sparrows only sing sporadically at night and deliver single songs, whereas during the day, they sing in long bouts or series of continuously repeated songs (Celis-Murillo et al., 2016).

We used descriptive and experimental approaches to address the functional role of nocturnal song in mated territorial field sparrows, particularly to explore whether nocturnal song has a role in repelling intruders (intrasexual function) and/or attracting females (intersexual function) during extrapair mating interactions. First, we used autonomous acoustic recording units (ARUs) and an automated detection and classification system to examine the associations of singing behaviour of mated field sparrows with social factors. Specifically, we explored whether fertility stage, presence

of neighbour song and presence of intruder song were reliable predictors of finding mated male field sparrows singing simple and complex songs at night. We expected that, if the primary role of nocturnal song is to repel intruders, then a male field sparrow's songs on a given night should be correlated with the occurrence of conspecifics (neighbours and/or intruders) singing near or within his territory on that night. Furthermore, if the primary role of nocturnal songs is to attract extrapair mates, then we would not expect to find males singing (or males countersinging) on the same night and we would expect singing to be more common after the fertile period of a male's social mate, when males are usually more inclined to seek extrapair mates. Second, using an automated radiotelemetry system (ARTS), ARUs and automated playback systems, we conducted a nocturnal playback experiment to explore how mated male and female field sparrows responded to nocturnal single songs at night and across pre-fertile, fertile and post-fertile stages. Although field sparrows are usually sleeping and inactive at night (Slay et al., 2012), if nocturnal single songs play a role in extrapair mating interactions (intersexual and/or intrasexual), simulated field sparrow songs at night should elicit responses in mated male and female sparrows, via singing or movement. We expected that, if nocturnal songs play a role in repelling intruders, then males should respond to simulated intruders' nocturnal songs through countersinging and movements, and that their response is likely to be greatest during their mate's fertile period. Alternatively, if nocturnal songs play a role in male–female interactions, then females should respond to simulated intruders by moving and their response should be strongest during their fertile period.

METHODS

Study Species and Location

The field sparrow is a diurnal, socially monogamous songbird that has sexually monomorphic plumage. It is migratory, breeds in Canada and the eastern United States, and winters in the southeastern United States (Carey, Burhans, & Nelson, 2008). The field sparrow breeding season last 10–12 weeks (Best, 1977). Most females arrive on the breeding grounds between 15 April and 15 May (10–20 days after males), and pair formation usually occurs within 2 days of their arrival (Best, 1977). Males tend to follow females during nest building; however, only females participate in nest construction and incubating eggs (Carey et al., 2008). Field sparrows engage in extrapair matings, with reports of at least 19% of offspring sired through extrapair mating (Petter, Miles, & White, 1990).

The study was conducted in Kennekuk Cove County Park, IL, U.S.A. (40°11.5'N, 87°42.9'W), composed of discreet grassland patches of varying sizes (2–10 ha) surrounded by oak–hickory forest. Each year three to eight field sparrows established territories in each of these grassland patches, creating spatially clumped aggregations of territories separated by forest patches (hereafter 'neighbourhoods'). In each of these neighbourhoods, individual males interacted with their neighbours daily via dawn singing behaviour (countersinging; Zhang, Celis-Murillo, & Ward, 2015). During this study, Kennekuk Park was closed to the public during the night, with no artificial light disturbing territorial birds.

Ethical Note

This project was carried out following ethical approval by the Institutional Animal Care and Use Committee of the University of Illinois (IACUC protocol number 10127) and in accordance with the United States Geological Survey (USGS Bird Banding Permit number 23277).

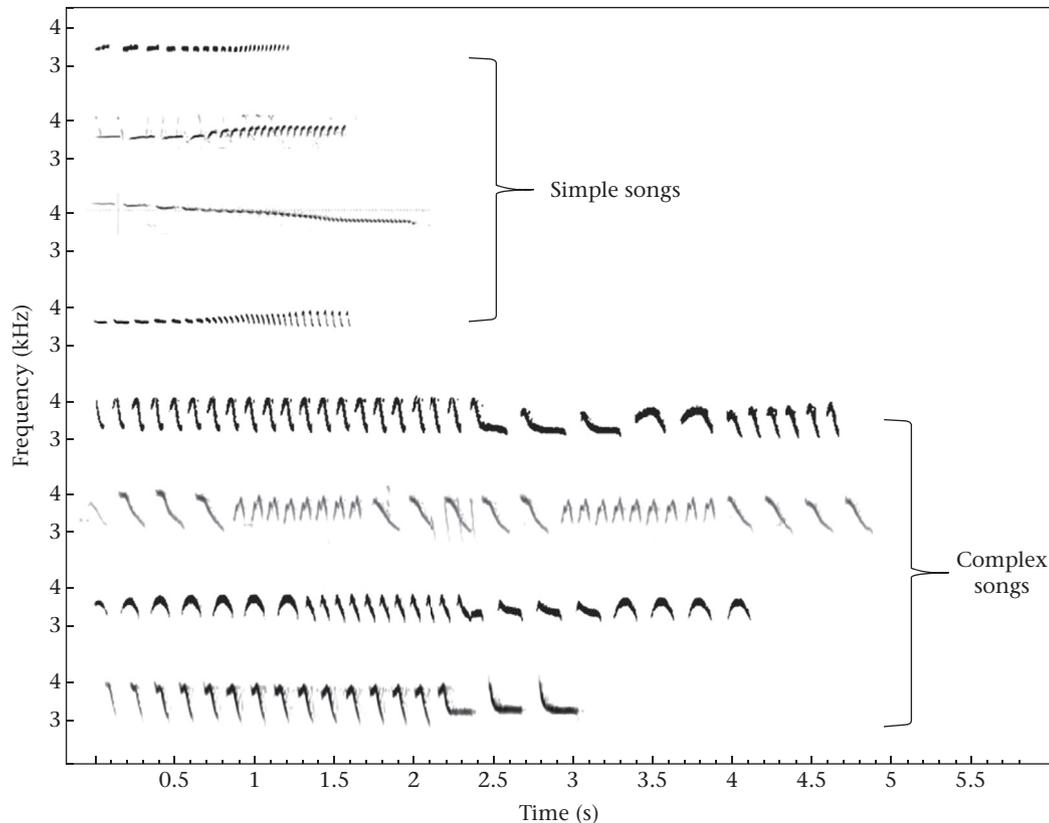


Figure 1. Spectrographic representation of differences in song characteristics (notes and syllables) among individual field sparrows. The figure shows four examples of simple songs and four examples of complex songs of four individuals. Data are from birds recorded in Kennekuk Cove Park, Vermilion County, IL, U.S.A. during the years 2012–2014.

