

EXTRAPAIR MATING BEHAVIORS IN THE FIELD SPARROW: NOCTURNAL SINGING  
AND EXTRATERRITORIAL FORAYS

BY

ANTONIO CELIS MURILLO

DISSERTATION

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Doctoral Committee:

Assistant Professor Michael P. Ward, Chair  
Professor Jeffrey Brawn, Director of Research  
Assistant Professor Thomas J. Benson  
Professor Andrew V. Suarez

## ABSTRACT

While there has been much research on the mating behaviors of birds, most attention has focused on elaborate and/or conspicuous mating displays, such as diurnal songs, ornaments, or mating dances. Much less attention has been devoted to investigating the role of more subtle behaviors, particularly nocturnal signing by diurnal birds and extra-territorial forays (movements off territory). My research explored the function of nocturnal singing and extra-territorial forays in the Field Sparrow (*Spizella pusilla*). I determined that nocturnal complex song serves to announce the presence of extra-pair males to females and that extra-territorial forays serve primarily in prospecting and soliciting extra-pair matings. While forays are common among both male and female Field Sparrows, a higher foraying rate did not result in greater extra-pair paternity (EPP). Rather, my data provide strong evidence that extra-pair matings are determined by current and previous relationships; females chose extra-pair sires that were current neighbors or neighbors or social mates during previous breeding seasons. Given female preference for extra-pair matings with neighbors, males who have information on the fertility status of neighboring females and coordinate their nocturnal vocalizations in relation to the fertility stage of neighboring females may be able to increase their EPP. Contrary to other studies, I did not find a relationship between the traits of males, females, or females' social mates (age and tarsus length) and EPP. Thus, proximity to females, rather than male characteristics, appears to be key for a male's success at acquiring extra-pair paternity. Finally, my findings are consistent with the hypothesis that female choice for extra-pair mates coupled with female foray behavior are driving patterns of extra-pair paternity and nocturnal singing behavior. By integrating research on nocturnal singing, extra-territorial foray behavior, and extra-pair paternity, my work has led to a more comprehensive understanding of extra-pair mating behavior in birds.

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## CHAPTER 1

### GENERAL INTRODUCTION

While there has been much research on the mating behaviors in birds (Borgia 1979, Dias et al. 2009), most attention has focused on the elaborated and/or conspicuous mating displays, including, diurnal songs, ornament displays or mating dances, and substantially less attention onto understanding the role of more subtle behaviors, in particular nocturnal signing and extra-territorial forays (movements off territory). In birds, male song often serves as an honest signal of individual quality (Kroodsma and Byers 1991, Hoeschele 2010). Bird song, especially long or frequent songs and songs with particular structural parameters (e.g., trills), provide reliable information to other males and females that influences the outcome of male-male and female-male interactions (Catchpole and Slater 2008). Song characters such as greater song rate/output (songs/min), song complexity (number of syllables and song types), and vocal performance (in the form of a relationship among frequency bandwidth and trill rate), among other song parameters, have been used to measure individual quality due to their positive correlation with reproductive success (e.g., Kempenaers et al. 1997, Ballentine et al. 2004, Nelson and Poesel 2012). To date, our understanding of the function of bird song is based largely on studies of diurnal song, with the exception of species such as Nightingales (*Luscinia megarhynchos*) that, while diurnal, have regular and well-developed nocturnal singing habits (La 2012). Many diurnal birds sing at night as well as during the day, however, the amount of nocturnal singing varies from regular to occasional and even rare (La 2012). Previous studies have hypothesized that nocturnal song may serve similar reproductive functions as diurnal song, including mate attraction (Tyler and Green 1996, Roth et al. 2009) or repulsion of intruders from territories during their social mate's fertile stage (Luschi and Del Seppia 1996, Naguib et al. 1999).

Although these explanations are reasonable, they are almost entirely based on data from a small subset of diurnal species with regular and well-developed nocturnal singing habits (i.e., Nightingale, Amrhein et al. 2002; Corncrake, *Crex crex*, Tyler and Green 1996), and not from diurnal species that less frequently sing at night. In a comprehensive review of nocturnal singing in diurnal birds, La (2012) reported that out of 126 species that she was able to classify based on how frequent they vocalized at night, 52% were classified as regular nocturnal singers (singing long bouts of repeated song and continuously across the night), 27% as occasional nocturnal singers, and 20% as rare nocturnal singers. For the species that sing repeatedly and continuously (regularly) during the night, it is clear that nocturnal singing might provide singers the ability to effectively signal information regarding their location, identity, and quality, supporting the hypotheses proposed for the functions of nocturnal song. However, for the species that only sing infrequently (occasionally or rarely) nocturnal singing may serve different functions as it is unlikely they provide large amounts of information on individual quality to effectively attract mates or repel intruders.

In chapter 2, I report hourly and seasonal patterns of nocturnal song in the diurnal Field Sparrow, *Spizella pusilla*, using a standardized passive recording approach to characterize patterns in nighttime singing. Diurnal singing behavior in Field Sparrows has been studied extensively (Nelson and Croner 1991), and one study have reported nocturnal singing in this species (Walk et al. 2000). During the day, Field Sparrows regularly sing two song types (simple and complex) which are distinguished by their acoustic structure and time of delivery. Simple song consist in 2-3 notes and is sung throughout the day, while complex song type is 4-6 notes and is sung almost exclusively at dawn (Nelson and Croner 1991). Information about the nocturnal song in the Field Sparrows, however, remains unknown. Diurnal song in Field



Sparrows functions as a tactic for attracting mates and repelling intruders (Nelson and Croner 1991) and nocturnal song may serve similar functions. I used autonomous acoustic recording units (ARUs) and automated detection and classification algorithms (Songscope) to quantify nocturnal singing behavior in different grassland patches in Kennekuk Cove County Park in Vermillion County, IL. I sampled songs produced in the neighborhood of the soundscape recorder during 7,938 10-minute recordings collected each hour from 21:00 hrs to 04:30 hrs. throughout the breeding season. I described temporal patterns of each of the two song types sung by the Field Sparrow, simple songs used in male-female interactions during the day, and complex songs used for male-male interactions (counter-singing) at dawn (Nelson and Croner 1991). Based on the different functions of the song types, I expected them to have different seasonal patterns. If simple songs are used to attract females, then I expected males to use simple songs early in the season when most pairing of social mates occurs. If complex songs are used primarily in male-male interactions, particularly territory and mate defense, then I expected them to be used more frequently later in the season, after most social pairing is complete. I sampled hourly nocturnal singing behavior to identify any patterns such as clustering of singing activity and the time of clustering that might provide additional insight into the function of the singing behavior. For example, clustered singing of complex songs shortly before dawn may represent an extension of dawn singing activity.

In chapter 3, I investigated the functional role of Field Sparrow nocturnal song in male-male vs. male-female interactions, particularly in the context of acquiring extra-pair mates, using two approaches: (1) associations of singing behavior with social factors (e.g., fertility stage and singing of other males in the neighborhood), and (2) experimental presentation of vocalizations by intruder males. First, I examined whether social factors were reliable predictors of simple and

complex nocturnal songs in mated male Field Sparrows (hereafter, residents). I considered simple and complex songs independently based on differences in seasonal patterns documented in Chapter 2 and hypothesized differences in the specific reproductive function of each song type. I used ARUs, Songscope, and an individual acoustic identification approach to quantify the nocturnal singing effort (simple and complex songs) of resident males, neighboring males, and intruding males across the different fertility stages. *Residents* refers to males holding a territory where I placed the autonomous recorders, *neighbors* refer to males holding territories in the same grassland patch (i.e. same neighborhood) adjacent to or within 200 m of the resident, and *intruders* are males with territories in a different grassland patch and in most cases >300m from the residents' territories.

I conducted a nocturnal playback experiment to explore how mated male and female Field Sparrows responded to simulated intruder songs at night. I focused my experiment on complex calls, because while simple calls demonstrated a seasonal pattern in Chapter 2, I observed no relationship between simple song activity and any of the social variables, leaving the interpretation of the seasonal patterns and their relationship to reproductive activity unclear. Additionally, simple calls are much less common than complex calls during nocturnal singing. I evaluated responses to the playbacks in two ways: (1) counter singing response of males recorded using ARUs placed in the territory of the social pair, and (2) activity responses (activity/no activity) of both the male and female via automated radio telemetry systems (ARTS). I carried out the experiment across different fertility stages to determine if resident males or females changed their response in relation to the female's fertility status. If complex calls play a role in male-male interactions, then I predicted that males would respond to a simulated intruders nocturnal songs through counter singing and presence of activity, and that responses would be

greatest during the female's fertile period. Alternatively, if complex calls play a role in male-female interactions, I predicted that females would actively respond to simulated intruders, and similarly, female response should be strongest during her fertile period.

The development and widespread use of genetic paternity analyses had provided insight into the mating systems of socially monogamous birds (Griffith et al. 2002, Westneat and Stewart 2003). While genetic parentage studies have revolutionized our view of avian mating and reproductive systems (Griffith et al. 2002), our understanding of the behavioral mechanisms used to acquire extra-pair matings and how these behaviors vary among individuals is limited (e.g., in relation to size, age, and sex; Lindstedt et al 2007, Akcay and Roughgarden 2007). Extraterritorial forays are hypothesized as the behaviors used by birds to acquire extra-pair matings (Yezerinac and Weatherhead 1997, Chiver et al. 2008), although some evidence supports a role of forays in prospecting for new breeding territories or general public information (Neudorf et al. 1997). The most widely-used approach for studying extra-pair behaviors is tracking songbirds and estimating foray rates via manual radio-telemetry (e.g., Stutchbury et al. 2005, Kleeven et al. 2006, Pedersen et al. 2006). Manual telemetry has enhanced our knowledge of extraterritorial forays, but it has technical and logistical constraints, specifically most manual telemetry of diurnal birds is conducted during the day (presumably when most diurnal birds are most active), long movements made over short periods of time may be difficult to detect and accurately record, and the average total effort devoted to tracking individuals is generally no more than 20 hours, which usually is achieved by tracking each bird a few hours a day every 2-3 days (e.g., Stutchbury et al. 2005, Pedersen et al. 2006, Kleeven et al. 2006). Recent studies have shown that some bird species make nocturnal forays (Nightingale, Naguib et al. 2001, Yellow-breasted Chat, Ward et al 2014), underscoring the limitations of manual telemetry. Manual

telemetry, at best, provides a snapshot of foraging behavior and at worse biases our understanding of the patterns of foray behavior and its relative contribution to an individual's overall reproductive performance (in the form of extra-pair paternity).

In Chapter 4, I used ARTS and microsatellite DNA analyses to investigate extra-territorial foray behavior in male and female Field Sparrows and the contribution of this behavior to extra-pair paternity (EPP). Field Sparrows are known to have extra-pair mates, and an estimated 19% of offspring are sired through extra-pair matings (Petter et al. 1990). First, I quantified foray behavior of Field Sparrows by simultaneously and continuously tracking male and female Field Sparrows over 24-hour periods across multiple breeding stages and a large spatial extent (50-60 territories) using an ARTS. Using the telemetry data, I quantified male and female extraterritorial foray rates (foray/hr), and examined relationships between foray rates and age, tarsus length, time of day (day vs. night), and fertility stage (prefertile, fertile and postfertile). I used tarsus length as a proxy of individual quality because it has been found to vary due to environmental conditions (Kunz and Ekman 2000), and there is a relationship between tarsus length and survival (see Dhondt 1982, Kempenaers et al. 1997); larger tarsus individuals are considered of higher quality. Second, I used a microsatellite analysis to estimate the patterns of paternity in my study population and to assess the relationship between the extra-territorial foray behavior and EPP. Specifically, I examined whether the frequency of extra-territorial forays was positively correlated with extra-pair paternity (offspring outside their social mate's nest), and whether females that foray more are more likely to have extra-pair young in their nest. Third, to gain further insight into how extra-pair paternity occurs, and using my detailed and extensive foray data, I assessed whether extra-pair young in a particular female's nest were the

result of extra-pair males foraging into the cuckolded male's territory or due to females foraging into extra-pair sires' territories.

In addition to the main objectives of Chapter 4, I also examined individual and social correlates of extra-pair paternity. First, I examined the relationship between male characteristics (age and tarsus length) and male extra-pair paternity as well as the relationship between the female and her social mate's characteristics (age and tarsus length) and the presence of extra-pair young in the female's nest. Second, I investigated differences in the characteristics (age and tarsus length) between social mates and extra-pair mates of females that engaged in extra-pair copulations. Third, I quantified the distance between the territories of females and her extra-pair sires. Fourth, I examined the relationship between the number of adjacent neighbors for each female and the probability of extra-pair young in the female's nest. Studies have suggested that males and females may construct a social network centered on their territories (in males) or their nests (in females) and that individuals may benefit from relationships with long-term and familiar neighbors (Beletsky and Orians 1989, Eliassen and Jorgensen 2014). This social network may benefit females through the acquisition of additional food resources; protection from their neighbors through enhanced vigilance, alarm calls, and predator mobbing; and extra-pair paternity, which also benefits extra-pair males (Graboska-Zhang et al. 2012, Eliassen and Jorgensen 2014).

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## CHAPTER 2

### SEASONAL AND HOURLY PATTERNS OF NOCTURNAL SINGING IN THE DIURNAL FIELD SPARROW (*SPIZELLA PUSILLA*)

#### INTRODUCTION

Nocturnal behavior in diurnal birds outside of migration is poorly described and not well understood (Barclay et al. 1985, Roth et al. 2009, Ward et al. 2014). The lack of information regarding nocturnal behavior is likely due to the misconception that diurnal birds sleep through the night, remaining quiet and stationary (Slay et al. 2012). However, a growing body of evidence has documented that diurnal birds are more active at night than previously believed (Mukhin et al. 2004, 2005, Roth et al. 2009, Ward et al. 2014).

There is also accumulating evidence that diurnal birds sing at night (Barclay et al. 1985, Tyler and Green 1995, Loughheed and Handford 1999, Koublec and Capek 2000, Perrault et al. 2014); where night is defined as the period of darkness between sunset and sunrise. Birds may sing at night for numerous reasons. Diurnal vocalizations are often used to enhance reproductive performance by attracting mates, maintaining pair bonds, stimulating reproductive activity in females, guarding fertile females, or defending territories (Kroodsma and Byers 1989, 1991, Catchpole and Slater 1995), all of which also may apply to nocturnal song. Males may also use nocturnal song to attract migrating females to a particular site (Betts et al. 2008, Alessi et al. 2010), reduce predation risk (Thomas et al. 2003), reduce acoustic competition and communicate more effectively (Hill et al. 2005, Fuller et al. 2007), or enhance acoustic transmission due to more favorable atmospheric conditions (La 2012). Singing at night also could be a response to increased natural or artificial light pollution (Miller 2006, Kempenaers et al. 2010, York et al.

2014) or simply an extension of dawn and dusk song when it is concentrated early or late in the nighttime period, respectively (Otter et al. 1997).

While nighttime song is more widespread than previously believed (La 2012), nocturnal communication varies among species, populations, and individuals. La (2012) reports that out of 126 diurnal species singing at night, 52% vocalized regularly, while 27% vocalized occasionally, and 21% vocalized rarely. Much of the variability in nocturnal singing among species and populations may be driven by the reasons underlying why birds sing at night (Thomas et al. 2003). Unfortunately, the majority of research on nocturnal singing behavior has simply established the occurrence of nocturnal song. Also, the few studies that addressed nocturnal singing patterns and function were conducted in species that regularly sing at night such as the Nightingale, *Lucinia megarhynchos*, (Amrhein et al. 2002,) or Corncrake, *Crex crex*, (Tyler and Green 2010), and not on species that only occasionally or rarely sing at night (La 2012). To better understand the function of nocturnal singing behavior it is crucial to also examine birds that occasionally or rarely sing and to intensively monitor their singing behavior throughout the night and across the breeding season.

I used autonomous acoustic recording units and automated detection and classification algorithms to describe seasonal and hourly patterns of nocturnal singing behavior of the Field Sparrow, *Spizella pusilla*, a common and widely-distributed North American diurnal songbird. Diurnal singing behavior in Field Sparrows has been studied extensively (Nelson and Croner 1988, 1989a, 1989b, 1991, Carey et al. 2008), and one study has reported nocturnal singing in this species (Walk et al. 2000). During the day, Field Sparrows regularly sing two song types distinguished by their acoustic structure and function; a simple song type (2-3 notes, Fig. 2.1) is regularly used in male-female interactions and a longer, and more complex song type (4-6 notes,

Fig. 2.1), is used exclusively in male-male counter-singing interactions during dawn (Nelson and Croner 1991, Carey et al. 2008). Based on the different functions of the song types during the day, I expected nocturnal songs to have different seasonal patterns throughout the breeding season. If simple songs during the day are used to attract social mates, then I expected males using nocturnal simple songs early in the season when most pairing of social mates occurs. If complex songs during the day are used primarily in male-male interactions, particularly territory and mate defense, then I expected nocturnal songs them to be used more frequently later in the season, after most social pairing is complete and during the peak period of reproduction (egg laying and incubation periods). I also expected that if nocturnal songs clustered after dusk or before dawn, nocturnal singing might simply be an extension of dusk and dawn chorusing. These information would provide additional insight into the function of the singing behavior.

## **METHODS**

### **Study site**

I collected sound recordings from April 6<sup>th</sup> to July 15<sup>th</sup> of 2012 at Kennekuk Cove County Park, Illinois, USA (40° 11.5' N, 87° 42.9' W). Discreet grassland patches surrounded by oak-hickory forest dominate Kennekuk Cove Park. The area was closed to the public and not artificially lit at night. I recorded Field Sparrows in six grassland patches varying in size from 2-10 ha.

### **Study species**

The Field Sparrow is a common and widely distributed socially monogamous songbird in eastern North America. Field Sparrows breed in old successional fields, brushy pastures and woodland openings and edges (Nice 1943, Best 1977a). Field Sparrows are considered partial migrants

because individuals from the southern part of the species' range remain on the breeding grounds in winter and individuals from my study area migrate south for the winter (Carey et al. 2008). Females arrive in Kennekuk Cove Park, IL between April 15 through May 15<sup>th</sup> (10-20 days after males) and pair formation usually occurs within two days after their arrival. The breeding season of the Field Sparrow lasts 10-12 weeks with first clutches laid the last week of April and the last nests fledging young birds at the end of July (Best 1977b). Double brooding is common in Field Sparrows and pairs usually re-nest after predation or desertion (Best 1978). Field Sparrows engage in extra-pair mating behavior and an estimated 19% of offspring are sired through extra-pair mating (Petter et al. 1990).

### **Nocturnal Song Recording**

I recorded nocturnal song on 100 nights using six Stereo Autonomous Acoustic Recording Units (SM2<sup>®</sup> - Wildlife Acoustics, Inc., Concord, MA). SM2 recorders were placed within a male territory located near the center of each grassland patch. I recorded every night from 21:00 to 04:30 hrs to avoid recording dusk and dawn singing activity periods. Recorders were scheduled to turn on every 30 minutes and collect sound for a 10 minute period. Recorders were able to effectively record sound within a 100 m radius (Celis-Murillo in prep.), therefore, I recorded primarily the male of the territory in which the SM2 recorder was placed and at most 2-3 individual neighbors. Field recordings were made in stereo at 16 bits and 44.1 kHz.

### **Interpretation of Acoustic Recording via Automatic Recognition and Detection Data**

I used Songscope 4.1.3A software (Wildlife Acoustics, Concord, MA) to automatically scan through audio recordings and find the most likely occurrences of a specific vocalization of

interest. I built “recognizers” using a catalog of recordings taken from the individual males in established territories within the study site and at the time of the study. Recordings of focal males were made using Telinga Stereo Parabolic microphones and Sony M10 digital recorders. I made an acoustic signal recognizer for each of the two song types of Field Sparrow (simple and complex) using relevant samples. The recognizers used training data in the form of annotations highlighting each song category in the song catalog recordings. The recognizer made for simple songs was limited to a range of 2460.94 to 5000Hz as all simple calls recorded in the catalog fell within this range. I used 256-point Fast Fourier Transform (FFT) with an overlap of  $\frac{3}{4}$  to output the frequency spectrum. The simple recognizer had a maximum syllable length of 301ms, maximum syllable gap of 96ms and a maximum song length of 4045ms. The recognizer made for complex vocalizations was limited to a range of 2375 to 8000Hz and had a 256-point FFT with an overlap of  $\frac{3}{4}$ . The maximum syllable length was 308ms, the maximum syllable gap was 100ms, and the maximum song length was 6400ms.

I manually examined the data in 168 randomly chosen ten-minute recordings using the program Audacity (open source software) to ensure Songscope provided accurate identification and detection data. Audacity allowed me to open individual 10-minute audio files, use the spectrogram view mode, and scan visually for detection of Field Sparrow songs. Using Audacity and zooming and moving through the spectrogram I were able to locate nocturnal songs even if they were low amplitude (faint) and incomplete. I then compared the manually scanned recordings to the Songscope recognizers. Songscope detected only 37 of the 74 songs I detected via manual scanning. All signals missed by Songscope were very faint signals and in most cases these signals were not discernable unless the “zoom in” function in Audacity was applied directly to the song. I considered low amplitude signals as songs produced by birds singing  $>100$

m from my recorders, and most likely from different grassland patches. Therefore, I did not include them in the data and used Songscope to detect only high quality and high-amplitude signals. Finally, the 10-minute recordings were amplified by 10 dB and scanned using both recognizers. All detections by Songscope were manually examined to screen out false positives and I identified time, date and type of song category (simple or complex) for each song detected.

### **Statistical analyses**

I used a generalized linear mixed model with a logit link and binomial distribution to investigate the patterns in the probability that a simple and complex song was recorded during each 10-minute observation period within a territory. I fit six different models investigating the influence of Julian date and daily time period within the season to reveal seasonal and nightly patterns. Time period was included as a fixed effect because each period represented a discrete 10 minute period. I accounted for the dependence among male territories by incorporating the location of the recorder as a random effect. I compared model fit using Bayesian Information Criterion (BIC, Schwarz 1978, Aho et al. 2014). All models were fit using the glmer option in the lme4 package in R (R Development Core Team 2008).

### **RESULTS**

I collected 7,938 ten-minute recordings across six different grassland patches on 100 nights throughout the breeding season. I detected Field Sparrow song (simple and complex) in approximately 10% (821) of recordings. Field Sparrows sang simple songs in 3.6% (304) and complex songs in 6.9% (573) of all recordings. I found a distinct seasonal pattern in Field Sparrow song, but little evidence for any pattern throughout the night. For instance, the

probability of detecting a simple song peaked at the start of the breeding season and began tapering off within 2-3 weeks (Figure 2.2). The probability of detecting a complex song increased for approximately a month following the arrival of males, peaking during the period when most females were incubating eggs, before tapering off as the breeding season wound down (Figure 2.2). The probability of detecting a simple and a complex song were best described by models with the quadratic of Julian date (Table 2.1), suggesting a strong seasonal pattern in the occurrence of simple and complex songs. There was little support for any nocturnal pattern in night song, (i.e. models with time across the night showed little support; Table 2.1), suggesting that songs were randomly spread across the night and not clustered around dusk or dawn. Additionally, nocturnal songs at night were produced as single, isolated songs and are sung irregularly throughout the night; in contrast to both song types being regularly sang in long bouts (series of continuously repeated songs) during the day.

## **DISCUSSION**

Male Field Sparrows sang both complex and simple songs at night. I recorded both song types during the early stages of territory settlement and mate acquisition. However, as the breeding season progressed the frequency of the simple song decreased, while the occurrence of complex song increased, reaching its peak approximately one month after arrival on the breeding grounds and during the height of reproductive activity (late nest-building and egg-laying). While these data does not provide sufficient information needed to evaluate the specific reproductive function(s) of nocturnal song, the seasonal patterns of nocturnal singing suggest that nocturnal singing is not a random behavior occurring at night and appears to be a behavior associated with



the reproductive activities of the Field Sparrow. Furthermore, the seasonal patterns of simple and complex songs suggest they may serve similar functions to at night as they do during the day.

In my study, the arrival of females on the breeding grounds and the peak period of reproductive activities corresponded with the occurrence of each of the two song types, simple and complex, respectively. Although song types may not contain exclusive information for intra- and inter-sexual functions (Kroodsma et al. 1989, Morse 1966, Price and Crawford 2013), song types in the Field Sparrow appear to be determined largely by the different reproductive activities across the breeding season and serve different functions. Other studies have also found similar patterns in dawn and mid-morning singing behaviors. For example, during the early phase of the breeding season, established but unpaired territorial male Yellow Warblers (*Setophaga petechia*) and Chestnut-sided Warblers (*Setophaga dominica*) use one song type to attract females moving through their territories, while later in the season they use another song type to defend territories, repel male intruders prospecting, and attract for extra-pair mates (Morse 1966, Kroodsma et al. 1989, Weary et al. 1994). Similar patterns have also been found in other diurnal species that vocalize at night. For instance, Nightingales have two distinct song types (whistle and non-whistle song) that are used for different functions (Hultsch and Todt, 1996, Naguib et al. 2002); the whistle song appears to be important in attracting females, while non-whistle songs in male-male interactions (Kunc et al. 2005).

While the seasonal patterns of nocturnal simple and complex songs in Field Sparrows are consistent with the functions of these song types during the day, I observed important differences between day and night. Nocturnal songs are produced as single, isolated songs and are sung irregularly throughout the night. In contrast, during the day, both song types are produced regularly in long bouts (series of continuously repeated songs). Long song bouts and frequent

delivery are likely to improve their effectiveness at attracting social mates and defending territories and repelling intruders through counter-singing. Consequently, the short, irregular songs may serve different functions during the night than the day, such as communication between social mates (Vickery et al. 1996), signaling to extra-pair mates (Naguib et al. 2001), or repelling male intruders seeking extra-pair copulations with their mates (Amrhein et al. 2003). Additionally, while I could not rule out the possibility that some sporadic songs were produced in response to disturbance events, such as wind, rain or predation pressure, as documented in other species (*Larus* Gulls, Southern et al. 1983; Jays, *Aphelocoma coerulescens*, Carter et al. 2007; Peahens, *Pavo cristatus*, Yorzinsky and Platt 2012), the seasonal pattern of song types found in my study suggest that disturbance is not the primary reason for the occurrence of nocturnal songs in the Field Sparrow.

I could not characterize individual nocturnal singing rates because my data only allowed us to estimate the number of songs detected within an area of recording (soundscape level). Male prospecting behavior is well documented in some species that also sing at night (Amrhein et al. 2003, Chiver et al. 2008, Roth et al. 2009, Ward et al. 2014) and usually occurs at the peak of reproductive activities (Naguib 2001). Therefore, if male intruders are also responsible for the nocturnal songs I detected, simple songs may be attributed to intruder males trying to attract mated females, while complex songs may be used by intruders challenging resident males (Norton et al. 1982, Arcese 1987, Sprau et al. 2014).

In summary, nocturnal song in the Field Sparrow likely plays a similar role in reproductive activities as diurnal song. Simple songs may serve primarily for inter-sexual interactions while complex songs may serve for intra-sexual interactions. Studies of nocturnal song are very limited, often encompass a short period of time, or are anecdotal in nature. The

variation between studies may be due the different reproductive stages experienced by males in those studies (Tyler and Green 1996, Naguib 2001, Sprau et al. 2012). While nocturnal song is not nearly as prevalent as diurnal song, understanding the function of nocturnal song may provide key information in understanding the reproductive strategies of Field Sparrows and the many other species that sing at night. Further studies on the nocturnal songs of diurnal birds, particularly studies that quantify individual variation in nocturnal singing and playback studies that reveal conspecific responses to different song types would provide additional insight into this unique behavior.

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## FIGURES

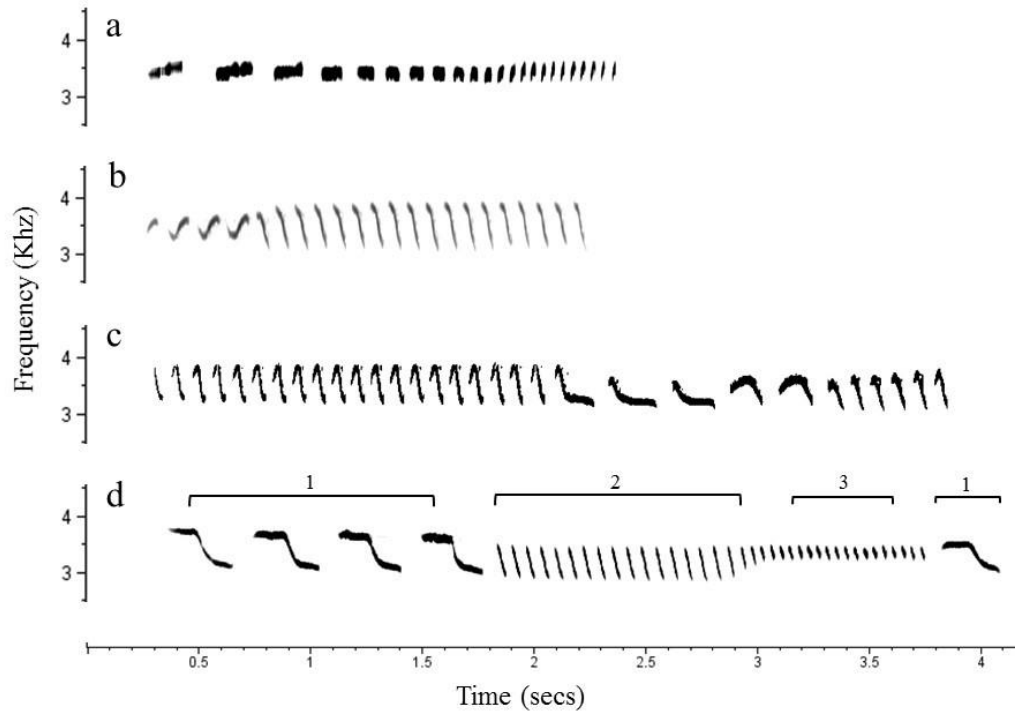


Figure 2.1. Examples of simple (a-b) and complex (c-d) song of the field sparrow. Complex song (d) denotes three syllable types (1, 2, 3) and one repeated syllable within the song. Songs were recorded during the breeding season 2012 in Kennekuk Cove Park, Vermilion County, IL.

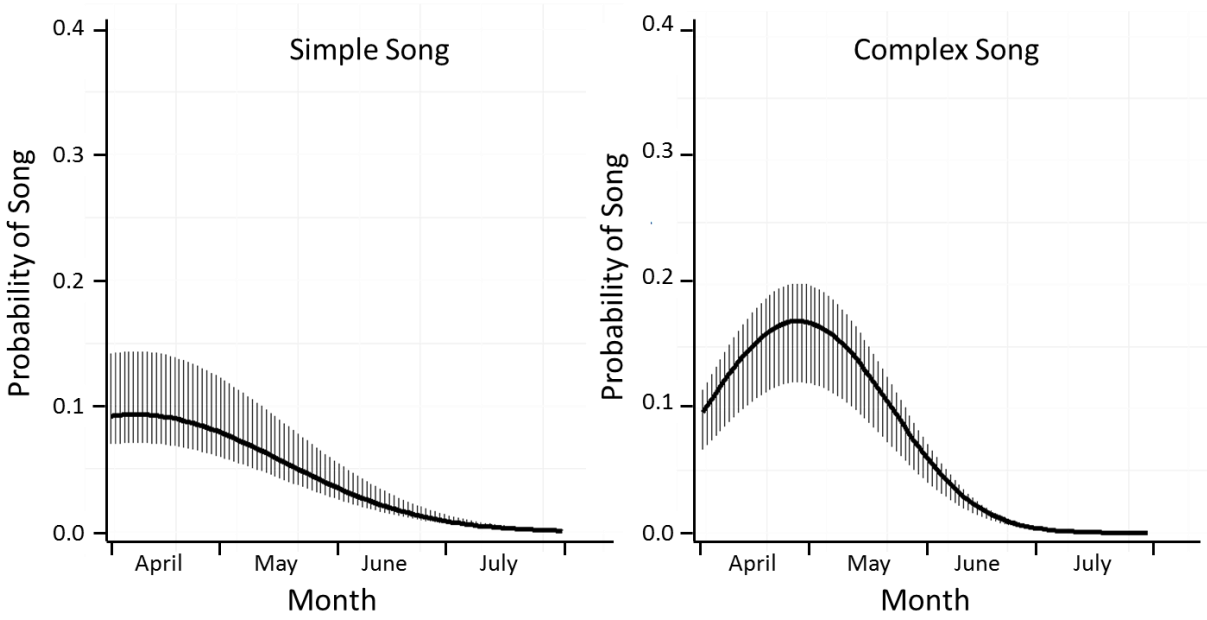


Figure 2.2. Probability of detecting Field Sparrow simple and complex nocturnal songs in a 10-minute recorded session in Kennekuk Cove County Park, Illinois, USA. Data are from six grassland patches recorded during breeding season 2012. 95% confidence intervals are included.