General Field Methods

We studied 28 mated territorial field sparrows from April to July of 2012 and 2013; 11 males were studied in 2012 and 17 males were studied in 2013. Only one male was studied during both years. Each year, we used spot-mapping and behavioural observations at the beginning of the season to delineate the territories of males distributed among seven different neighbourhoods of varying size; these territories were also examined via behavioural observations throughout the breeding season, ensuring that territory boundaries were accurately estimated and did not change in size or shape. In each territory, we captured and banded male and female field sparrows using targeted mist netting. We banded individuals with unique-numbered USGS aluminium and coloured plastic leg bands. We recorded age (second year, SY, and after second year, ASY), sex and morphometric variables (tarsus, bill and wing length and mass) for all individuals. To age the birds, we used a combination of plumage characteristics (shape and wear of primary coverts, primaries and secondaries, following Pyle, 1997); however, we could not age 26% of our birds. We identified sex by observing the cloacal protuberance in males or brood patches in females. For each territorial male and its mate, we collected information on their reproductive behaviours (mating–not nesting, nest building, laying eggs, incubating, feeding nestlings and caring for fledglings). We combined breeding stages into prefertile (not nesting), fertile (nest building and laying eggs) and postfertile stages (incubating, feeding nestlings and caring for fledglings). We also monitored territory ownership and establishment date for each individual throughout the season. This helped us to ensure that ownership of territories was not changing through time. Territory switching appeared to be rare as we only found two individuals that switched territories to a

different neighbourhood during the study, and we omitted these individuals from analyses.

Recordings, detection, individual song variation and identification of individuals

Manual acoustic recordings. We manually recorded the songs of each individual territory holder in the population and over the 2 years of the study. We collected recordings at day using a combination of Telinga parabolic microphones (Telinga Microphones, Uppsala, Sweden), Wildtronic parabolic microphones (Wildtronic, LLC, Newton Falls, OH, U.S.A.) or Sennheiser MKH60 shotgun microphones (Sennheiser, Wedemark, Germany), and a Sound Devices 722 digital recorder (Sound Devices, LLC, Reedsburg, WI, U.S.A.) or a Sony M10 digital recorder (Sony, Tokyo, Japan) at 16 bits and 44.1 kHz.

Autonomous acoustic recordings. We used six stereo autonomous acoustic recording units (SM2, Wildlife Acoustics, Inc., Concord, MA, U.S.A.) to collect the nocturnal singing of field sparrows. We placed SM2 recorders at the centre of territories of males previously captured, banded and identified as paired. We rotated recorders throughout neighbourhoods to collect data on different males throughout the season. We set up the machines to record sound for 10 min periods every 30 min from 2100 to 1600 hours. Our field observations suggest that the recorders effectively recorded the male of the focal territory and between two and three neighbouring males (within about 100 m of the recorder).

Field sparrow song detection. Detailed information about automatic recognition and detection can be found in Celis-Murillo et al. (2016), but briefly, we automatically scanned the SM2 audio recordings to

find the occurrences of field sparrow songs using Songscope 4.1.3A software (Wildlife Acoustics, Inc.). We used manually collected high-quality recordings (of both simple and complex song) with low-level background noise and no overlapping sounds to construct Songscope recognizers for field sparrow simple and complex songs. The recognizer built for scanning for simple songs had a range of 2460–5000 Hz, 256-point fast Fourier transform (FFT) with an overlap of three-fourths to output the frequency spectrum, a maximum syllable length of 301 ms, a maximum syllable gap of 96 ms, a maximum song length of 4045 ms and a dynamic range of 20 dB. The recognizer for the complex song type had a range of 2375–8000 Hz, 256-point FFT with an overlap of three-fourths, a maximum syllable length of 308 ms, a maximum syllable gap of 100 ms, a maximum song length of 6400 ms and a dynamic range of 20 dB. This set-up provided accurate identification and detection data, allowing Songscope software to detect only high-quality signals (see Celis-Murillo et al., 2016, for further details about the validation procedure for this method).

Individual song variation and identification of individuals. To assess whether multiple songs came from the same individual, we compared variation within and between songs of focal field sparrows (Foote, Palazzi, & Mennill, 2012). We randomly selected up to 10 songs per individual from a large set of focal recordings collected in the study site. Our selection procedure resulted in 338 complex songs from 39 individuals (average \pm SD songs per individual: 8.6 ± 1.8) and 355 simple songs from 46 individuals (average \pm SD songs per individual: 7.7 ± 2.7). To test whether songs differed significantly between individuals, we compared each song against all other songs from our samples using the correlation tool in Raven 1.4 software (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). The correlation analysis was based on spectrograms (DFT size: 512; hop size: 13; overlap: 94.9), using a band-pass filter from 2 to 6 kHz, and linear power values from the spectrograms. We reduced effects of background noise, such as low-level wind and other nonfocal sounds, by setting the power level to 0 dB of any signal with an amplitude below -70 dB using the clipping function (Foote et al., 2012). Correlation values were standardized, resulting in values between 0 and 1 (with values of 1 indicating that two samples are identical). Before the analyses, we normalized all recordings to -1 dB using the software Audacity (<http://audacity.sourceforge.net>). We examined whether variation in songs within individuals was lower than variation in songs among individuals using analysis of similarities (ANOSIM) in the R package 'vegan' (version 2.0-10; Oksanen et al., 2013; R Development Core Team, 2008) using 10 000 permutations. The ANOSIM showed that both simple and complex song types were more similar within individuals than across individuals. Based on pairwise comparisons among individuals, the average correlation was $R = 0.8$ ($P = 0.00009$) for simple songs and $R = 0.9$ ($P = 0.00009$) for complex songs. We then catalogued all of the songs collected with our autonomous acoustic recorders as coming from a resident male, a neighbouring male, or an intruder male. 'Resident' refers to males holding a territory where an SM2 recorder was placed; 'neighbour' refers to males holding territories in the same grassland patch (i.e. same neighbourhood), and 'intruder' refers to males with territories in a spatially separated grassland patch (i.e. different neighbourhood). We could not identify 195 songs, as these songs were incomplete or their signal-to-noise ratio (audio quality) was too weak to assign an identity category. These unidentified songs were not included in the analyses.

Automated nocturnal playback experiments

Playback trials and stimuli. We created seven tracks (trials), each with three random stimuli: (1) a relatively long complex song; (2) a

relatively short complex song; and (3) a control song of either northern cardinal, *Cardinalis cardinalis*, or Carolina wren, *Thryothorus ludovicianus*. We used two different song lengths in our playback experiment because recent studies on other sparrow species have shown that song length variation may convey information about the aggressive motivation of individuals (Nelson & Poesel, 2012). The seven long complex songs (4–5 s long) and seven short complex songs (2–3 s long) were selected from our large collection of field sparrow songs. All songs were from different individual field sparrows within the state of Illinois, and not from the population of this study. We used complex song in the experiments because they are more common at night than simple songs, and we used single songs in the experiments to simulate the natural occurrence of field sparrow songs at night (Celis-Murillo et al., 2016). We used two different species as controls (five songs from different northern cardinals, and two songs from different Carolina wrens) because songs of these species also differ in length; however, we observed no difference in response and therefore we combined the controls in subsequent analyses. The whole trial lasted approximately 31 min and included 5 min of silence before and after each stimulus (i.e. song).