## TABLES

Table 2.1. Comparison of candidate models predicting the probability of simple and complex song during the night in the Field Sparrow. Data were collected during the breeding season of 2012 in Kennekuk Cove County Park, Illinois, USA. Models were ranked based Bayesian Information Criterion (BIC).  $K$  is the number of model parameters and  $\Delta\text{BIC}$  is the difference in BIC from the top model.

Model	Simple Song				Complex Song		
	K	Dev.	BIC	$\Delta\text{BIC}$	Dev.	BIC	$\Delta\text{BIC}$
Date + Date <sup>2</sup> (Seasonal pattern and quadratic effect on Julian date)	4	3506.6	3542.7	0	2329.9	2366.0	0
Time + Date + Date <sup>2</sup> (Seasonal and nightly patterns and quadratic effect on Julian date)	19	3469.7	3641.1	98.4	2231.4	2402.8	36.8
Date (Seasonal pattern)	3	3660.1	3687.2	144.5	2379.2	2379.2	13.2
Time + Date (Seasonal and nightly patterns)	18	3621.6	3784.0	241.3	2254.2	2416.6	50.6
Constant	2	3957.7	3975.8	433.1	2524.8	2542.8	176.8
Time (nightly pattern)	17	3912.8	4066.1	523.4	2418.8	2572.2	206.2

## CHAPTER 3

### THE FUNCTION OF NOCTURNAL SONG IN THE FIELD SPARROW

(*SPIZELLA PUSILLA*)

#### INTRODUCTION

Nocturnal vocalizations are typically considered a characteristic of nocturnal birds. Nonetheless, recent evidence has shown that many diurnal birds also sing at night (Barclay et al. 1985, Loughheed and Handford 1999, Perrault 2014). Studies suggest that singing at night may serve similar reproductive functions as diurnal song, attracting females (Tyler and Green 1996, Betts et al. 2008, Roth et al. 2009) and/or territory or mate defense (Luschi and Del Seppia 1996, Naguib et al. 1999). Although these explanations for nocturnal song in diurnal birds are reasonable, they are almost entirely based on a small subset of diurnal species with regular and well-developed nocturnal singing habits (i.e., Corncrake, *Crex crex*, Tyler and Green 1996; Nightingale, *Luscinia megarhynchos*, Amrhein et al. 2002), and do not consider the many diurnal species that only sing occasionally or rarely at night (La 2012). In a comprehensive review of nocturnal singing in diurnal birds, La (2012) reported that out of 126 species that she was able to classify based on how frequent they vocalized at night, 52% were classified as regular nocturnal singers (singing long bouts of repeated song and continuously across the night), 27% as occasional nocturnal singers, and 20% as rare nocturnal singers. For the species that sing repeatedly and continuously (regularly) during the night, it is clear that nocturnal singing might provide singers the ability to effectively signal information regarding their location, identity, and quality, supporting the hypotheses proposed for the functions of nocturnal song. However, for the species that only sing infrequently (occasionally or rarely), nocturnal singing may serve different functions as it is

unlikely they provide large amounts of information on individual quality to effectively attract mates or repel intruders. In the previous Chapter, I documented that Field Sparrows sing the two song types documented for the species (simple and complex) both during daylight hours and at night. During daylight hours, complex songs serve an intra-sexual function and they are sung almost exclusively during the dawn, while simple songs serve an inter-sexual function and they are sung throughout the day (Nelson and Corner 1991). During the night, however, the function of nocturnal songs remain unknown. Chapter 2 documented the occurrence of Field Sparrows song types at night and highlighted a strong seasonal pattern; simple songs reach their peak frequency early in the season, coinciding with the arrival of female sparrows 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. Interestingly, Field Sparrow delivery of simple and complex songs at night was very different than during the day; songs at night are delivered sporadically as single, isolated songs, whereas during the day they are delivered in long bouts or series of continuously repeated songs.

Nocturnal prospecting for extra-pair mates at night has been documented in males and females of many species (Pedersen et al. 2006, Chiver et al. 2008), therefore, nocturnal singing in the Field Sparrow may function to signal extra-pair mates (inter-sexual function) or repelling intruders (intra-sexual function). Studies of female nocturnal prospecting behavior have shown that female prospecting coincides with nighttime singing by males (e.g. Naguib et al. 2001, Dalziell and Cockburn 2008), suggesting that short nighttime songs may attract extra-pair mates to males' territories while minimizing attention from the female's social mate, which could result in retaliation (e.g., withholding parental care Westneat 1988, Weatherhead et al. 1994). Short and infrequent calls may also represent a response from territory holders to male intruders, and serve

as a means to let intruders know that the territory holder is on his territory and aware of the intruder's presence (Arcese 1987).

The goal of this study is to understand the functional role of nocturnal song in Field Sparrows, particularly in the context of reproduction and acquiring extra-pair mates. To accomplish this goal, I used two approaches: (1) correlations of singing behavior with social factors (fertility stage and singing of other males in the neighborhood), and (2) experimental playbacks of vocalizations by intruder males. First, I used autonomous acoustic recording units (ARUs) and an automated detection and classification software (Songscope, Wildlife Acoustics, Inc., Concord, MA) to examine whether fertility stage, presence of neighbor song, and presence of intruder song were reliable predictors of simple and complex nocturnal songs in mated male Field Sparrows. If nocturnal songs have an intra-sexual function and serves for attracting mates, Field Sparrows should sing when their social mate was fertile. Alternatively, if nocturnal songs have an intra-sexual function and serves in territory and mate defense, nocturnal singing in Field Sparrows should be correlated with the presence of conspecifics singing near or within their territory. Second, I conducted a nocturnal playback experiment to explore how mated male and female Field Sparrows responded to simulated intruder songs at night. This experiment provides insight into the precise reproductive function of complex songs, specifically to distinguish between male-male and male-female interactions. I carried out the experiment across different fertility stages to determine whether resident males or females changed their response with female's fertility. If complex songs play a role in male-male interactions, then males should respond to simulated intruders nocturnal songs through counter singing and activity (i.e., movements at night), and that response would be greatest during the female's fertile period. Alternatively, if complex songs play a role in male-female interactions, females should respond

(become active and move at night) to simulated intruders, and similarly, female response should be strongest during her fertile period.

## **METHODS**

### **Study species and location**

The Field Sparrow is a diurnal, socially monogamous songbird that is sexually monomorphic with respect to plumage. They differ slightly in size; males are usually larger than females (Carey et al. 2008). The breeding season of the Field Sparrow last 10-12 weeks (Best 1977a). Females arrive on the breeding grounds between 15 April and 15 May (10-20 days after males), and pair formation usually occurs within two days of their arrival. Males tend to follow females during nest building, however, only females build nests and incubate eggs. Field Sparrows engage in extra-pair matings and at least 19% of offspring may be sired through extra-pair matings (Petter et al. 1990). The study was conducted in Kennekuk Cove County Park, IL, USA (40° 11.5' N, 87° 42.9' W). Kennekuk Park is composed of discreet grassland patches of varying sizes (2-10 ha) surrounded by oak-hickory forest. Each year 3-8 Field Sparrows established territories in each of these grassland patches and spatially formed clumped aggregations of territories separated by forest patches (hereafter 'neighborhoods'). In each of these neighborhoods, individual males interacted with their neighbors daily via dawn singing behavior (counter-singing). Kennekuk Park was closed to the public during the night and did not have artificial light at night during the study.

### **General Field Methodology**



I studied 28 mated territorial Field Sparrows from April to July of 2012 and 2013. Eleven males were studied in 2012 and 17 males in 2013. Only one male was studied in both years. Each year, I used spot-mapping and behavioral observations at the beginning of the season to delineate the territories of 60-70 males distributed along 7-10 different neighborhoods of varying sizes. I also captured and banded male and female Field Sparrows using targeted mist-netting. Individuals were banded with unique-numbered USGS aluminum and colored plastic leg bands. Age (when possible), sex, and morphometric variables were recorded for all individuals. A small proportion of birds were aged using a combination of plumage characteristics (primary coverts, primaries and secondary) following Pyle (1997) and large proportion of individuals were not aged. Sex was identified by observing cloacal protuberance (males) and brood patches (females). For each territorial male and its mate, I collected information on their reproductive behaviors (mating-no nesting, nest building, laying eggs, incubating, feeding nestlings and caring for fledglings). Breeding stages were later combined in more conservative periods: prefertile (no nesting), fertile (nest building and laying eggs), and postfertile (incubating, feeding nestlings and caring for fledglings) following Akcay et al. (2012). I also monitored territory ownership and establishment date for each individual throughout the season. This helped me to ensure that ownership of territories was not changing through time. Territory switching in my population appears to be rare as I only found two individuals that switched territories to a different neighborhood during my study. These individuals were not included in my analyses. In addition to monitoring reproductive behaviors, I recorded the songs of each individual territory-holder in my population and over the three years of the study. Recordings were collected as a daily basis during the three year study. Recordings were collected using a combination of Telinga Stereo Dat microphones, Wildtronics Parabolic microphones, and Sennheiser MKH60 shotgun microphones. Recordings

were made using Sound Devices 722 and Sony M10 digital recorders at 16 bits and 44.1 kHz. During the years of the study, I also obtained data on moon illumination for each day of the breeding season. Data was requested to the U.S. Naval Observatory.

### **Recordings, detection and song classification**

*Autonomous acoustic recordings.* I used six stereo Autonomous Acoustic Recording Units (SM2, Wildlife Acoustics, Inc., Concord, MA) to collect nocturnal singing behavior of Field Sparrows throughout their reproductive activities. Recorders were placed at the center of territories of males previously captured, banded, and identified as paired. Recorders were rotated throughout neighborhoods to collect data on different individual males throughout the season. I never recorded two territories simultaneously in the same neighborhood. Recorders were programmed to collect sound for 10 minute periods every 30 minutes throughout the night (21:00 – 4:30 hrs.), collecting a total of 16 recording periods per night. Recorders effectively recorded the male of the territory in which the SM2 recorder was placed and at most 2-3 individual neighbors within each neighborhood (approximately recorded sound within 100 m radius).

*Detection of Field Sparrow songs.* I used Songscope 4.1.3A software (Wildlife Acoustic, Concord, MA) to automatically scan the audio recordings I collected using SM2 recorders and to find the most likely occurrences of a Field Sparrow vocalizations. I built recognizers of each of the two song types of the Field Sparrow (simple and complex) using recordings of focal males in established territories within the study site and at the time of the study. These high-quality recordings with low-level background noise and no overlapping sounds were used for Songscope recognizers. Recognizers used the recordings in the form of annotations and to build a set of

training data to scan throughout all the audio recordings collected via SM2 recorders. The recognizer built for scanning for simple song type had a range of 2460 – 5000 Hz, 256-point Fast Fourier Transform (FFT) with an overlap of  $\frac{3}{4}$  to output the frequency spectrum, maximum syllable length of 301ms, maximum syllable gap of 96ms, and limited to maximum song length of 4045ms. The recognizer for the complex song type had a range of 2375 to 8000Hz, 256-point FFT with an overlap of  $\frac{3}{4}$ , maximum syllable length of 308ms, the maximum syllable gap of 100ms, and was limited to a maximum song length was 6400ms. These settings were very conservative and allowed the detection of many more detections than just the Field Sparrows (e.g. insects or other sounds at the same frequency bands).

To ensure Songscope and my recognizers provided accurate identification and detection data, I manually examined data in randomly chosen 168 ten-minute recordings using the program Audacity (open source software). Audacity allowed me to visually scan and detect Field Sparrow songs, while checking that no songs were missed. Using Audacity I located nocturnal songs even if they were of very low amplitude (faint) and incomplete. Once the 168 10-minute recordings were scanned manually, I ran the Songscope recognizers on the same recordings and assessed results. Out of 74 songs detected at night via manual scanning using Audacity, only 37 songs were detected by Songscope. However, I noted that all signals missed by Songscope had very low amplitude and appeared as faint signals in spectrograms (in most cases not discernable unless the “zoom in” function in Audacity was applied directly to the song). These low amplitude signals are likely songs produced by birds singing very far away (>400 m) from my recorders, and most likely from different grassland patches. Therefore, I did not include them in the data and let Songscope detect only high quality and high-amplitude signals (only signals within the territory where the recorder was placed and at most 2-3 contiguous neighbors). After

confirming that Songscope accurately detected and identified nocturnal vocalization of Field Sparrows within the territory and the grassland patch of interest, each of the 10-minute recordings was scanned using both, simple and complex recognizers. All detections by Songscope were examined manually to screen out false positives. I manually reviewed each individual detection and confirmed identifications by visual observation and in some instances, by listening. Ultimately, for each detection, I identified the exact time of each recording, the date and whether the song was simple or complex.

*Individual identification of residents, neighbors and intruders via acoustic signals.* I used an individual acoustic identification approach to identify and quantify the nocturnal singing effort (simple and complex songs) of resident males, neighboring males, and intruding males across the different fertility stages. This method has been used as an alternative marking technique to monitor and census diurnal and nocturnal animal populations (Peake et al. 1998, 2001, Rebbeck et al. 2001, Grava et al. 2008), to examine long-distance movements (Mikkelsen et al. 2003), residency and adult turnover (Delpont et al. 2002), and to monitor specific singing behaviors (duetting, Klenova et al. 2008), particularly in situations where individuals are difficult to detect or when they are sensitive to disturbance (Terry 2002, Terry et al. 2005, Budka et al. 2015). In order to use this method and accurately classify each Field Sparrow song as resident, neighbor, or intruder, I followed Foote et al. (2012) to assess whether the variation in song characteristics was greater among individuals than within individuals.

I selected the highest quality recordings from my large set of focal recordings (see general methods) and randomly, when possible, selected 10 songs per individual from these recordings. My selection procedure resulted in 338 complex songs from 39 (average  $\pm$ SE songs

per individual:  $8.6 \pm 0.3$ ) individuals and 355 simple songs from 46 individuals (average  $\pm$ SE songs per individual:  $7.7 \pm 0.4$ ). To test whether songs differ significantly between individuals, I compared each song against all other songs from my samples using the correlation tool in Raven 1.4 (Cornell Lab of Ornithology, Ithaca, NY). 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. I reduced any effects of background noise, such as low-level wind and other non-focal sounds, by setting the power level to 0 dB of any signal with an amplitude below -70 dB using the clipping function. Correlation values were standardized resulting in values between 0 and 1 (with values of 1 indicating that two samples are identical). Previous to the analyses, all recordings were normalized to -1 dB in Audacity (version 2.0.5; Open source). I tested whether variation in songs within individuals was lower than variation in songs among individuals by performing an analysis of similarities (ANOSIM) in the R package *vegan* (version 2.0-10; Oksanen et al. 2013; R Core Team 2013). ANOSIM tested whether there were significant differences between groups of sampling units. ANOSIM tests were based on 10,000 permutations. The analysis of similarities (ANOSIM) showed that Field Sparrow simple and complex songs were more similar within individuals than across individuals (Simple song:  $R = 0.8$ ,  $p = 0.00009$ . Complex song:  $R = 0.9$ ,  $p = 0.00009$ ). Using this information, I created a catalog of song samples for each individual in the population (Figure 3.1). Once the song catalog was built, each individual Field Sparrow song in my recordings was easily matched to a resident territorial male, neighboring males, intruder, or unknown individuals. *Residents* refers to males holding a territory where I placed the autonomous recorders, *neighbors* refer to males holding territories in the same grassland patch (i.e. same neighborhood) adjacent to or within 200 m of the resident, and *intruders* are males with

territories in a spatially separated grassland patch and in most cases >300m from the residents' territories. Some songs in my recordings were not identified and they were classified as unknown birds.

### **Experimental playback experiments**

*Nocturnal automated playbacks.* I conducted nocturnal playback experiments on 15 Field Sparrow pairs (subjects) in June 2014. I focused my experiment on complex songs because they were more common at night than simple songs. Playbacks were conducted in an automated fashion using FOX PRO speakers (Model NX4) connected to a digital timer switch (TM618-4) and a Powersonic 12V battery (Model PS-12120). Digital timers allowed me to program the playback systems to start the trials at specific times of the night and days. Having a programmable and automatic playback systems allowed me to simulate singing intruders while avoiding potential disturbance on sleeping birds. I conducted playbacks on each Field Sparrow pair at the border of each of the pair's territory. Due to the short length of the nocturnal song of the Field Sparrow, the stimulus I used for my experiments were also very short (2 to 5 seconds of length). Because my interest to test if subjects responded differently across fertility stages, I conducted up to seven different playback experiments to each subject over the different fertility stages of each mated pair. Due to the nature of stimulus presented to subjects (very short stimulus), I expected subjects not to be influenced if more than one playback experiment was conducted over different days. I never conducted more than one trial per day for a single bird, as suggested by Kroodsma (1989). Trials were conducted randomly at 23:00, 0:00 or 2:00 hrs.

*Playback stimuli.* Using Field Sparrow recordings collected within the state of Illinois but not from my population, I constructed seven different playback tracks composed of three different stimulus in varying orders – an example of a relatively long complex song, a relatively short complex song, and a control song of either Northern Cardinal (*Cardinalis cardinalis*) or Carolina Wren (*Thryothorus ludovicianus*). In contrast to most studies that used playback stimulus of repeated songs over several minutes, my stimulus were only single songs that lasted between 2 to 5 seconds; simulating Field Sparrow nocturnal songs as they usually occur at night (sporadically and only single songs, Chapter 2). I used examples of two different song lengths of the complex song because, although no study has examined responses of Field Sparrows to song length variation, recent sparrow studies have shown that song length variation contains information about the aggressive motivation of individuals (Nelson and Poesel 2012), therefore, different lengths in complex songs could influence subject's responses. I used two different species as controls (Northern Cardinal and Carolina Wren) because they also differ in song length. Within a playback track, each of the three stimulus were separated by 10 minutes of silence. The total length of each playback track was 31 minutes. The three stimulus in each track were arranged in random and different sequence.

*Quantifying male and female activity responses.* To monitor male and female activity (active-not active) responses to simulated intruders, I radio-tagged 8 males and 15 mated females. Sparrows were fitted with radio-transmitters weighting 0.5 to 0.6 g (JBJC Corp., Fisher, IL, US). This weight represented ~5% of birds' average weight (average weight of Field Sparrows is 12g). The transmitters used to track birds were glued to birds' backs following Raim et al. (1977). I used automated radio telemetry systems (ARTS, JBJC Corp., Fisher, IL, US) to

track activity (active-not active) of male and female Field Sparrows during playback experiments. ARTS system was comprised of four towers with autonomous radio-telemetry receiving units located 400-950 meters apart and strategically placed in the study area to collect data from each radio-tagged bird of study (Figure 3.2). The height of towers was 12-14 meters. Each receiving unit was connected to an array of six three-element Yagi antennas (Nighthawk model - JDJC Corp., Fisher, IL) attached to the top of towers. The six Yagi antennas were positioned at 0°, 60°, 120°, 180°, 240° and 300° to 360° detection coverage. Receiving units collected up to three activity reading per minute per bird over the duration of the transmitter's battery life ( $24 \pm 6$  days). ARTS recorded the signal strength (in dB) and the pulse interval (ms) characteristic of each radio transmitter mounted in birds and subsequently, used to estimate whether the bird was active or not after stimulus during playback experiments. Although males appear to be occasionally active and irregularly sing during the night, Field Sparrows were expected to sleep, being inactive throughout most of the night. Therefore, I considered any activity within 5 minutes after my play back stimulus to be a response to my simulated male intruders (Figure 3.3). I used a threshold of change of 3.0 dB and a bearing change of  $1.8^{\circ}$  to determine a movement, these thresholds were determined from the same study system (Ward et al. 2013). For further details on this methodology see Kays et al. (2011), Steiger et al. (2013) and Ward et al. (2013).

*Quantifying male singing responses.* To monitor male singing responses (singing-no singing) to simulated singing intruders, I placed ARUs (SM2s) on the center of the territory of the focal male to assess their singing activity immediately after being exposed to playback treatments. ARUs allowed me to monitor all singing activity. Recorders were programmed to



collect sound for the entire night on the day of the trial (from 9:00 – 4:00 hrs.). Recorders collected sound at 16 bits and 44.1 kHz. Although males sing occasionally during the night, male Field Sparrows were expected to sleep throughout the night and being quite most of the time. Therefore, I considered any singing activity within 5 minutes of being exposed to my play backed stimulus to represent a response to my simulated male intruders.

### **Statistical analyses**

*Factors influencing nocturnal song in the Field Sparrow.* I used generalized linear mixed models (GLMM, GLIMMIX procedure, SAS 9.3) with binomial distribution and logit link function (Littell et al. 2006) to examine factors influencing nocturnal singing in the Field Sparrows. I examined song types (simple and complex songs) separately. My response variable was the presence and absence of nocturnal song (coded as Yes = 1 and No= 0). I treated nocturnal singing data as binomial distribution because the nocturnal singing events across the night were very infrequent. I combined the 16 recording periods within nights into a single measure of presence or absence of nocturnal song in a single night. I treated the presence of territorial neighbors singing, intruders singing, fertility stages of resident's mates, moon illumination and interactive combinations as fixed effects, and bird identity as a random effect. To take into account that the nocturnal song in the Field Sparrow shows a strong seasonal pattern (Chapter 2), I included a quadratic term of Julian date in each candidate model. A quadratic term allowed me to examine the variable of interest (fertility stage and songs of conspecifics), without confounding my results with seasonal patterns of the nocturnal songs. To assess goodness-of-fit of my models, I compared AICc scores of candidate models to a model with only the quadratic effects (null model). Throughout the chapter the term Julian date always includes the quadratic

term; however, I simply refer to it as Julian date. I also included moon illumination in my models to account for the possibility of increased activity associated with elevated light levels (Hill et al. 2005, Miller et al. 2006, Kempenaers et al. 2010, York et al. 2014). I evaluated candidate models using Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson 2002).

*Playback responses.* I used generalized linear mixed models (GLMM, GLIMMIX procedure, SAS 9.3) with binomial distribution and logit link function (Littell et al. 2006) to test whether males and females responded with activity (active-not active) to simulated territorial intrusions (short and long versions of the complex song or to control songs). My binary response variable was activity/no activity (coded as Yes = 1 and No= 0). I treated song type (coded as 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 and trial were treated as a random effects to account for potential non-independence for repeated samples (Kroodsma 1989). To assess whether males responded by singing to simulated territorial intrusions (short and long versions of the complex song or to control songs), I used generalized linear mixed models (GLMM, GLIMMIX procedure, SAS 9.3) with binomial distribution and logit link function (Littell et al. 2006). My binary response variable was song/no song from the territorial male (coded as Yes = 1 and No= 0). I 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 and trial were treated as a random effects.

## **RESULTS**

I investigated nocturnal singing in 28 mated male Field Sparrows. I collected 11,756 10-min recording periods across the 28 male territories, which represented nocturnal data on 1,624 nocturnal surveys (1126 in 2012 and 498 in 2013). I detected resident songs on 202 nights (70 simple songs and 132 complex songs), neighbor songs on 127 nights (44 simple songs and 83 complex songs), intruder songs in 141 nights (65 simple songs and 76 complex songs) and unidentified songs in 144 nights (52 simple songs and 92 complex songs) (Figure 3.4). The two best fitting models ( $<2 \Delta AICc$ ,  $\sum w_i = 0.78$ ) for predicting Field Sparrow nocturnal complex vocalizations included the presence of intruders and neighbors singing, breeding stage and Julian date. The next best model predicting complex songs ( $<4 \Delta AICc$ ,  $w_i = 0.17$ ) also included breeding stage and Julian date. The three models combined received most the weight of evidence ( $\sum w_i = 0.95$ , Table 3.1), indicating that the songs of conspecifics (neighbors and intruders) and breeding stage were correlates of Field Sparrow nocturnal complex song. Complex songs varied across the breeding stages; birds vocalized more during the fertile and postfertile periods than the prefertile period (Figure 3.5). As opposed to complex song, I did not find support for any of my investigated variables predicting the occurrence of Field Sparrow simple song (Table 3.2). Furthermore, simple songs did not vary across the breeding stages (Figure 3.6). I did not find any evidence of moon illumination or single fixed effects predicting nocturnal complex or simple songs (Table 3.1).

I investigated activity responses (active-not active) using ARTS on 6 males and 14 females. I conducted a total of 101 playback trials across the 20 experimental birds and over the breeding season of 2014. The average number of playback trials I conducted per birds was five (range = 1-7). I found that both males and females became equally active when exposed to nocturnal simulated singing intruders ( $F_{1,7} = 0.22$   $P = 0.65$ ). However, their responses varied

significantly by the type of the stimulus. Males and females responded significantly more to both short and long versions of the complex songs of the Field Sparrow than to control stimulus ( $F_{2,7} = 9.97$   $P < 0.009$ ) (Figure 3.7).

While males responded equally during prefertile and postfertile stages (I did not have data in the fertile stages because radios fell off, battery of radios died or due to other logistical issues), females responded more during the prefertile and fertile stages than the postfertile stages ( $F_{4,9} = 3.55$   $P = 0.053$ ) (Figure 3.8). In the case of males, I planned to analyze the singing responses of males to simulated singing intruders, however, although I collected acoustic data during the nights of each playback trial and on each focal experimental pair, I never detected a singing response from males. Therefore, I could not analyze these data. The finding that males never sang in response to simulated singing intruders was also supported by the data I collected using acoustic recordings across the years. When I quantified the detections of each song for the Field Sparrow detected by the automated detection and classification application (11,756 10-min recording periods among 28 territories), only in four occasions was more than one song recorded. Together, these two observations demonstrated that males do not sing in response to simulated singing intruders (i.e., counter singing) at night.

## **DISCUSSION**

Nocturnal complex song in the Field Sparrow, despite being an uncommon behavior, appears to have a role in extra-pair mate attraction and not in repelling intruders. Nocturnal complex songs of the Field Sparrow were predicted by the presence of singing by neighbors and intruders as well as the breeding stage of their social mate. However, the playback experiment demonstrated that resident males never sang in response to intruders. Additionally, while counter-singing using

complex songs is common during the dawn (Nelson and Croner 1991), I only found four instances where counter-singing occurred at night (out of 11,756 10-min recording periods). Overall, my results suggest that all males (residents, neighbors and intruders) were singing in response to the same social factor, i.e., the fertile stage of females in the neighborhood. Recent studies have demonstrated similar patterns. Taff and others (2014) in a study quantifying singing effort in a territorial bird demonstrated that they changed their effort according to the number of females fertile in their neighborhood. Their results suggested that males are aware of female fertility periods, even females with territories 400 m away.

The nocturnal playback experiment found that females become active (respond) upon exposure to simulated singing intruders and that they were more responsive when fertile. These results demonstrate that females are aware of males singing at night, and further supports the expectation that males should sing more when females are fertile. Further, these observations are consistent with nocturnal song in the Field Sparrow occurring more frequently during the peak period of reproductive activities (see Chapter 2). Female fertility in the Field Sparrows is known to be synchronous during the initial part of the breeding season (Best 1977b, Carey et al. 2008); however, as the season progresses, males minimize their effort at the nest and may sing to attract potential additional mates. While I do not know whether neighboring or intruder males were entering the resident male's territory when singing at night, it is highly likely that the resident male's social mate 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 extra-pair copulations.

From the female perspective, although nocturnal song is relatively rare compared to diurnal song on any given day, females were nevertheless likely to hear a non-social mate song.

Of all the nocturnal songs detected in my surveys, resident male songs (her mate) were detected only 43% of nights, while neighbors and intruders song on 27% and 30%, respectively. If females are engaging in extra-pair copulations at night (Pedersen et al. 2006, Chiver et al. 2008, Chapter 4), it is likely that potential extra-pair sires need to advertise their presence. The extra-pair sires likely need to sing in order to potentially alert (wake up) the female, and to coordinate a meeting location.

During daylight hours male Field Sparrows commonly sing loud and long bouts of complex and simple songs. In contrast, songs at night is much more rarely but may be easily detected as it occurs when there is less acoustic interference from songs of heterospecific and conspecific species. This advantage may help males attract the attention of females, even if they use 2-5 seconds songs. Network theory suggests that in social animals that have clumped territories, like the Field Sparrow, acoustic signals should be heard by most neighbors (McGregor and Dabelsteen 1996). Females, therefore, might be listening to all males displaying at night (Naguib et al. 2011). Interestingly, my playback experiment showed that, instead of singing, males physically responded (moved) in response to the playback stimulus, suggesting that males may attempt to repel intruders by approaching them and not by singing at night.

Nocturnal songs of the Field Sparrow are characterized by single, isolated vocalizations. Delivering single songs could be a tactic to achieve some level of “privacy” analogous to quite or soft songs in other species (e.g., Blackbirds, *Turdus merula*, Dabelsteen 1984, Robin, *Erithacula rubecula*, Dabelsteen et al. 1997). Single songs in the Field Sparrow may help them to attract females without attracting predators (Lima et al. 2005, Schmidt and Belinsky 2013) or causing conflicts with neighboring males (especially if their females are the ones being attracted). Quiet and soft songs have multiple functions depending on the species (Dabelsteen et al. 1998);

however, they are generally thought to be associated with secretively courting females. For example, Dunnocks, *Prunella modularis*, display quiet songs during the reproductive periods and their “secretive” vocalizations appear to help males to secure copulations, especially because multiple mates compete for access to fertile females and males attempt to disrupt their extra-pair copulations (Davies 1992). Similarly, Great Tits, *Parus major*, possess a short and quite-like vocalization that serves for courtship feeding and copulation (Gompertz 1961). Soft and quiet songs also serve in male-male interactions in Common Yellowthroats, *Geothlypis trichas*, for cooperative and/or non-cooperative purposes (Titus 1998).

Complex songs may be better suited for attracting potential extra-pair mates as they have more syllables and may provide more information on the quality of the individual producing them (Otter et al. 1997, Kempenaers et al. 1997, Poesel et al 2001). Additionally, the ability to identify individuals via song is increased when they contain more information (i.e., complexity). Recent research on the dawn singing behavior of Field Sparrows in the same system also has demonstrated that males change aspects of complex song (song rate, song length, song complexity) in response to their social mate’s fertility stage (Zhang et al. in review). Therefore, the use of complex songs at night might serve as an effective way to advertise the quality and identity of males to potential extra-pair mates.

I found that complex song was sung nearly twice as often as simple song. Simple songs are thought to have a role in male-female interactions and serve for long-distance communication (Nelson and Croner 1991), therefore, I expected simple songs to be more common at night if nocturnal songs were used for mate attraction. However, simple song was not predicted by the social or environmental factors I examined, despite the seasonal pattern observed in simple song when assessed at the neighborhood scale (Chapter 2). Thus, simple song does not appear to serve

a clear function in the reproduction of Field Sparrows. It is possible that the seasonal pattern of simple song reflects a different, yet possibly related seasonal factor. For example, simple song may serve as a way to attract migrating females to the site (for pairing), but not factor in the attraction of extra-pair mates once they have settled at the site. There remains the question of why roughly 40% of nocturnal songs are simple songs. Further research is required to understand why Field Sparrows sing simple songs at night.

More investigations are needed to reveal the function of single songs and irregular nocturnal singing in birds. Additional playback experiments on males and females at different times of the day, using simple and complex songs, and using songs from neighbors of different ages and individual quality would help further our understanding of the function of nocturnal song. These experiments also should examine the postures and physical displays during these nocturnal playback interactions as they may reveal whether responses are cooperative or non-cooperative and more importantly, if they lead to EPC. Generally, species that have more competitive interactions among conspecifics due to their dense populations exhibit more elaborated mating displays (e.g. singing modes) and demonstrate greater female choosiness for these displays (Darwin 1871, Anderson 1994, Price 2013). However, if the reason for the nocturnal interactions among males and females is prospecting for mates or extra-pair mates, then elaborate, repetitive, or loud displays may not be necessary. Instead, quiet, short and inconspicuous signals should be favored, similar to the nocturnal songs of Field Sparrows.