Playback procedure. We conducted nocturnal playback experiments from May to July 2014 to explore how mated male and female field sparrows would respond to nocturnal songs at night and across pre-fertile, fertile and post-fertile stages. We placed an automated playback system near the edge of the focal field sparrow territory to broadcast the stimuli. The automated playback system consisted of a speaker (model FoxPro NX4) connected to a digital timer switch (Sinotimer TM618-4) and a battery (model Power-sonic 12V PS-12120). We programmed the digital timer to randomly broadcast the tracks at 2300, 0000 or 0200 hours, broadcasting only one track per day to each subject individual. The playback volume of our stimuli was not measured in the field; however, we estimated a volume that resembled the volume (amplitude) of field sparrows singing at night within the field site. All playbacks used the same volume. Having programmable and automatic playback systems allowed us to simulate singing intruders while avoiding potential disturbance of sleeping birds. To explore whether the birds' responses changed across different fertility stages, we repeated the experiment to each individual on up to seven consecutive nights. The average number of playback trials per individual was five (range 1–7). Following Kroodsmma (1989), we never conducted more than one trial per pair per night. When we tested more than one pair per night, we made sure pairs were not neighbours and were not located within the same grassland patch.

Assessment of responses to playback. We measured male and female physical and vocal activity in response to the broadcasted stimuli. To investigate physical activity (movements) during playback experiments, we radiotagged eight mated males and 15 mated females (including 5 mated pairs) and used an automated radiotelemetry systems (ARTS, JBJC Corp., Fisher, IL, U.S.A.). We used radio transmitters weighing ~ 0.55 g (JBJC Corp.). This weight represented $\sim 5\%$ of birds' average mass (average mass of field sparrows = 12.0 g). We glued transmitters to birds' backs following Raim (1978). The adhesive method ensured that transmitters fell off birds after a few weeks, reducing stress and potential physiological impacts on birds. The ARTS was composed of four 12–14 m towers with autonomous radiotelemetry-receiving units located 400–950 m apart and strategically placed in the study area to collect data from each radiotagged bird of study (Fig. 2). Each tower and receiving unit was connected to an array of six three-element Yagi antennas (Nighthawk model, JBJC Corp.) attached to the top

of the towers. The six antennas were positioned at 0°, 60°, 120°, 180°, 240° and 300° to attain 360° of detection coverage. Receiving units collected up to three readings per minute per bird over the duration of the transmitter's battery life (24 ± 6 days). ARTS recorded the signal strength (dB), background noise (dB), pulse width (ms) and the pulse interval (ms) of each radio transmitter. To quantify movement, we investigated change in signal strength and bearing at the tower with the strongest signal strength.

We determined whether an individual moved or did not move within 5 min of the start of a stimulus (Fig. 3). We set a threshold of change in signal strength of 3.0 dB and a bearing change of 1.8° to determine a movement (Ward, Alessi, Benson, & Chiavacci, 2014; Ward, Sperry, & Weatherhead, 2013). These thresholds were developed from research on passerines in the same location using the same automated telemetry system (Ward et al., 2014, 2013). For further details on the automated telemetry techniques used in this study, see Kays et al. (2011), Staiger et al. (2013) and Ward et al. (2013). As a radiotagged bird moves, the orientation of its transmitter's antenna relative to the ARTS antenna changes, causing an increase or a decrease in the number of structures between the two antennas, and thus greater or lesser attenuation of the signal, respectively. With the subsequent change in signal strength and the ability to estimate a bearing from the tower, given the relative strength of the signal on the six different antennas, we were able to quantify birds' movements. Additionally, the birds spent most of the night inactive, likely sleeping, and the signal strength and bearing rarely changed at night; when a change did occur, it was relatively obvious and affected both signal strength and bearing (Fig. 3).

To simultaneously examine male singing in response to the playbacks, we placed SM2 recorders at the centre of the territory of focal individuals. We programmed recorders to collect sound continuously for the entire night of the playback experiment (from 2100 to 0400 hours). We programmed recorders to register sound at 16 bits and 44.1 kHz. As with the physical (activity) responses, we considered any focal male singing activity to be a response if it

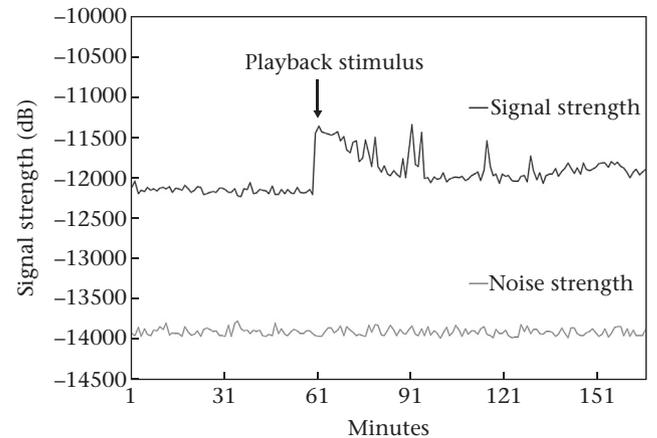


Figure 3. Activity of a radiotagged female field sparrow between 0100 and 0300 hours. Note that after 60 min of inactivity (likely sleeping), the female showed activity in response to a simulated singing intruder (playback stimulus). The stimulus given was a single field sparrow song. The black line shows signal strength (dB) from the radio transmitter and the grey line shows the constant noise strength (dB) of the environment during playbacks. Data are from a mated fertile female in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. during 2014.

occurred within 5 min of being exposed to a playback (simulated intruder song).