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## FIGURES

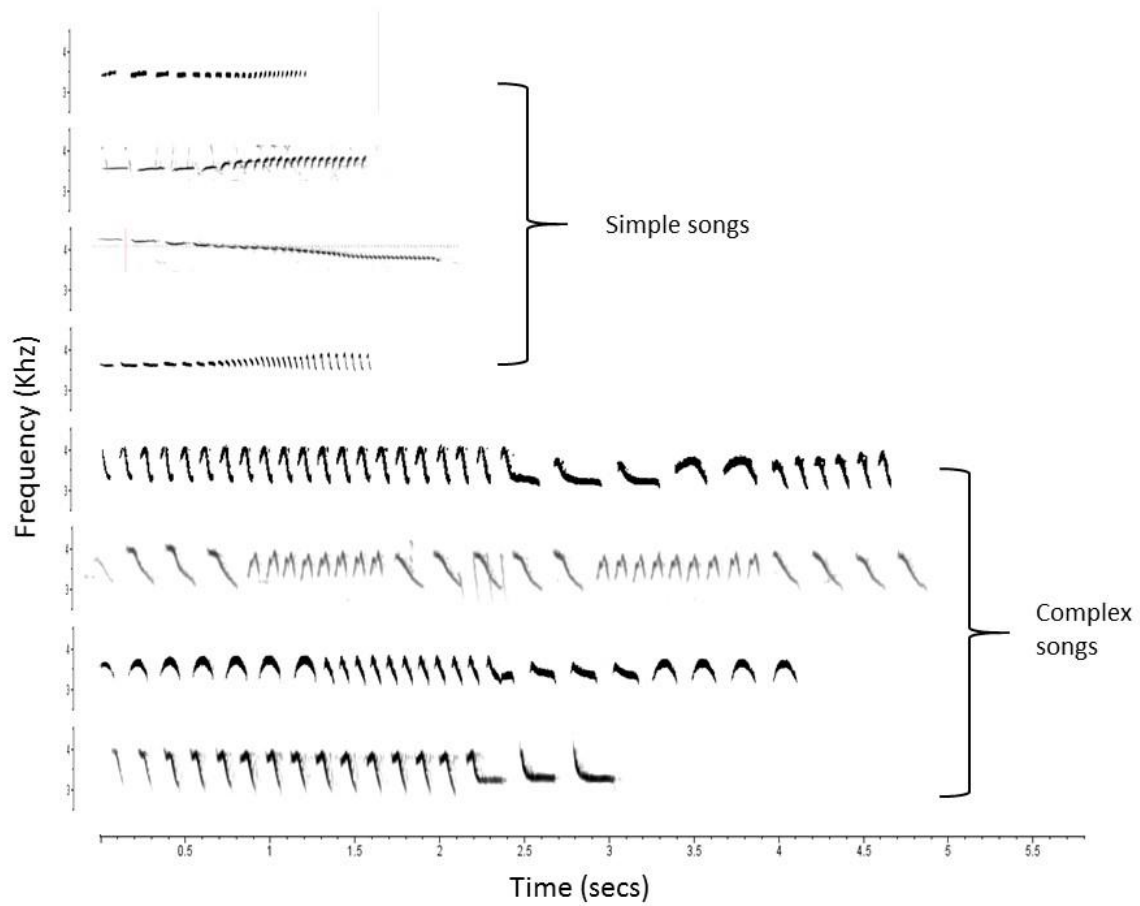


Figure 3.1. Spectrographic representation of differences in song characteristics (notes and syllables) among individuals. Figure shows four examples of simple songs and four examples of complex songs of four different Field Sparrow, *Spizella pusilla*. Data are from birds recorded in Kennekuk Cove Park, Vermilion County, Illinois, USA during the years 2012-2014.



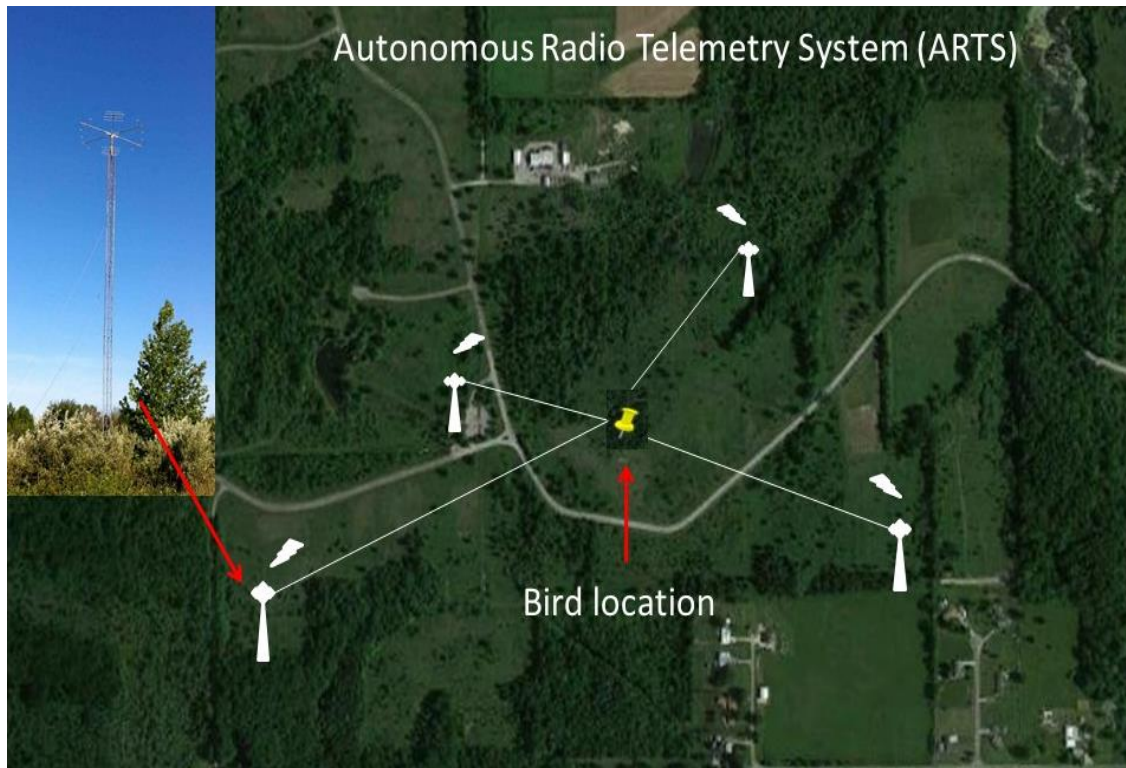


Figure 3.2. Graphic representation of the Automated Radio Telemetry System (ARTS) deployed in Kennekuk Cove County Park, Vermilion County, IL, USA to detect activity responses of males and females of Field Sparrows, *Spizella pusilla*, to simulated singing intruders.

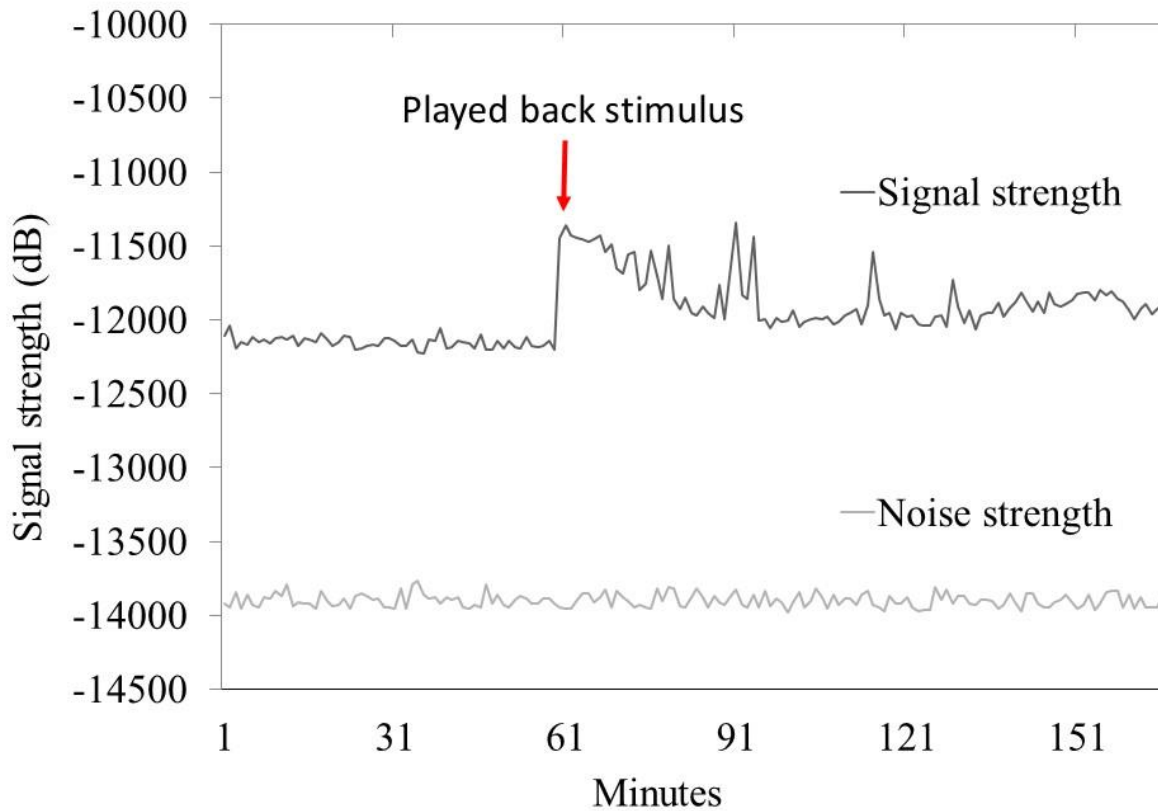


Figure 3.3. Graphic representation of the activity of a female Field Sparrow, *Spizella pusilla*, between 01:00 and 03:00 hrs. Note that after 60 minutes of inactivity (sleeping), a radio-tagged female showed activity in response to a simulated singing intruder (playback trial). The stimulus given was a single song of Field Sparrow. Black line shows signal strength (dB) from the radio-transmitter and gray 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, USA during 2014.

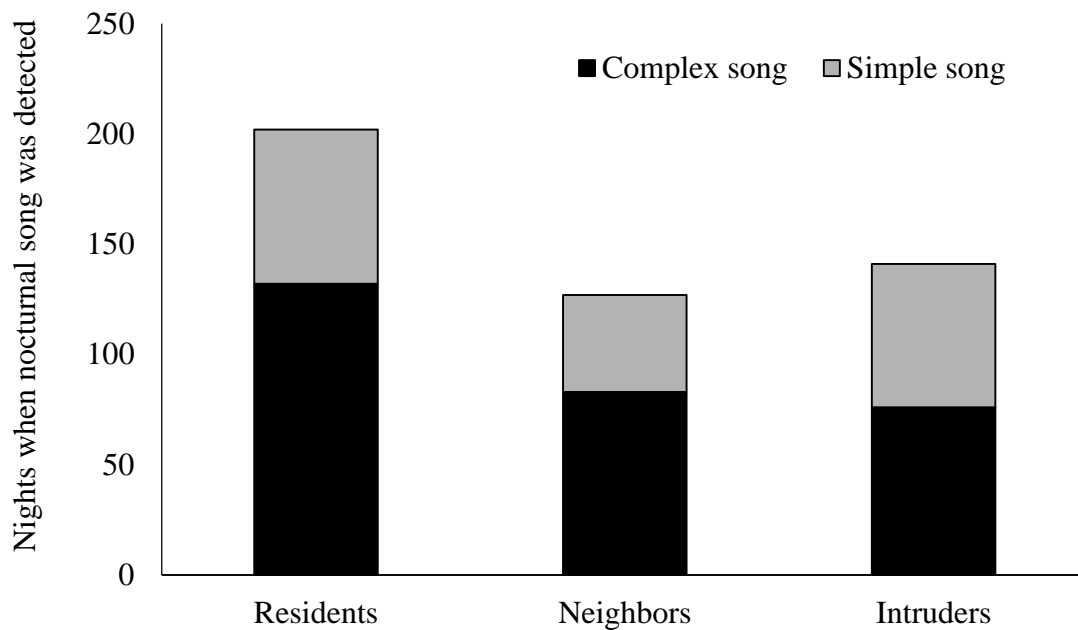


Figure 3.4. Total number of nights where Field Sparrow complex and simple songs were detected at least once during my surveys. Data are from soundscape recordings of 28 different resident bird male locations distributed across 10 grassland patches, representing a total of 1624 nocturnal surveys during the months of April and July of 2012-2013. Recordings were collected in Kennekuk Cove County Park, Vermilion County, IL, USA.

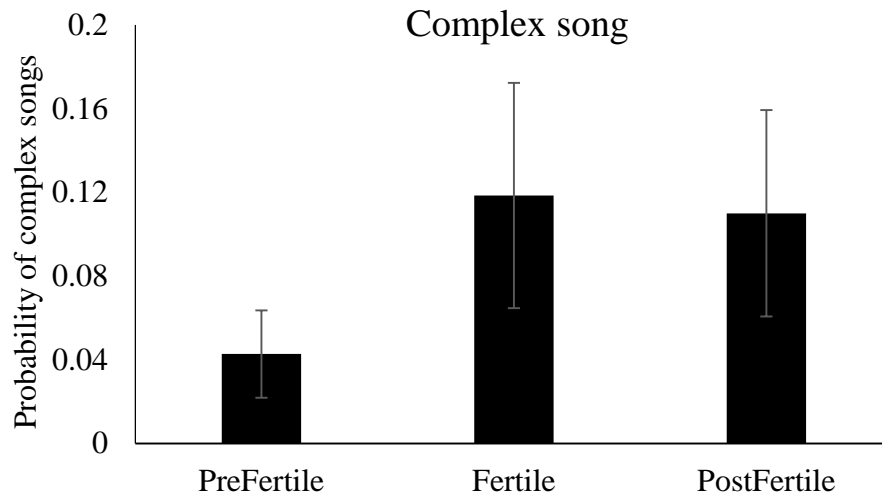


Figure 3.5. Probability and  $\pm$  SE of nocturnal complex songs in mated Field Sparrows, *Spizella pusilla* (n=28) across their mate's fertility stages. Recordings were collected in Kennekuk Cove County Park, Vermilion County, IL, USA during the years 2012-2013.

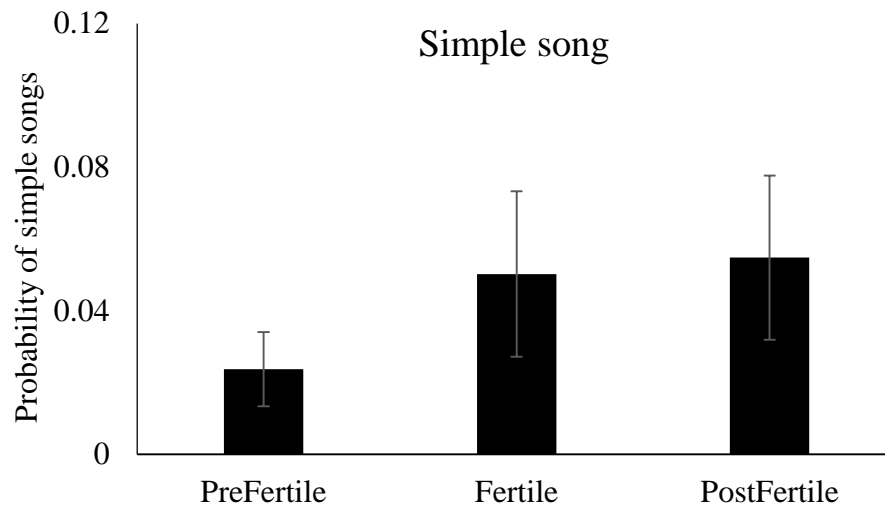


Figure 3.6. Probability and  $\pm$  SE of simple songs in mated Field Sparrows, *Spizella pusilla* (n=28) across their mate's fertility stages. Recordings were collected in Kennekuk Cove County Park, Vermilion County, IL, USA during the years 2012-2013.