Statistical Analyses

Factors influencing nocturnal singing in the field sparrow

We used generalized linear mixed models (GLMM, GLIMMIX procedure, SAS 9.3, SAS Institute, Cary, NC, U.S.A.) with a binomial distribution and logit link function (Littell, Milliken, Stroup, Wolfinger, & Schabenberger, 2006) to examine factors influencing nocturnal singing in male field sparrows. We examined song types (simple and complex songs) separately. The response variable was

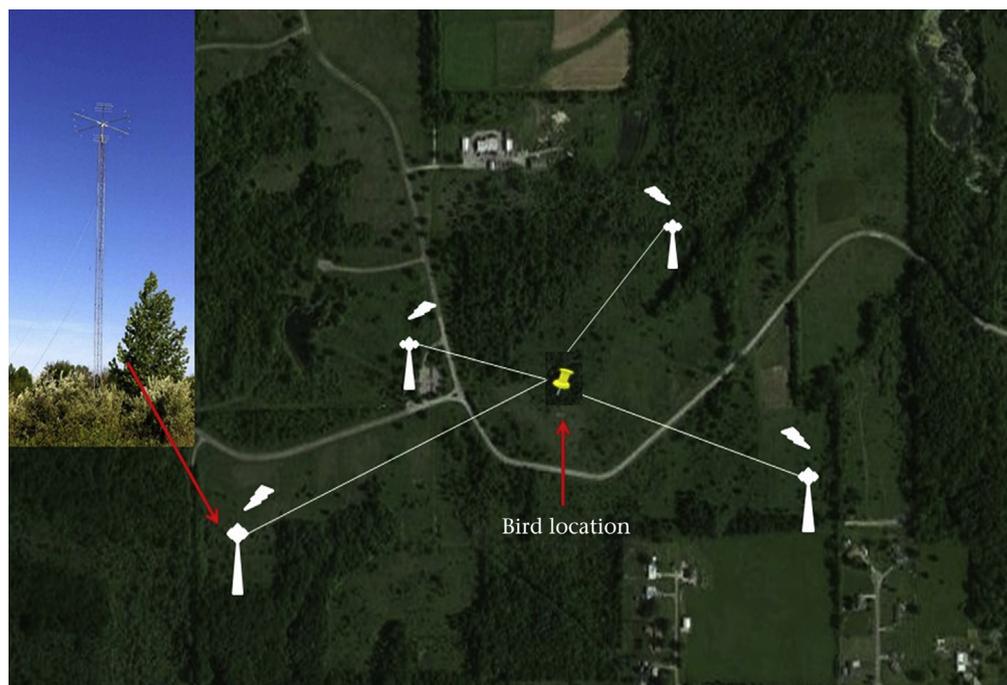


Figure 2. Automated radiotelemetry system (ARTS) deployed in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. to detect activity responses of male and female field sparrows to simulated singing intruders.

the presence or absence of nocturnal song for each monitored individual per night. Because we originally recorded 15 10-minute recording periods for each monitored individual on each night, we combined these periods to obtain the presence or absence of nocturnal song for that individual for the entire night. We treated the presence of singing neighbours and intruders within a night, fertility stage of the resident's mate, moon illumination and all interactions between these variables as fixed effects. We treated bird identity as a random effect to account for the nonindependence of including multiple observations for each individual (i.e. similar to a repeated measures approach with a general linear model). Our approach of focusing on the nightly probability of singing was necessary, rather than aggregating responses for each individual, because the predictor variables of interest (singing of conspecifics, fertility stage, moon illumination) were temporally dynamic. We included moon illumination to account for the possibility of increased activity associated with elevated light levels (Hill, Copenhaver, Gangler, & Whaley, 2005; Kempenaers, Borgström, Loës, Schlicht, & Valcu, 2010; Müller, 2006; York et al., 2014). We retrieved data on moon illumination for each day of the sample period from the United States Naval Observatory website (<http://www.usno.navy.mil/USNO>). To account for the strong seasonal pattern in the occurrence of nocturnal song in field sparrows (Celis-Murillo et al., 2016), we included a quadratic effect of ordinal date in each candidate model. We evaluated candidate models using Akaike's information criterion adjusted for small sample sizes, AIC_c (Burnham & Anderson, 2002). To assess goodness of fit of models, we compared AIC_c scores of candidate models to a model with only the quadratic effect of date (null model).

Playback responses

We used GLMM (GLIMMIX procedure, SAS 9.3) with a binomial distribution and logit link function (Littell et al., 2006) to examine whether males and females responded to simulated territorial intrusions (short and long versions of the complex song or to control songs) with activity (active versus not active). We treated sex, song type (coded as short complex song, long complex song or control song) and breeding stage (prefertile, fertile and postfertile) as fixed effects. We treated bird identity, sequence of stimuli and trial number as random effects to account for potential nonindependence data collected from the same individual and the effects of stimulus order and use of repeated playbacks. We also included pair as a random effect to account for the potential nonindependence of response from an individual and the effects of the behaviour from their mate during the playbacks. To assess whether males responded by singing to simulated territorial intrusions, we again used GLMM with a binomial distribution and logit link function. The binary response variable was song or no song from the territorial male. We treated song type (short complex song, long complex song or control song) and breeding stage (prefertile, fertile and postfertile) as fixed effects, and bird identity, sequence of stimulus, trial and pair as random effects.

RESULTS

We conducted 812 nocturnal surveys (563 in 2012 and 249 in 2013) across 28 resident male territories. Each resident male was surveyed on 29 ± 30.18 nights (mean \pm SD; range 5–97 nights, $N = 28$). Only 57% (16) of resident males sang at night. These males sang 1.63 ± 1.32 songs per night (mean \pm SD; range 0.07–5.79 songs per night, $N = 16$); 1.12 ± 1.11 complex songs per night (mean \pm SD; range 0–4.34 complex songs per night, $N = 16$) and 0.50 ± 0.47 simple songs per night (mean \pm SD; range 0–1.44 simple songs per night, $N = 16$).

Across all nocturnal surveys, we detected 1130 field sparrow single songs (749 complex songs and 381 simple songs); 387 songs from resident males (274 complex songs and 113 simple songs), 231 songs from neighbouring males (159 complex songs and 72 simple songs) and 251 songs from intruder males (146 complex songs and 115 simple songs) (Fig. 4). The two best-fitting models ($\Delta AIC_c < 2$, $\sum w_i = 0.78$) for predicting nightly occurrence of complex song by individual field sparrows included the presence of intruders singing, presence of neighbours singing, fertility stage and ordinal date. The third-best model ($\Delta AIC_c < 4$, $w_i = 0.17$) for predicting nightly occurrence of complex song also included breeding stage and ordinal date. The three models combined received most of the weight of evidence ($\sum w_i = 0.95$; Table 1). Birds were more likely to vocalize complex songs during the fertile and postfertile periods than during the prefertile period (Fig. 5). We found no support for any variables predicting the nightly occurrence of simple songs at night (Table 2); the presence of neighbour or intruder songs did not predict the occurrence of simple songs and simple songs did not vary across breeding stages (Fig. 6). Furthermore, there was no evidence for moon illumination predicting the nightly probability of recording complex or simple songs (Table 1).