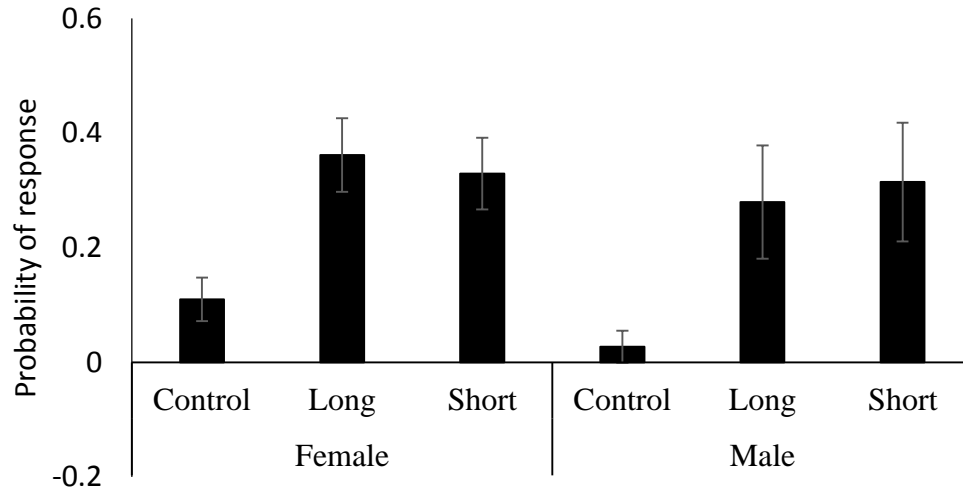


Figure 3.7. Probability of response (activity/no activity) and  $\pm$  SE of mated males and females of Field Sparrow, *Spizella pusilla* (n=20) to each of the stimulus presented during playback trials (control song, long complex song and short complex song). Responses were evaluated via automated radio telemetry systems (ARTS) in Kennekuk Cove County Park, Vermilion County, IL, USA during the year 2014.

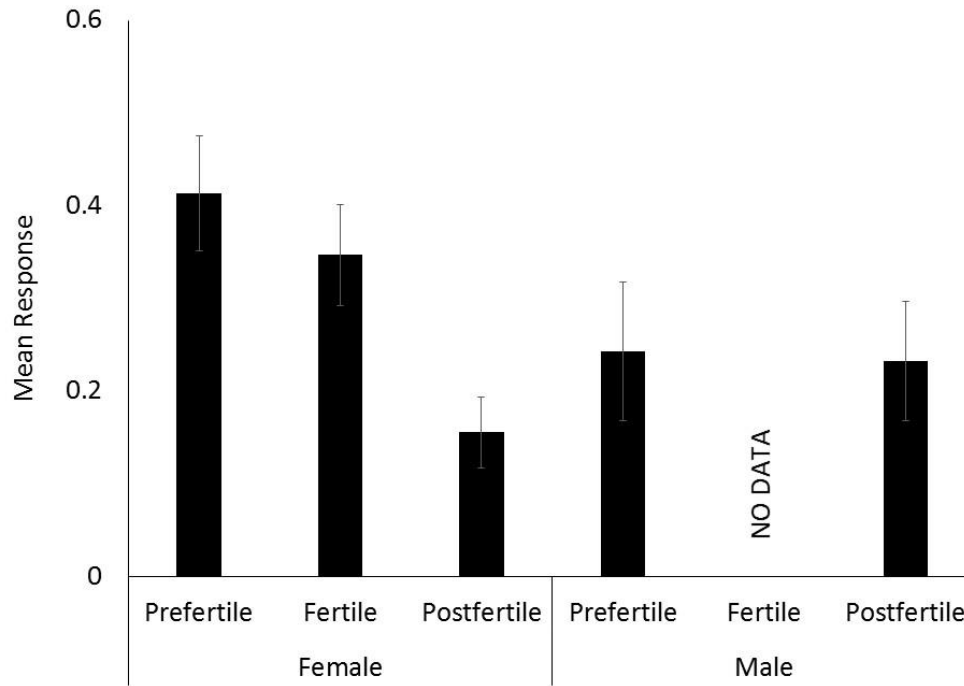


Figure 3.8. Probability of response (activity/no activity) and  $\pm$  SE of mated males and females of Field Sparrow, *Spizella pusilla* (n=20) across the fertility stages. Responses were evaluated via automated radio telemetry systems (ARTS) in Kennekuk Cove County Park, Vermilion County, IL, USA during the year 2014.

## TABLES

Table 3.1. Comparison of candidate models predicting the probability of detecting nocturnal complex songs in males of Field Sparrow, *Spizella pusilla*. Models were ranked based on Akaike's Information Criterion (AIC).  $K$  is the number of model parameters and  $\Delta AIC_c$  is the difference in AIC from the top model. Data is from 28 territory-holders distributed across 10 grassland patches in Kennekuk Cove County Park, Vermilion County, IL, USA during the years 2012-2013. \* = denotes interactive effects. + = denotes additive effects. Day<sup>2</sup> represents a quadratic term of Julian date.

Model	K	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
Intruder song + Breeding stage + Day <sup>2</sup>	6	610.47	0.00	0.55
Neighbor song + Breeding stage + Day <sup>2</sup>	6	612.24	1.77	0.23
Breeding stage + Day <sup>2</sup>	5	612.87	2.40	0.17
Intruder song * Breeding stage + Day <sup>2</sup>	6	615.87	5.40	0.04
Neighbor song * Breeding stage + Day <sup>2</sup>	6	618.26	7.79	0.01
Intruders + Day <sup>2</sup>	4	622.14	11.67	0.00
Neighbors + Day <sup>2</sup>	4	623.59	13.12	0.00
Null + Day <sup>2</sup>	3	625.08	14.61	0.00
Moon illumination + Day <sup>2</sup>	4	626.82	16.35	0.00



Table 3.2. Comparison of candidate models predicting the probability of detecting nocturnal simple songs in males of Field Sparrow, *Spizella pusilla*. Models were ranked based on Akaike's Information Criterion (AIC).  $K$  is the number of model parameters and  $\Delta AIC_c$  is the difference in AIC from the top model. Data is from 28 territory-holders distributed across 10 grassland patches in Kennekuk Cove County Park, Vermilion County, IL, USA during the years 2012-2013. \* = denotes interactive effects. + = denotes additive effects. Day<sup>2</sup> represents a quadratic term of Julian date.

Model	K	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
Null + Day <sup>2</sup>	3	427.13	0.00	0.30
Neighbor song + Day <sup>2</sup>	4	427.90	0.77	0.21
Moon illumination + Day <sup>2</sup>	4	428.64	1.51	0.14
Intruder song + Day <sup>2</sup>	4	429.09	1.96	0.11
Intruder song * Breeding stage + Day <sup>2</sup>	6	429.32	2.19	0.10
Breeding stage + Day <sup>2</sup>	5	430.35	3.22	0.06
Neighbor song + Breeding stage + Day <sup>2</sup>	6	431.25	4.12	0.04
Intruder song + Breeding stage + Day <sup>2</sup>	6	432.34	5.21	0.02
Neighbor song * Breeding stage + Day <sup>2</sup>	6	433.87	6.74	0.01

## CHAPTER 4

# PATTERNS, CORRELATES AND PATERNITY CONSEQUENCES OF EXTRATERRITORIAL FORAY BEHAVIOR IN THE FIELD SPARROW (*SPIZELLA PUSILLA*): AN AUTOMATED TELEMETRY APPROACH

### INTRODUCTION

The development and widespread use of genetic paternity analyses have led to an enormous body of research describing the genetic mating systems of monogamous birds (Birkhead and Møller 1992, Westneat and Stewart 2003, Griffith et al. 2002). These studies have shown that true monogamy is relatively rare among birds with most species having complex webs of reproductive interactions in which both sexes solicit extra-pair copulations (EPC) to enhance reproductive performance via extra-pair young (EPY) (Dias et al. 2009). Although genetic parentage studies have revolutionized my view of avian mating and reproductive systems, very little research has focused on understanding the behavioral mechanisms used by males and females to acquire extra-pair matings, how these behaviors vary among individuals, and the relative contribution of such behaviors to an individual's overall reproductive performance (Lindstedt et al 2007, Akcay and Roughgarden 2007).

Birds have two behavioral mechanisms for acquiring extra-pair matings: (1) a passive approach, where individuals mate with other individuals being attracted to their territories (or their mates' territories, in the case of females), or (2) an active approach, where individuals search for extra-pair mates beyond their territory boundaries via extraterritorial forays (hereafter forays) (Yezerinac and Weatherhead 1997, Dalziell and Cockburn 2008, Chiver et al. 2008). The costs of engaging in extra-pair matings within their territories or during forays differ between

females and males. Forays allow males to acquire extra-pair mates, but during forays, they reduce mate-guarding resulting in an increased risk of cuckoldry (Petrie and Kempenaers 1998, Dias et al. 2009). In females, searching for extra-pair matings via forays may improve a female's probability of locating a higher-quality individual than their mate (Mays and Hill 2004), locating a preferred male in the population (Bartsch et al. 2015), or increasing brood diversity (Arnold and Duvall 1994, Yasui 1998, 2001). However, females caught engaging in EPC or foraging outside their mate's territory may risk retaliation from their mate via withholding parental care (Westneat 1988, Dixon et al. 1994, Arnold and Owen 2002), reducing nest defense (Weatherhead et al. 1994).

The specific approach (passive or active) that a male or females chooses to employ may depend on age or individual quality. For example, empirical data suggest that the active approach may be an effective tactic for older or high-quality males (Weatherhead and Boag 1995, Stutchbury et al. 2005, Kleven et al. 2006), while younger or low-quality males may stay in their territory and guard their female (Evans et al. 2008). The risk of cuckoldry is known to differ between males of different quality; high-quality males are less cuckolded than low-quality males (Weatherhead and Boag 1995, Sherman and Morton 1998). Therefore, the difference in the likelihood of cuckoldry between individuals of different age or quality may explain the pattern of forays in males. Like males, females use forays to search for extra-pair copulations in addition to or in lieu of accepting solicitations from males intruding on their mate's territory (Kempenaers et al. 1997, Double and Cockburn 2000, Dalziel and Cockburn 2008). Female's ability to balance costs and benefits of foraging during reproductive activities may vary depending on age or quality, and this may lead to differences in foraging behavior. In this scenario, female age and indicators of her social mate's individual quality are predicted to influence female foray

behavior, specifically whether or not a female forays, how often she forays and even who she visits (Kempnaers and Dhondt 1993, Kleven et al. 2006, Chiver et al. 2008).

Differences in foray behavior among individuals of different sex, age, and quality may not only be reflected in the rate of foraging (number of forays/hr) but also when they conduct their forays (Murkhin et al. 2004, Roth et al. 2009). For example, older and high-quality males may conduct more forays during the day because they can selectively intrude into territories of low-quality male and obtain EPCs (Pedersen et al. 2006), while young and low-quality males may stay in their territories and mate-guard due to their risk of intrusions from high-quality males (Westneat 1988, Griffith et al. 2002). Young and low-quality males, however, may conduct forays at night because they can more easily “sneak” into neighboring territories to acquire matings without confronting resident males; making the best of a bad situation (Gross 1996). Benefits of foraging at night can also be extended to females (Roth et al. 2009). Females may opt to foray at night to avoid their social mates learning about their extraterritorial forays and the subsequent costs associated with foraging (Weatherhead et al. 1994). For instance, in some species females are known to foray at night and seek copulations (e.g. Superb Fairy-wren, *Malurus cyaneus*, Double and Cockburn 2000, Yellow-breasted Chats, *Icteria virens*, Ward et al. 2014). Furthermore, the patterns of foray behavior in males and females appear to vary with fertility stages. Male and female Song Sparrows (*Melospiza melodia*) commonly remain together in the prefertile period, but afterwards males and females tend to foray separately (Akçay et al. 2012). Males tend to foray frequently during the postfertile periods, as their role in reproductive activities with their mate are reduced (Akçay et al. 2012, Ward et al. 2014). In contrast, females tend to foray more during their fertile stage (Stutchbury et al. 2005, Chiver et al. 2008, Ward et

al. 2014), and reduce foray effort after their fertile stage when they need to attend their offspring (Neudorf et al. 1997).

The most widely-used approach for studying extra-territorial foray behaviors is tracking songbirds and estimating foray rates via manual radio-telemetry (e.g., Stutchbury et al. 2005, Kleven et al. 2006, and Pedersen et al. 2006). While manual telemetry has enhanced our knowledge of extraterritorial forays, it has technical and logistical constraints. For example, it is difficult to track movements of individual birds if they move large distances, especially over short time periods. Consequently, the average total effort devoted to tracking foraging individuals is generally < 20 hours, which usually is achieved by tracking each bird a few hours a day every 2-3 days (e.g., Stutchbury et al. 2005, Pedersen et al. 2006, Kleven et al. 2006). Additionally, recent studies have shown that some bird species make nocturnal forays (Nightingale, *Luscinia megarhynchos*, Naguib et al. 2001, Yellow-breasted Chat, Ward et al 2014), but most radio telemetry studies are conducted during daylight hours. Manual telemetry, at best, provides a snapshot of foraging behavior and at worse biases our understanding of the patterns of foray behavior and its relative contribution to an individual's overall reproductive performance (in the form of EPPs).

I used a combination of an automated radio telemetry system (ARTS) and microsatellite DNA analyses to investigate extraterritorial foray behavior in male and female Field Sparrows (*Spizella pusilla*) and the contribution of this behavior to extra-pair paternity (EPP). First, I quantified foray behavior of Field Sparrows using ARTS. ARTS allowed me to continuously and simultaneously track male and female Field Sparrows over 24-hour periods across multiple breeding stages and over a large spatial extent (50-60 territories). Specifically, I explored relationships between male and female extraterritorial foray rates (forays/hr) and age, tarsus

length (a proxy of individual quality, Dhondt 1982, Kempenaers et al. 1997), time of forays (day vs. night), and fertility stage (prefertile, fertile and postfertile). I used tarsus length as a proxy of individual quality because it is sensitive to environmental conditions (Kunx and Ekman 2000). Also tarsus length often correlates positively with survival (see Dhondt 1982, Kempenaers et al. 1997). Second, I used a microsatellite analysis to estimate the patterns of paternity in my study population and to assess the relationship between the extra-territorial foray behavior and EPP. Specifically, I examined whether males that foray more have more EPP (outside their nest), and whether females that foray more are more likely to have extra-pair young in her nest. Third, to gain further insight into how EPP occurs, and using my detailed and extensive foray data, I assessed whether EPY in a particular female's nest were the result of extra-pair males foraying into the cuckolded male's territory or due to females foraying into extra-pair sires' territories.

While examining the patterns and correlates of foraying behavior and examining the relationship between foray behavior and EPP were the main focus of this manuscript, I also examined individual and social correlates of EPP. First, I assessed the relationship between male characters (age and tarsus length) and male EPP as well as the relationship among the female's characteristics (age and tarsus length), her social mate's characters (age and tarsus length), and the presence of EPY in their nest. Second, I investigated differences in the characteristics (age and tarsus length) between social mates and extra-pair mates of females that engaged in extra-pair copulations. Third, I quantified the distance between the territories of females and her extra-pair sires. Fourth, I evaluated the relationship between the number of adjacent neighbors for each female and the probability of EPY in the female's nest. Studies have suggested that males and females may construct a social network centered on their territories (in males) or their nests (in females) and benefit from relationships with long-term and familiar neighbors (Beletsky and

Orians 1989, Eliassen and Jorgensen 2014). This social network may benefit females by allowing them to acquire additional food resources; protection from their neighbors through alarm calls, vigilance, and predator mobbing; and also extra-pair paternity, which also benefits extra-pair males (Graboska-Zhang et al. 2012, Eliassen and Jorgensen 2014).

I made the following predictions. (1) Both males and females conduct forays; however, males will foray more frequently than females, because of their low parental investment. Females will foray less than males as they seek fewer extra-pair copulations due to greater selectivity. (2) Older and larger males and females will foray more than SY individuals because they are better able to seek extra-pair mates and balance the costs and benefits of foraying. (3) Older and larger males and females will conduct their forays mostly during the day, because it should be more effective to find extra-pair mates during daylight hours. Young and smaller tarsus males and females, instead, may conduct their forays mostly during the night. Young males could obtain EPCs while reducing interactions with older or dominant territory holders and the risk of cuckoldry by high-quality males that intrude into their territories during the day. Young females could minimize the risk of harassment or guarding from their social mate. (4) Males will foray more during their social mate's prefertile and postfertile stages, when they do not need to guard their mate. In contrast, females will foray more during their prefertile and fertile periods. (5) Males and females that foray more frequently will acquire more EPY. (6) Older and larger males and females will gain more EPP, and females mated with younger and smaller males will gain more EPP. (7) Extra-pair sires in general will be older and have larger tarsus and when compared to females' social mates. (8) The quality of a female's social mate and the extra-pair sire, rather than the number of females adjacent to a female, will predict the occurrence of EPP.