We investigated singing and activity (movement versus no-movement) responses to simulated territorial intrusions in six mated males and activity responses in 14 mated females. Of these birds, 10 of them were paired to each other, forming five experimental mated pairs. We conducted 101 nocturnal playback trials using these 20 birds. There was no difference in the activity response between males and females in response to simulated intruders ($F_{1,264} = 0.17$ $P = 0.68$). However, we found a significant difference in the activity responses due to song type (short, long and control song) ($F_{2,264} = 10.38$ $P < 0.001$) and breeding stages ($F_{2,264} = 2.62$ $P = 0.074$). Males and females responded equally to short and long versions of complex song (females: $t_{264} = 0.41$ $P = 0.68$; males: $t_{264} = -0.31$ $P = 0.75$), but they responded significantly more to short and long versions of complex songs than they did to control stimuli (females: short song versus control: $t_{264} = -3.23$ $P = 0.0014$; long song versus control $t_{264} = -3.58$ $P = 0.0062$. Males: short song versus control $t_{264} = -2.47$ $P = 0.014$; long song versus control $t_{264} = -2.29$ $P = 0.023$; Fig. 7). Although no data were collected for males during the fertile stages of their mated females because radios either fell off the bird or the batteries died, we found that males responded equally during prefertile and postfertile stages ($t_{265} = -0.65$ $P = 0.51$). In contrast,

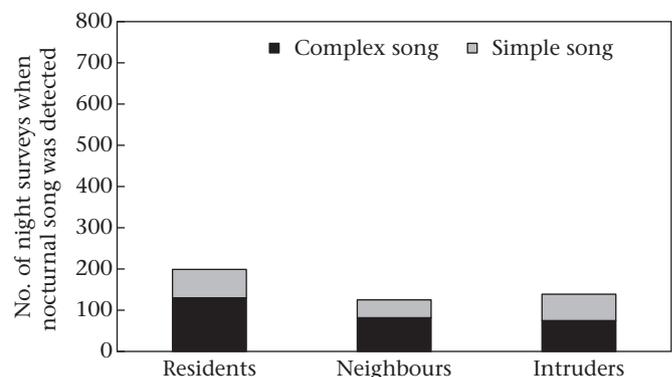


Figure 4. Total number of night surveys on which at least one field sparrow song (complex and simple) was detected. Data are from 812 nocturnal surveys across 28 different resident male territories (mean \pm SD = 29 ± 30.18 survey nights per individual) conducted from April to July of 2012–2013. Focal males were distributed across 10 grassland patches in Kennekuk Cove County Park, Vermilion County, IL, U.S.A.

Table 1
Comparison of candidate models explaining the nightly probability of detecting field sparrow complex songs

Model	K	AIC _c	ΔAIC _c	w _i
Intruder song+breeding stage+day ²	6	610.47	0.00	0.55
Neighbour song+breeding stage+day ²	6	612.24	1.77	0.23
Breeding stage+day ²	5	612.87	2.40	0.17
Intruder song*breeding stage+day ²	6	615.87	5.40	0.04
Neighbour song*breeding stage+day ²	6	618.26	7.79	0.01
Intruders+day ²	4	622.14	11.67	0.00
Neighbours+day ²	4	623.59	13.12	0.00
Day ² (null)	3	625.08	14.61	0.00
Moon illumination+day ²	4	626.82	16.35	0.00

We ranked models based on Akaike's information criterion corrected for small sample size (AIC_c). K is the number of model parameters, ΔAIC_c is the difference in AIC from the top model and w_i is Akaike weight. day²: quadratic effect of ordinal date. Data are from 28 territory holders distributed across 10 grassland patches in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. during the years 2012–2013.

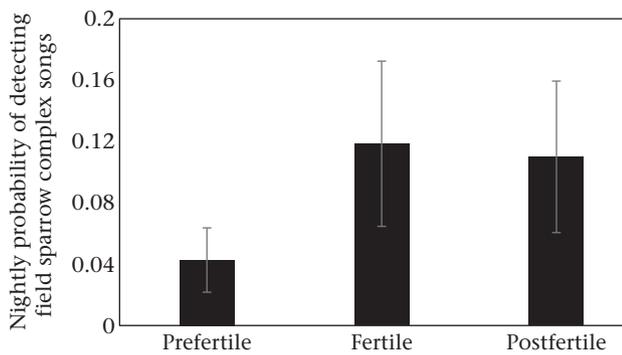


Figure 5. Nightly probability (±SE) of detecting complex songs of male field sparrows across their mate's fertility stages. Data are from 28 territory holders distributed across 10 grassland patches in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. during the years 2012–2013.

Table 2
Comparison of candidate models explaining the nightly probability of detecting field sparrow simple songs

Model	K	AIC _c	ΔAIC _c	w _i
Day ² (null)	3	427.13	0.00	0.30
Neighbour song+day ²	4	427.90	0.77	0.21
Moon illumination+day ²	4	428.64	1.51	0.14
Intruder song+day ²	4	429.09	1.96	0.11
Intruder song*breeding stage+day ²	6	429.32	2.19	0.10
Breeding stage+day ²	5	430.35	3.22	0.06
Neighbour song+breeding stage+day ²	6	431.25	4.12	0.04
Intruder song+breeding stage+day ²	6	432.34	5.21	0.02
Neighbour song*breeding stage+day ²	6	433.87	6.74	0.01

We ranked models based on Akaike's information criterion corrected for small sample size (AIC_c). K is the number of model parameters, ΔAIC_c is the difference in AIC from the top model and w_i is Akaike weight. day²: quadratic effect of ordinal date. Data are from 28 territory holders distributed across 10 grassland patches in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. during the years 2012–2013.

females responded more to simulated intruders during the pre-fertile and fertile stages than during the postfertile stage (prefertile versus fertile: $t_{265} = -1.2$ $P = -1.2$; prefertile versus postfertile: $t_{265} = -3.01$ $P = 0.0029$; fertile versus postfertile: $t_{265} = 2.2$ $P = 0.028$; Fig. 8). For males, our original plan was to analyse the singing responses of males to simulated singing intruders and expected countersinging events; however, we never detected a singing response (i.e. countersinging) from males during the

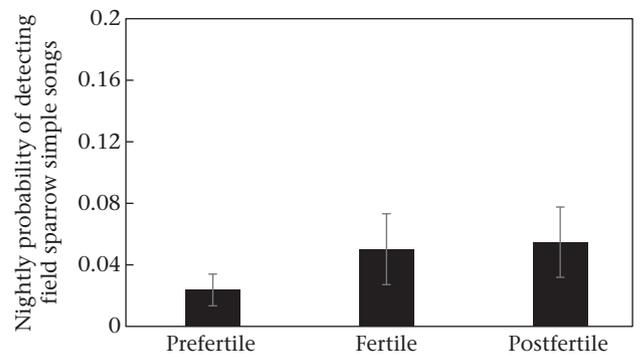


Figure 6. Nightly probability (±SE) of detecting simple songs of male field sparrows across their mate's fertility stages. Data are from 28 territory holders distributed across 10 grassland patches in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. during the years 2012–2013.