## **METHODS**

### **Study species**

Field Sparrows, a socially monogamous songbird, are known to engage in extra-pair matings (at least 19% of offspring may be sired through extra-pair matings, Petter et al. 1990) and to be active at night (Walk et al. 2000, Chapter 1). Field Sparrows are sexually monomorphic with respect to plumage, but differ slightly in size; males are usually larger than females. Field Sparrows are partial migrants, with some individuals remain on the breeding grounds in winter (Carey et al. 1994). Females arrive on the breeding grounds between 15 April and 15 May (10-20 days after males), and pair formation usually occurs within a couple days of their arrival. Field Sparrows breed in successional old fields, brushy pastures, and woodland openings and edges (Carey et al. 1994). They typically place their nests at the base of woody vegetation, near the ground (Best 1977). Only females build the nest and incubate eggs, but males follow mates during the late stages of the nest building. Both sexes provide food to the young. Double brooding is common in Field Sparrows, and pairs usually re-nest immediately after nest failure.

### **Study site and general field methods**

From May 1<sup>st</sup> to July 31<sup>st</sup> of 2012 to 2014, I studied male and female Field Sparrows at Kennekuk Cove County Park, Illinois, USA (40° 11.5' N, 87° 42.9' W). Kennekuk Park is composed of discreet grassland patches of varying sizes (2-10 ha) surrounded by oak-hickory forest. Each year 3-8 Field Sparrow males established territories in each of these grassland patches and spatially formed clumped aggregations of territories separated by forest patches (hereafter 'neighborhoods'). Each year at the beginning of the season, I used spot-mapping and



behavioral observations during dawn and morning periods to delineate the territories of 50-60 territorial males distributed across 10 different neighborhoods of varying sizes (2-8 ha). Territory boundaries were delineated over the course of several visits to each territory by observing males while singing at dawn or bird behaviors during the day. Field Sparrows usually sing at dawn and counter-sing with their neighbors near their territory boundaries. This facilitated the delineation of territory boundaries for each male. Once birds were confirmed to be settled in their territories, I captured male and female birds using targeted mist-netting. Sparrows were banded with unique-numbered USGS aluminum and colored plastic leg bands. Age (when possible), sex, and morphometric variables (i.e., wing, tail, tarsus and bill length, and mass in grams) were recorded for all individuals. Age was estimated as SY and ASY by following Pyle (1997). Second Year (SY, birds that were in their first breeding season) and after second year (ASY). Sex was identified by observing cloacal protuberance (males) and brood patches (females). Sparrows were fitted with radio-transmitters weighting 0.5 to 0.6 g (JDJC corp, Fisher, IL). This represented ~5% of birds' average weight (12g). The transmitters used to track birds were glued to birds' backs following Raim et al. (1977). This method ensured that transmitters fell off of birds by the end of the field season, reducing stress and physiological impacts on birds.

I also conducted behavioral observations and visited territories every three days to monitor pairing status and reproductive status (paired but not nesting, building a nest, laying eggs, incubating eggs, nestlings and fledglings). Reproductive stages were later combined in more conservative periods following Akcay et al. (2012); prefertile period (paired but not nesting, and initial 4 days of building nest), fertile period (four days before the first egg is laid and the period of laying eggs), and postfertile period (incubating, feeding nestlings and caring for fledglings). In addition to monitoring pairing status and reproductive behaviors across the

season, I monitored territory ownership and establishment for each individual throughout the season. I ensured that the ownership of territories in my population were not changing throughout my study. I only observed a couple individuals per year switching territories to a different neighborhood during my study. Individuals that switched territories were not included in my analyses.

### **Automated radio telemetry and tracking birds**

I documented foray behavior in mated male and female Field Sparrows using an automated radio telemetry system (ARTS; Kays et al. 2011, Steiger et al. 2013, Ward et al. 2013; 2014). The ARTS was comprised of four towers with autonomous radio-telemetry receiving units (JDJC Corp., Fisher, IL) located 400-950 meters apart and strategically placed in the study area to collect data from each radio-tagged bird of study (Figure 4.1). The height of towers was 12-14 meters. Each ARU was connected to an array of six three-element Yagi antennas (Nighthawk model - JDJC Corp., Fisher, IL) attached to the top of towers. The six Yagi antennas were positioned at 0°, 60°, 120°, 180°, 240° and 300° to 360° detection coverage. Receiving units collected up to three detections per minute per bird over the duration of the transmitter's battery life ( $24 \pm 6$  days). The receiving units recorded the signal strength (in dB), electromagnetic noise (dB), and pulse width of the transmitter (milliseconds) of each radio transmitter mounted on birds; subsequently, I estimated the bearing of the signals detected from radio tagged birds. Custom scripts developed in R 2.15.2 software (Open source) were used to estimate the locations of each bird via triangulation based on detection records collected from multiple receiving units (Ward et al 2013). As in previous studies (Ward et al 2013, 2014) I used thresholds for signal strength, noise, and pulse width to remove potential locations caused by multipath effects

(signals bouncing off of manmade objectives or spurious radio signals). After applying filters and removing spurious data, I estimated X and Y coordinates for each intersection of signals and used the harmonic mean of the X and Y values for each coordinate to estimate location. The locations of birds were plotted in Google Earth in order to facilitate interpretation of the data. Because it is important to quantify error when tracking birds via ARTS, multiple tests were previously conducted using ARTS in my study site and with the system used in this study (see Ward et al. 2013, 2014). In the core area of the study (the area within the four telemetry towers), the mean accuracy was  $28.6 \pm 12.6$  m (mean difference of a radio transmitter attached to a tree and where the ARTS estimated the location of the radio transmitter). While Field Sparrows were located outside of the core area I only radio-tagged individuals in areas with good coverage by the ARTS.

Forays have typically been identified by visually watching focal individuals leave their territories (Dalziel and Cockburn 2000, Kleven et al. 2006, Barron et al. 2015). In most cases the territories are analogous to the behavioral home ranges I identified. An assumption of this approach is that the male and female have the same home range. While this assumption may be correct, I took a more rigorous approach and determined which utilization distribution (UD) best matched behavioral home ranges of males. UD's are the relative frequency distributions of an animal's occurrence in space and time (Keating and Cherry 2009). I estimated each individual's UD from 20% to 95% by units of 5%. The UD's were estimated using the dynamic Brownian Bridge estimators in the R package 'move' (Kranstauber et al. 2012). The contribution of each location is smoothed out to form a kernel estimate (polygon) (Silverman 1982). The data on UD's showed that 50-55% kernel estimates matched well in size and shape to the territories of the Field Sparrows (Celis-Murillo in prep; Figure 4.2). I then used a conservative approach to

identify forays. First, I used 60% UD as the individual's home range (Figure 4.2) this was slightly larger than the behavioral distribution and allow us to account for some of the error inherent in the ARTS. I then filtered the forays such that only forays with three consecutive points were used. This approach resulted in forays that lasted at least a couple minutes but removed several forays that were likely spurious. Communication radios, lightning strikes, and aircraft (communication can under certain situations create signals that meets all the filters used in this study). Many of these very short forays were also biologically questionable (a foray in an inappropriate habitat hundreds of meters away from a home range for a period of less than a minute). Thus, forays were consecutive locations outside of an individual's 60% UD, each foray ended when the individuals returned to the 60% UD. Data were collected on 92 Field Sparrows but due to transmitters failing off, transmitter failure, and dispersal from the site, I only analyzed data from 62 individuals all of which had at least 228 locations. Once forays were quantified for each bird, I estimated foray rates (forays per hour) for each individual bird (Figure 4.3). I estimated the maximum distance a foray was from an individual's home range using the R package Ggplots (Wickman 2009).

### **Extra-pair paternity analyses**

Blood samples were collected from a total of 399 birds. I collected 30  $\mu$ l of blood from the birds' brachial veins via venipuncture. Nestlings were banded and sampled for blood at five days of age. Blood in the field was stored in Queen's lysis buffer (Seutin et al. 1991) and stored in the lab at ambient temperatures. I used DNeasy Blood kit (Qiagen, Valencia, CA, USA) to extract DNA from blood samples. To determine paternity I used seven microsatellite loci identified from other species including five from Worthen's Sparrow (*Spizella wortheni*) (Canales-Delgadillo et

al. 2010) and three from Brown-headed Cowbird (*Molothrus ater*) (Strausberger and Ashley 2001, 2003) (Table 4.1). I searched for cross-amplification of each locus for Field Sparrows first on a temperature gradient. Once I identified an optimal annealing temperature I checked for allelic polymorphisms for each locus. Forward primers were labeled with either 6-FAM or HEX (Eurofins MWG operon, Huntsville, AL, USA) or NED (Applied Biosystems, Foster City, CA, USA) 5'-fluorescent labels for genotyping. PCR reactions were performed in 96-well plates using a BioRad T-100 thermal cycler (Bio-Rad, Hercules, CA, USA). The cycling profile was either a standard, single-temperature PCR with 1 cycle at 94°C for 3 min, 35 cycles of 30 s at 94°C, 60 s at the locus-specific annealing temperature (Appendix A), and 60 s at 72°C followed by a final extension cycle of 5 min at 72°C or a touchdown cycle that lowers the annealing temperature from a starting temperature (see Table 4.1) by 0.5°C over 30 cycles and ends with 30 additional cycles at 45°C. Each 15- $\mu$ l reaction contained at least 30 ng genomic DNA, 0.25  $\mu$ M of each primer, 250  $\mu$ M dNTPs, 1x PCR buffer, 0.5 U of *Taq* polymerase (5 Prime, Gaithersburg, MD, USA), and a primer-specific MgCl<sub>2</sub> concentration (1.5 to 2.5 mM). Fragment sizes for all PCR products were analyzed by the University of Illinois Biotechnology Core Lab using an ABI 3730 (Applied Biosystems Inc., Foster City, CA, USA). Fragment data were sized using GENEMAPPER 5 (Applied Biosystems Inc.).

Each set of primers was tested on the full set of breeding Field Sparrows ( $n = 182$ ) to assess allelic diversity, test for Hardy-Weinberg equilibrium, the frequency of null alleles [CERVUS, (Marshall et al. 1998)], and linkage disequilibrium [GENEPOP (Rousset 2008)] (Chapter 6, Appendix A). All individuals ( $n = 399$ ) were genotyped at more than four loci and the majority (> 99%) were genotyped at all seven loci. Allelic diversity ranged from 4 to 36 alleles and no locus deviated significantly from Hardy-Weinberg equilibrium nor did any loci

show evidence of linkage disequilibrium. The frequency of null alleles from all but one locus (i.e. Sw09) ranged from 0.003 to 0.051, which is considered rare, and should not cause sufficient concern over exclusion probability for paternity analyses (Dakin & Avise 2004). Because locus Sw09 had a high (0.10) frequency of null alleles I conducted my parentage analyses with and without this locus. The analyses did not differ in the identity of parents assigned to offspring so I included it in my analyses to maximize the potential to genetically identify sires. Since genotyping in this type of project is seldom 100% accurate, I used the likelihood-based approach implemented in application CERVUS 3.0 (Marshall et al. 1998, Kalinowski et al. 2007) to assign paternity. CERVUS uses the available data to calculate likelihood ratios for the possibility that the genotypes of parents and offspring are mistyped and to determine, via simulation, the level of confidence in the parentages it assigns. To determine the statistical significance of paternity assignments, I performed a simulation of 10,000 tests based on adult genotype frequencies using a genotyping error rate of 0.02 and assuming 75% of the candidate mothers and 90% of the candidate fathers were sampled. I used parentage assignments with  $\geq 95\%$  confidence, as determined by the likelihood-odds ratios (Kalinowski et al. 2007).

### **Statistical Analysis**

*Extraterritorial foray behavior.* I examined males and females separately because I expected males and females to have very different foraging behavior. I used Generalized Linear Mixed Models (GLMM, GLIMMIX procedure, SAS 9.3) with a negative binomial distribution and a logit link function (Littell et al. 2006) to examine the factors influencing extraterritorial foray behavior in males and females of Field Sparrows. I used a negative binomial distribution to account for potential over dispersion of my data. Number of forays, with a number of hours as an

offset were treated as response variable and age, tarsus length, time of forays, fertility stages, seasonality, year, and interactive combinations of these variables as fixed effects. I treated bird identity as a random effect to avoid potential effects of some individuals driving patterns of foray behavior. Tarsus length was a continuous variable and measured in mm. Because day and night differed in length of time (e.g., 16 and 8 hr. respectively), I examined the time of forays in 4 hr periods; 4 periods for day and 2 periods for night. I specified fertility stage as: prefertile, fertile or postfertile stage. I also assessed for potential seasonal effects in foray behavior in my data by including the date in which each foray occurred (Julian date). Finally, I included year to evaluate for potential year effects on my study. I evaluated a priori candidate models using Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ) (Burnham and Anderson 2002).

*Extra-pair paternity.* I used Generalized Linear Mixed Models (GLM, GLIMMIX procedure, SAS 9.3) with a binomial distribution and a logit link function (Littell et al. 2006) to examine whether the probability of obtaining EPY in males increased with foray behavior and whether the female probability of having EPY in their nest increased with foray behavior. I treated extra-pair paternity (coded as Yes = 1 and No= 0) as response variable and foray rates (forays/hr) as a fixed effect. I treated bird identity as a random effect. To examine the relationship among male characters (age and tarsus length) and male EPP, I used a Generalized Linear Models (GLM, GLIMMIX procedure, SAS 9.3) with a binomial distribution and a logit link function (Littell et al. 2006). I treated extra-pair paternity (coded as Yes = 1 and No= 0) as response variable and foray rates (forays/hr) and tarsus length (in mm) as a fixed effects. To examine the relationship among female characters (age and tarsus length), social mate characters (age and tarsus length) and female's EPP (EPY in the nest), I used a Generalized Linear Model (GLM, GLIMMIX procedure, SAS 9.3) with a binomial distribution and a logit link function

(Littell et al. 2006). I treated extra-pair paternity (coded as Yes = 1 and No= 0) as response variable and female's age (SY and ASY) and tarsus length (in mm), social mate's age and tarsus length as a fixed effects. Parameter estimates are presented with standard errors (SE) or  $\pm$  95% confidence intervals (CI).

To further understand the patterns of EPP, I assessed the differences in ages and tarsus length among extra-pair sires and social mates. I used a McNemar's test (FREQ procedure, SAS 9.3) to assess the significance of the differences in ages between the two matched groups (social mates vs. extra-pair sires). McNemar's test assess the marginal frequencies of two binary outcomes from matched-pairs of subjects (in my case, the number of ASY and SY birds from both, social mates and extra-pair sires). I used a paired t-test (TTEST procedure, SAS 9.3) to compare tarsus length among extra-pair sires and social mates. To examine whether extra-pair sires were from adjacent territories or from territories at least one territory away of female's territories, I used a binomial exact test (FREQ procedure, SAS 9.3). Adjacent territories were defined as a territory that shared a common border. I used the female's social mate behavioral home range as the "territory". To examine the relationship between females obtaining EPP and the number of neighbors, I used a Generalized Linear Model (GLM, GLIMMIX procedure, SAS 9.3) with a binomial distribution and a logit link function (Littell et al. 2006). I treated extra-pair paternity (coded as Yes = 1 and No= 0) as response variable and female's number of neighbors as a fixed effects. Lastly, I assessed whether EPY in a particular female's nest were the result of extra-pair males foraging into the cuckolded male's territory or due to females foraging into extra-pair male territories. For this, I examined the complete movements (including forays) of radio-tagged females with EPY in their nest and those of identified extra-pair fathers. I examined only females that had EPY in their nest, movement data over fertile periods, and the identity of



their extra-pair mates with movement information over the same periods of time (radio-tagged males). I used the location of territories from both, the female territory and the extra-pair father to assess who visited which territory that resulted in EPP.

## RESULTS

I banded 567 Field Sparrows (161 males, 74 females and 332 nestlings) over the course of the study. I documented foray behavior of 63 radio-tagged adult birds during the years 2012-2014; 39 males and 24 females. Of the 63 sparrows across the three years of the study, 13 birds were tracked in 2012, 23 birds in 2013 and 27 birds in 2014. Twenty of these 63 birds radio-tagged, were paired to a radio-tagged mate (10 pairs). I tracked each bird for an average of 331 hours (~14 days) and acquired an average of 5,394 locations per bird, with a maximum number of locations of 34,033 over the course of 28 days. I identified a total of 5,553 forays over the three year study (Appendix B).