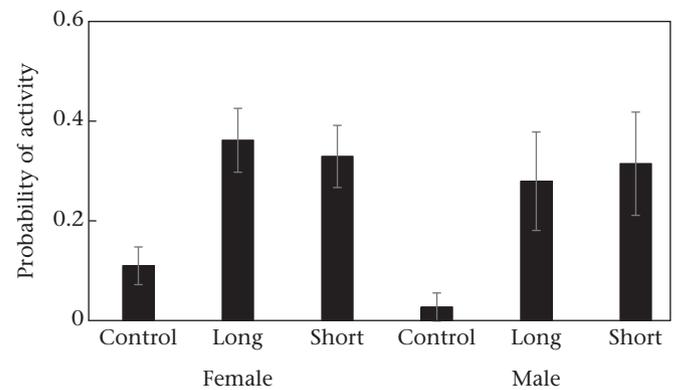


Figure 7. Probability of activity (±SE) of mated male and female field sparrows (FISP, N = 20) in response to each of the stimuli presented during playback trials. Control: northern cardinal song or Carolina wren song; Long: long complex FISP song; Short: short complex FISP song. We evaluated responses via automated radiotelemetry systems (ARTS) in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. during 2014.

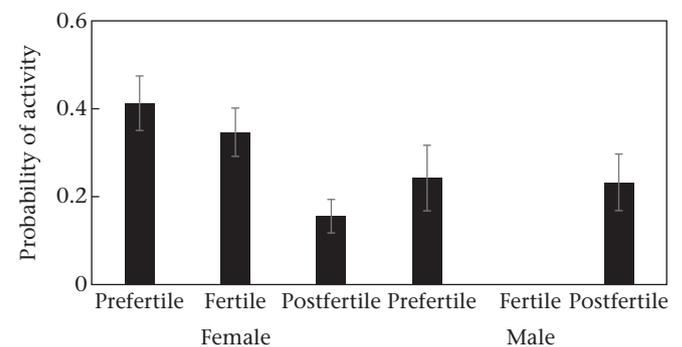


Figure 8. Probability of activity (±SE) of mated male and female field sparrows (FISP, N = 20) in response to 105 short and long FISP songs across the fertility stages. Note: there were no data for males during the fertile period. We evaluated responses via automated radiotelemetry systems (ARTS) in Kennekuk Cove County Park, Vermilion County, IL, U.S.A. during 2014.

experiment. Our larger automated-recorder data set (11756 10-minute recording periods among 28 territories) confirmed the lack of countersinging; we only recorded more than one song in four out of 1130 10-minute periods with detections of nocturnal songs of the field sparrow.

DISCUSSION

We used descriptive and experimental approaches to address the functional role of nocturnal song in mated territorial field sparrows. We found that the nightly probability of detecting complex songs by individual field sparrows was associated with the nocturnal singing activity of neighbouring and intruder males and the breeding stage of their social mate. Neighbours and intruder males tended to sing complex songs on the same night when the resident focal males sang. In addition, all birds (resident males, neighbours and intruders) tended to sing according to the fertility periods of the resident male's mate. Conversely, the probability of detecting nocturnal simple songs by individual field sparrows was not associated with any of the variables included in our analyses. Furthermore, our playback experiment demonstrated that although field sparrows were usually sleeping and inactive at night, males and females actively responded to simulated nocturnal single songs of field sparrows. Interestingly, males did not respond by singing or countersinging to simulated field sparrow intrusions. The experiment also demonstrated that male activity responses were similar during the prefertile and postfertile stages, while females responded more to simulated intruders during the prefertile and fertile stages than during the postfertile stage.

Our results suggest that the nocturnal singing behaviour of males (i.e. resident males, neighbours and intruders) in our study was driven by the same factor: the fertile stage of a fertile female, the focal male's mate. The increase in singing effort by mated males has been shown to correlate with the fertility stages of their mates in some species. For example, the dawn singing effort of male willow tits, *Poecile montanus*, peaks about 10 days before commencement of laying, coinciding with the fertility period of their mates (Welling, Koivula, & Lahti, 1995). In addition, changes in singing behaviours in blue grosbeaks, *Guiraca caerulea*, correspond to periods of female fertility (Ballentine, Badyaev, & Hill, 2003). Specifically in the field sparrow, changes in dawn song (complex song) performance also tend to correspond to different female breeding stages (Zhang et al., 2015), suggesting that resident males may sing more to attract their mates and possibly, to reinforce their mating relationship. Neighbouring males and males from nonadjacent territories (i.e. intruders) appear to know the reproductive stage of females and to sing near these females when they are fertile. Other studies have found evidence that neighbouring males know the reproductive stage of nonsocial males. Taff, Patricelli, and Freeman-Gallant (2014) demonstrated that male common yellowthroats, *Geothlypis trichas*, are usually aware of neighbouring females' fertility periods, even the fertility period of relatively distant females (~400 m away) and adjust their diurnal singing effort based on the number of fertile females in their neighbourhood.

Our observational and experimental data suggest that while nocturnal song in the field sparrow is uncommon, it may play a role in mate attraction and extrapair mate attraction, as opposed to repelling intruders, as suggested in other species that sing at night (e.g. nightingales: Amrhein et al., 2002; Naguib et al., 2001; Roth et al., 2009). This is also supported by the fact that, despite singing responses and/or countersinging using complex songs being commonly used with intruders during the daytime (Nelson & Croner, 1991), countersinging was rarely observed in our large nocturnal data set. For instance, we observed nocturnal countersinging only four times in >10 000 min of nocturnal recording.

Females responded to the singing of simulated intruders and were more responsive when fertile. These results suggest that females are aware of males singing at night, and further supports the expectation that males should sing more when females are fertile. These observations are also consistent with nocturnal song occurring more frequently during the peak period of reproduction (Celis-

Murillo et al., 2016). While we do not know whether neighbouring or intruder males were entering the resident male's territory when singing at night, the resident male's social mate likely was able to hear the songs of other males. Therefore, singing at night could be a good strategy for males to signal their presence to females and their willingness to engage in extrapair copulations (Amrhein et al., 2002). Nocturnal song is rare compared to diurnal song, but our experiment suggest that female field sparrows were likely to hear songs elicited by neighbouring or intruding males. In this study, of all the nocturnal songs detected, resident male songs were detected on only 43% of nights, while neighbour and intruder songs were detected on 27% and 30%, respectively. If females are engaging in extrapair copulations at night (Celis-Murillo, 2015; Chiver et al., 2008; Pedersen et al., 2006), potential extrapair sires likely need to advertise their presence.

During daylight hours, male field sparrows commonly sing loud and long bouts of complex and simple songs. In contrast, nocturnal songs are characterized by single, isolated vocalizations. Delivering single songs could achieve some level of 'privacy' analogous to soft songs in other species (e.g. blackbirds, *Turdus merula*: Dabelsteen, 1984; European robins, *Erithacula rubecula*: Dabelsteen, McGregor, Holland, Tobias, & Pedersen, 1997). Single songs in the field sparrow may help them to attract females without attracting predators (Lima, Rattenborg, Lesku, & Amlaner, 2005; Schmidt & Belinsky, 2013) or minimize conflicts with neighbouring males or mates. Quiet and soft songs have multiple functions depending on the species (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998); however, they are generally associated with secretively courting females. For example, dunnocks, *Prunella modularis*, display quiet songs during the reproductive period, and their secretive vocalizations appear to help males secure copulations, especially because multiple mates compete for access to fertile females and males attempt to disrupt their extrapair copulations (Davies, 1992). Similarly, great tits, *Parus major*, possess a short and quiet vocalization that serves for courtship feeding and copulation (Gompertz, 1961). Soft songs also serve in male–male interactions in common yellowthroats, for cooperative and/or noncooperative purposes (Titus, 1998).

We found that complex song was sung at night more often than simple song. Complex songs may be better suited for attracting potential extrapair mates as they have more syllables and may provide more information on the quality of the individual producing them (Kempnaers, Verheyen, & Dhondt, 1997; Otter, Chruszcz, & Ratcliffe, 1997; Poesel, Foerster, & Kempnaers, 2001). Additionally, the ability to identify individuals via song is better when songs contain more information (i.e. complexity). Recent research on the dawn singing behaviour of field sparrows in the same system also has demonstrated that males change aspects of complex song (e.g. song rate, song length, song complexity) in response to their social mate's fertility stage (Zhang et al., 2015). Therefore, males' use of complex songs at night might be an effective way for them to advertise their quality and identity as potential extrapair mates. In contrast, nocturnal simple songs do not appear to serve a clear function. Despite the fact that simple songs are thought to have a role in male–female interactions (Nelson & Croner, 1991), they were not predicted by the social or environmental factors examined in this study. Simple songs, however, could serve to attract migrating females, as suggested in yellow-breasted chats, *Icteria virens* (Alessi, Benson, & Ward, 2010), but not in the attraction of extrapair mates once they have settled at the site (Celis-Murillo et al., 2016).

While nocturnal singing is an infrequent behaviour of many diurnal birds, it may be important in the mating system of these birds. Many of the diurnal birds that sing infrequently at night are socially monogamous, with some extrapair mating behaviour (La,

2012). While during the day male song serves multiple purposes including defending territories and attracting a social mate (Catchpole & Slater, 2008), nocturnal song may have a more specific function associated with coordinating extrapair copulations (Alessi et al., 2010; Amrhein et al., 2002). Given that roughly a quarter of passerine species engage in infrequent singing at night (La, 2012), further research on this rare behaviour is needed to potentially understand its function, such as when, where and why males and females engage in extraterritorial forays.

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References

- Alessi, M. G., Benson, T. J., & Ward, M. P. (2010). Nocturnal social cues attract migrating yellow-breasted chats. *Wilson Journal of Ornithology*, *122*, 780–783.
- Amrhein, V., Korner, P., & Naguib, M. (2002). Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Animal Behaviour*, *64*, 939–944.
- Arcece, P. (1987). Age, intrusion pressure and defense against floaters by territorial-male song sparrows. *Animal Behaviour*, *35*, 773–784.
- Ballentine, B., Badyaev, A., & Hill, G. E. (2003). Changes in song complexity correspond to periods of female fertility in blue grosbeak (*Guiraca caerulea*). *Ethology*, *109*, 55–66.
- Barclay, R. M. R., Leonard, M. A., & Friesen, G. (1985). Nocturnal singing by marsh wrens. *Condor*, *87*, 418–422.
- Best, L. B. (1977). Nestling biology of the field sparrow. *Auk*, *94*, 308–319.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.
- Carey, M., Burhans, D. E., & Nelson, D. A. (2008). Field sparrow (*Spizella pusilla*). In A. Poole, & F. Gill (Eds.), *The birds of North America (No.103)*. Philadelphia, PA: Academy of Natural Sciences; Washington, D.C.: American Ornithologists' Union.
- Carter, G. M., Legare, M. L., Breininger, D. R., & Oddy, D. M. (2007). Nocturnal nest predation: a potential obstacle to recovery of a Florida scrub-jay population. *Journal of Field Ornithology*, *78*, 390–394.
- Catchpole, C. K., & Slater, P. J. B. (2008). *Bird song biological themes and variations* (2nd ed.). Cambridge, U.K.: Cambridge University Press.
- Celis-Murillo, A. (2015). *Extra-pair mating behaviors in the field sparrow: Nocturnal song and extraterritorial forays* (Doctoral dissertation). Champaign, IL: University of Illinois at Urbana-Champaign.
- Celis-Murillo, A., Stodola, K. W., Pappadopoli, B., Burton, J. M., & Ward, M. P. (2016). Seasonal and daily patterns of nocturnal singing in a diurnal bird: a case study of the field sparrow (*Spizella pusilla*). *Journal of Ornithology*. <http://dx.doi.org/10.1007/s10336-015-1318-y>. Advance online publication.
- Chiver, I., Stutchbury, B. J. M., & Morton, E. S. (2008). Female foray behavior correlates with male song and paternity in a socially monogamous bird. *Behavioral Ecology and Sociobiology*, *62*, 1981–1990.
- Dabelsteen, T. (1984). An analysis of the full song of the blackbird *Turdus merula* with respect to message coding and adaptations for acoustic communication. *Ornis Scandinavica*, *15*, 227–239.
- Dabelsteen, T., McGregor, P. K., Holland, J., Tobias, J. A., & Pedersen, S. B. (1997). The signal function of overlapping singing in male robins (*Erithacus rubella*). *Animal Behaviour*, *53*, 398–408.
- Dabelsteen, T., McGregor, P. K., Lampe, P. K., Langmore, H. M., & Holland, J. (1998). Quit song in songbirds: an overlooked phenomenon. *Bioacoustics*, *9*, 89–105.
- Davies, N. B. (1992). *Dunnock behavior and social evolution*. Oxford, U.K.: Oxford University Press.
- Foot, J. R., Palazzi, E., & Mennill, D. J. (2012). Songs of the eastern phoebe, a subsongbird, are individually distinctive but do not vary geographically. *Bioacoustics*, *22*(2), 137–151.
- Gompertz, T. (1961). The vocabulary of the great tit. *British Birds*, *54*, 369–394.
- Hill, C. E., Copenhaver, K. A., Gangler, R. K., & Whaley, J. W. (2005). Does light intensity influence song output by northern mockingbirds? *Chat*, *69*, 61–67.
- Kays, R., Tilak, S., Crofoot, M., Fountain, T., Obando, D., & Ortega, A. (2011). Tracking animal location and activity with an automated telemetry system in a tropical rainforest. *Computer Journal*, *54*, 1931–1948.
- Kempnaers, B., Borgström, P., Loès, P., Schlicht, E., & Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, *20*, 1735–1739.
- Kempnaers, B., Verheyen, G. R., & Dhondt, A. A. (1997). Extra-pair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behavioral Ecology*, *8*, 481–492.
- Kroodsma, D. E. (1989). Suggested experimental designs for song playbacks. *Animal Behaviour*, *37*, 600–609.
- La, V. T. (2012). Diurnal and nocturnal birds vocalize at night: a review. *Condor*, *114*, 245–257.
- Lima, S. L., Rattenborg, N. C., Lesku, J. A., & Amlaner, C. J. (2005). Sleeping under the risk of predation. *Animal Behaviour*, *70*, 723–736.
- Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D., & Schabenberger, O. (2006). *SAS for mixed models* (2nd ed.). Cary, NC: SAS Institute.
- Lougheed, S. C., & Handford, P. (1989). Night songs in the rufous-collared sparrow. *Condor*, *91*, 462–465.
- Luschi, P., & del Seppia, C. (1996). Song-type function during territorial encounters in male Cetti's warbler, *Cettia cetti*. *Ibis*, *138*, 479–484.
- Miller, M. W. (2006). Apparent effects of light pollution on singing behavior of American robins. *Condor*, *108*, 130–139.
- Naguib, M. (1999). Effects of song overlapping and alternating on nocturnally singing nightingales. *Animal Behaviour*, *58*, 1061–1067.
- Naguib, M., Altenkamp, R., & Griebmann, B. (2001). Nightingales in space: song and extra-territorial forays of radio tagged songbirds. *Journal of Ornithology*, *142*, 306–312.
- Nelson, D. A., & Croner, J. L. (1991). Song categories and their functions in the field sparrow (*Spizella pusilla*). *Auk*, *108*, 42–52.
- Nelson, D. A., & Poesel, A. (2012). Responses to variation in song length by male white-crowned sparrows. *Ethology*, *118*, 24–32.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., et al. (2013). *Vegan: Community ecology package* (R package version 2.0-9). Vienna, Austria: R Foundation for Statistical Computing <http://CRAN.R-project.org/package=vegan>.
- Otter, K., Chruszcz, B., & Ratcliffe, L. (1997). Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology*, *8*, 167–173.
- Pedersen, M. C., Dunn, P. O., & Whittingham, L. A. (2006). Extraterritorial forays are related to a male ornamental trait in the common yellowthroat. *Animal Behaviour*, *72*, 479–486.
- Perrault, K., Lobert, L. M., Ehnes, M., & Foote, J. R. (2013). Nocturnal singing in a temperate bird community. *Journal of Ornithology*, *155*, 1059–1062.
- Petters, S. C., Miles, D. B., & White, W. M. (1990). Genetic evidence of mixed reproductive strategy in a monogamous bird. *Condor*, *92*, 702–708.
- Poesel, A., Foerster, K., & Kempnaers, B. (2001). The dawn song of the blue tit *Parus caeruleus* and its role in sexual selection. *Ethology*, *107*, 521–531.
- Pyle, P. (1997). *Identification guide to North American birds (Part 1)*. Bolinas, CA: Slate Creek Press.
- R Development Core Team. (2008). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Raim, A. (1978). A radio transmitter attachment for small passerine birds. *Bird Banding*, *49*, 326–332.
- Roth, T., Sprau, P., Schmidt, R., Naguib, M., & Amrhein, V. (2009). Sex-specific timing of mate searching and territory prospecting in the nightingale: nocturnal life of females. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 2045–2050.
- Schmidt, K. A., & Belinsky, K. L. (2013). Voices in the dark: predation risk by owls influences dusk singing in a diurnal passerine. *Behavioral Ecology and Sociobiology*, *67*, 1837–1843.
- Slay, C. M., Ellison, K. S., Ribic, C. A., Smith, K. G., & Schmitz, C. M. (2012). Nocturnal activity of nesting shrubland and grassland passerines. In C. A. Ribic, F. R. Thompson, III, & P. J. Pietz (Eds.), *Studies in avian biology: Vol. 43. Video surveillance of nesting birds* (pp. 105–116). Berkeley, CA: University of California Press.
- Staiger, S. S., Valcu, M., Spoelstra, K., Helm, B., Wikelski, M., & Kempnaers, B. (2013). When the sun never sets: diverse activity rhythms under continuous daylight in free-living Arctic-breeding birds. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131016.
- Taff, C. C., Patricelli, G. L., & Freeman-Gallant, C. R. (2014). Fluctuations in neighborhood fertility generate variable signaling effort. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 1974.
- Titus, R. (1998). Short-range and long-range songs: use of two acoustically distinct song classes by dark-eyed juncos (*Junco hyemalis*). *Auk*, *115*, 386–393.
- Tyler, G. A., & Green, R. E. (1996). The incidence of nocturnal song by male corn-crakes *Crex crex* is reduced during pairing. *Bird Study*, *43*, 214–219.

- Ward, M. P., Alessi, M., Benson, T. J., & Chiavacci, S. J. (2014). The active nightlife of diurnal birds: extraterritorial forays and nocturnal activity patterns. *Animal Behaviour*, *88*, 175–184.
- Ward, M. P., Sperry, H. J., & Weatherhead, P. J. (2013). Evaluation of automated telemetry for quantifying movements and home ranges of snakes. *Journal of Herpetology*, *47*, 337–345.
- Weatherhead, P. J., Montgomerie, R., Gibbs, H. L., & Boag, P. T. (1994). The cost of extra-pair fertilizations to female red-winged blackbirds. *Proceedings of the Royal Society B: Biological Sciences*, *258*, 315–320.
- Welling, P., Koivula, K., & Lahti, K. (1995). The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. *Journal of Avian Biology*, *26*, 241–246.
- Westneat, D. F. (1988). Male parental care and extrapair copulations in the Indigo bunting. *Auk*, *105*, 149–160.
- York, J. E., Young, A. J., & Radford, A. N. (2014). Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase. *Biology Letters*, *10*, 20130970.
- Yorzinski, Y. L., & Platt, M. L. (2012). The difference between night and day: anti-predator behavior in birds. *Journal of Ethology*, *30*, 211–218.
- Zhang, V. Y., Celis-Murillo, A., & Ward, M. P. (2015). Conveying information with one song type: changes in dawn song performance correspond to different female breeding stages. *Bioacoustics*, *25*, 19–28. <http://dx.doi.org/10.1080/09524622.2015.1076348>.