The foraging behavior of males was best explained by two factors: age and time of day. ASY males conducted more forays per 24 hour period than SY males (0.29 and 0.12 forays/hr, respectively) (Figure 4.4). Like males, ASY females forayed more than SY females, (0.23 forays/hr and 0.14 forays/hr, respectively) (Figure 4.5). ASY and SY males forayed more during the day than during the night (ASY, day=0.43 forays/hr and night=0.19 forays/hr, SY day=0.16 forays/hr and night=0.08 forays/hr) (Figure 4.6). These patterns were best described with the two best-fitting models ( $\Delta AIC_c = <2$ , Burnham and Anderson 2006) that included age (ASY and SY) and time of forays (Day/Night); these two models received nearly all the weight of evidence ( $\sum w_i = 0.878$ ) (Table 4.1). I found little support for tarsus length, fertility stage, seasonality, year, or interactions among these variables for influencing foray behavior (Table 4.1). Female foray

rates differed in the time in which they conduct forays and in the period of fertility. During the day, ASY females forayed significantly more during the prefertile and fertile stages than postfertile stages, while during the night, they forayed equally across fertility stages (Figure 4.7). SY females forayed more during the prefertile stage than the other stages, however, during the prefertile period, they forayed more during the night than during the day (Figure 4.7). These patterns of foraying were best described in the best two-fitting models ( $\Delta AIC_c = <2$ ) that included fertility stages and an interaction among age and time of forays (Day/Night); these two models received nearly all the weight of evidence ( $\sum w_i = 0.750$ ), Table 4.1). Further evidence for age and fertility stage influencing female foray behavior was seen in the two subsequent models that received some additional weight of evidence ( $\Delta AIC_c = <4$ ,  $\sum w_i = 0.17$ ). These four best-fitting models combined provided a substantial weight of evidence ( $\sum w_i = 0.92$ ) of the importance of age and fertility stages in female foray behavior. There was little support for other factors (i.e. tarsus length, fertility stages, seasonality, year or interactions among these variables) explaining female foray behavior (Table 4.2). The average distance of forays occurring during the day was 158.2 m for males and 191.6 m for females, while at night the average distance was 106.6 m for males and 161 m for females (Appendix C and D).

I included the microsatellite genotypes of all known territorial adults for maximum-likelihood simulations and to estimate the confidence of paternity assignments. The allelic frequencies for each loci were in Hardy-Weinberg Equilibrium (chi-squared test:  $P > 0.07$ ). Extra-pair paternity was found in 40.0 % (32/80) of the broods and 13.3 % (30/225) of the offspring sampled were sired by an extra-pair male. I identified 24 of the extra-pair fathers in 26 broods. Four nests had EPY from two extra-pair fathers. There was no support for foray effort explaining EPP in males or females; males or females that forayed more frequently did not gain more EPY (GLM for

males:  $n = 20$ ,  $\beta = 0.16 \pm 2.26$  SE,  $t_{1,18} = 0.07$ ,  $P = 0.94$ ; GLM for females:  $n = 21$ ,  $\beta = 1.72 \pm 3.6$  SE,  $t_{1,19} = 0.48$ ,  $P = 0.63$ ). I also found no relationship among EPP and male characters: age (GLM:  $n = 58$ ,  $\beta = 0.90 \pm 0.66$  SE,  $t_{1,55} = 1.37$ ,  $P = 0.17$ ) or tarsus length (GLM:  $n = 58$ ,  $\beta = -0.49 \pm 0.55$  SE,  $t_{1,55} = -0.89$ ,  $P = 0.37$ ). I found no relationship among EPP and female characters: age (GLM:  $n = 54$ ,  $\beta = 1.39 \pm 1.13$  SE,  $t_{1,46} = 1.23$ ,  $P = 0.22$ ) or tarsus length (GLM:  $n = 58$ ,  $\beta = 0.17 \pm 0.45$  SE,  $t_{1,46} = 0.38$ ,  $P = 0.70$ ), or social mate's characteristics: age (GLM:  $n = 54$ ,  $\beta = 0.14 \pm 0.89$  SE,  $t_{1,46} = 0.16$ ,  $P = 0.87$ ) or tarsus length (GLM:  $n = 54$ ,  $\beta = 0.27 \pm 0.52$  SE,  $t_{1,46} = 0.53$ ,  $P = 0.59$ ). When I compared age among extra-pair sires and social mates, I found that SY birds were more likely to be extra-pair sires than social mates, whereas ASY were more likely to be social mates than extra-pair sires (McNemar's test:  $X^2 = 3.6$ ,  $df = 1$ ,  $P = 0.05$ ). The difference in tarsus length between extra-pair sires and social mates was minimal ( $0.17$  mm  $\pm 0.23$  SE) and not significant (Paired test:  $t_{24} = 0.75$ ,  $P = 0.46$ ).

While age and tarsus length did not explain EPP, the arrangement of territories did. I found that 14 (54%) of the 26 extra-pair sires were from territories adjacent to the female's territory and 7 (27%) from at least one territory away; the identity of the remaining 5 extra-pair sires and their relationship to the female could not be determined because I did not find a match in my blood samples. This is consistent with the maximum foray distances (Appendix C and D). On average an individual would have to go at least 100m to reach a territory that was not adjacent and 56% of female forays and 71% of male forays were less than 100m from their home range. The distances between females' territories and those of the extra-pair sires' territories that were not adjacent were: 331, 340, 427, 491, 601, 738 and 885 m away. These distances were measured from the centroid of extra-pair sire's territory to centroid of female's territory. Despite my limited sample of extra-pair sires, my results showed that extra-pair sires were more likely to be

from adjacent territories than from more distant territories (Binomial test:  $P = 0.06$ ).

Furthermore, I found that the likelihood of female's EPP increased as the number of territorial neighbors (i.e., adjacent territories) increased (GLM:  $n = 54$ ,  $\beta = 0.84 \pm 0.24$  SE,  $t_{1,46} = 3.44$ ,  $P = 0.0009$ ; Figure 4.8). Of the seven birds who were not from territories adjacent to the female's territory, I had data on at least one of the parents for four of these situations. Telemetry data for three males showed that the extra-pair sires never entered the territories of the females they had EPY with and were never less than 225, 250, and 300 m from the edge of the females' territory. Although no data were available for the three females, these data demonstrate that the EPY were the result of forays by the female into the extra-pair sires' territories. Additionally, one female from a fourth pair was documented entering the territory of the extra-pair sire who sired young in her nest; no data were available on the extra-pair father.

## **Discussion**

With the unprecedented spatial and temporal resolution of my foraging behavior and data on extra-pair paternity, I gained new insights into the behavioral mechanisms that males and females use to gain extra-pair matings. As expected, and has been shown in other species (Pedersen et al. 2006, Evans et al. 2008, Akcay et al. 2012), both male and female Field Sparrows regularly engaged in extraterritorial forays. Males forayed more than females, and older birds forayed more than younger ones. Overall forays occurred more frequently during the day than night, and all individuals, regardless of sex, forayed farther from their territories during the day. Males forayed consistently across all fertile periods, whereas females forayed more during the prefertile and fertile period. Despite the variation I observed in foraging behavior, these behaviors did not correlate with the probability of EPY in males or females. In total, over

5,000 forays were identified; however, only 40% of nests had EPY, and only 13% of young came from extra-pair sires. These results suggest that, although forays may help birds to find extra-pair mates, foray behavior alone does not determine extra-pair fertilizations.

EPP appears to be determined by familiar relationships and occurs primarily between neighbors or familiar individuals (previous mates or neighbors). Out of the 26 extra-pair sires, 95% were familiar males: 14 were current neighbors, 4 were previous neighbors, 2 were previous social mates; the remaining 6 individual's previous relationship with the female could not be determined because there was no match in my blood samples, so this percentage is conservative. This predominance of neighboring males as extra-pair sires is consistent with other studies examining EPP in songbirds (Stutchbury et al. 2005, Cleasby and Nakagawa 2012). However, contrary to other studies (Pedersen et al. 2006, Kleeven et al. 2006, Patrick et al. 2012), I found no relationship between male age or tarsus length and EPP or a difference in quality between females' social mates and extra-pair mates. Of course, I cannot rule out the possibility that male quality in the Field Sparrow is determined by characteristics not considered in my study, such as vocal performance (Ballentine et al. 2004).

In this study, I provided empirical support for the hypothesis that males and females may construct a social network centered at their territories (in males) or their nests (in females) and potentially experience fitness benefits through extra-pair relationships with current and past neighbors (Beletsky and Orians 1989, Eliassen and Jorgensen 2014). This social network may provide "direct benefits" to females by acquiring additional food resources; protection from their neighbors through alarm calls, vigilance, predator mobbing; as well as extra-pair paternity, which may also benefits extra-pair males (Graboska-Zhang et al. 2012, Eliassen and Jorgensen 2014). Although the quality of females' social and extra-pair mates did not differ, and females

appeared to select males based on familiarity, it is possible that females also receive indirect benefits through increasing brood diversity (Arnold and Duvall 1994, Yasui 1998, 2001). Building relationships may also have benefits for future matings; neighbors in one year may make good social mates in future years. An important finding in my study is that not only do social networks in Field Sparrows play an important role in reproduction, namely through the prevalence of neighbors among extra-pair mates, but also that the influence of social networks may extend beyond the current breeding season, as individuals not only select extra-pair sires who currently occupy neighboring territories but also extra-pair mates who were neighbors in previous breeding seasons. Beletsky and Orians (1989) presented several lines of evidence that long-term familiarity among breeding blackbirds may be beneficial to female and male breeding success.

I found that SY males were more likely to be extra-pair sires than social mates, and ASY males were more likely to be social mates than extra-pair mates. These observations are inconsistent with nearly all published studies (e.g. Pedersen et al. 2006, Kleeven et al. 2006, Patrick et al. 2012). In my system SY males may be positioning themselves in areas where they have a higher probability of acquiring EPP, in particular establishing territories in densely populated neighborhoods. ASY birds may tradeoff the opportunity for access to EPP for better quality territories and are therefore preferred by social mates.

While the amount of extra-territorial foray activity by females does not appear to determine the probability of having extra-pair young in the nest, females may be using forays to determine the presence and location of familiar males. For four extra-pair matings in which the sire was not a neighboring male and for which I have tracking data for one of the parents, I documented that in at least 75% of those cases (3 out of 4), the female was responsible for the

EPY as the extra-pair sires had never entered or neared the female's territory. While I have a limited sample, these data provide compelling support that females are driving patterns of extra-pair paternity in the population through their foray behavior and apparent preference for familiar males.

I found that ASY females forayed more during the day while SY tended to foray more at night during the pre-fertile period. Older and more experienced females may foray mostly during the day because it may be more optimal to acquire public information and fulfill their needs (extra-pair mates, future mates or breeding sites) during daylight hours. SY females presumably could gain the same advantages of foraying during the day; however, the costs of daytime forays may be greater for younger, less experienced females. The costs females incur with foraying are associated with their social mate being aware of the foray and providing less parental care to the nestlings and fledglings (Weatherhead et al. 1994). The reduction in parental care may be more detrimental for younger less experienced females as compared to older more experienced females. Nocturnal forays, however, pose an additional issue for females; how to locate and assess potential mates at night. Studies have shown that females looking for mates tend to foray specifically when other territorial males are singing and can easily be assessed (Naguib 2001, Double and Cockburn 2008, Roth et al. 2009). The Field Sparrows, despite being considered a diurnal bird for conducting most of their activities during the day, they are known to vocalize at night (Chapter 3). This nocturnal singing appears to have role in mate attraction or at least advertising for potential mates (Chapters 2, 3). The nocturnal singing of males may allow SY females to assess territorial males and possibly find an extra-pair mates.

For males, extra-territorial foray behavior may be used primarily for prospecting. Evidence from other species suggests that prospecting allows males to acquire information on

the quality of other territories at the breeding site for use in selecting territories in subsequent years (Eadie and Gauthier 1985, Doligez et al. 2004, Betts et al. 2008, Pärt et al. 2011). For instance, 75% of nests in the Field Sparrow are usually depredated, and those individuals who experience depredation events may move territories among years. However, prospecting may also serve to assess the reproductive status (e.g., fertility stage) of females in his neighborhood, as seen in other species (Doligez et al. 2004, Pärt et al. 2011). Given female preference for extra-pair matings with neighbors, males who have information on the fertility status of neighboring females and coordinate their nocturnal vocalizations in relation to the fertility state of neighboring females may be able to increase their number of extra-pair offspring. Thus, proximity to females, rather than male quality, could be key for male's success at acquiring extra-pair paternity. The finding that male foray activity is constant across the breeding season, i.e., is not related to the fertility stage of social mates, is consistent with this conclusion, as there may always be some fertile females in the neighborhood due to lost nests or lost mates. Furthermore, the greater amount of foray behavior among males is expected based on their minimal investment in parental care compared to that of females (Bateman 1948, Birkhead and Moller 1992).

An alternative explanation for the lack of relationship between forays and EPP for males or females is that forays are being used for foraging; however, I believe that foraging is not the main reason for conducting forays. During my three-year study I conducted daily behavioral observations and described male-male and male-female interactions of birds within and outside their territories, and I never observed birds foraging outside their territories.

My findings support the conclusion that females are driving EPP in my system and that extra-pair sires are chosen based on familiarity with the female. I suggest that forays may help at



acquiring extra-pair mates but do not determine EPP. Forays may play an important role in acquiring information about their social (current and future neighbors, potential mates and extra-pair mates) and ecological (potential new territories, nesting sites, habitats.) environment. This information may ultimately help to achieve higher reproductive success but not necessarily in the form of EPP. Foraging behavior is relatively common and it likely extremely important in developing and maintaining a social network with which female occasionally use to acquire EPP.

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## FIGURES

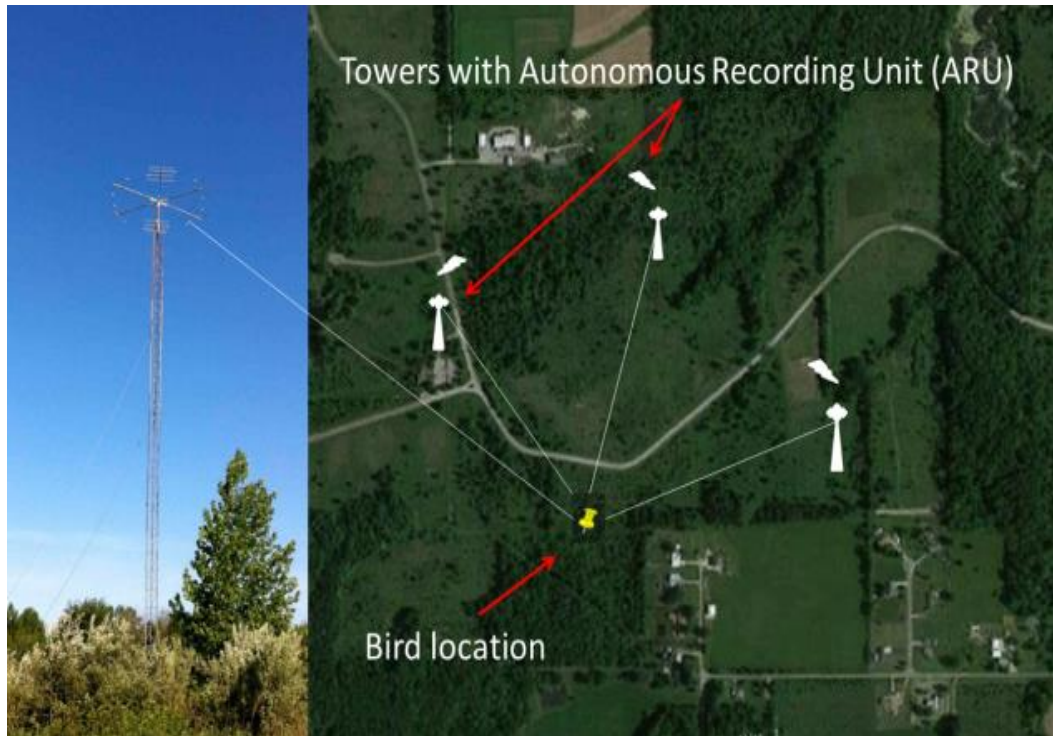


Figure 4.1. Automated Radio Telemetry System (ARTS). Representation of four automated radiotelemetry towers and triangulating signals to obtain a bird location in Kennekuk Cove County Park, Illinois, USA.



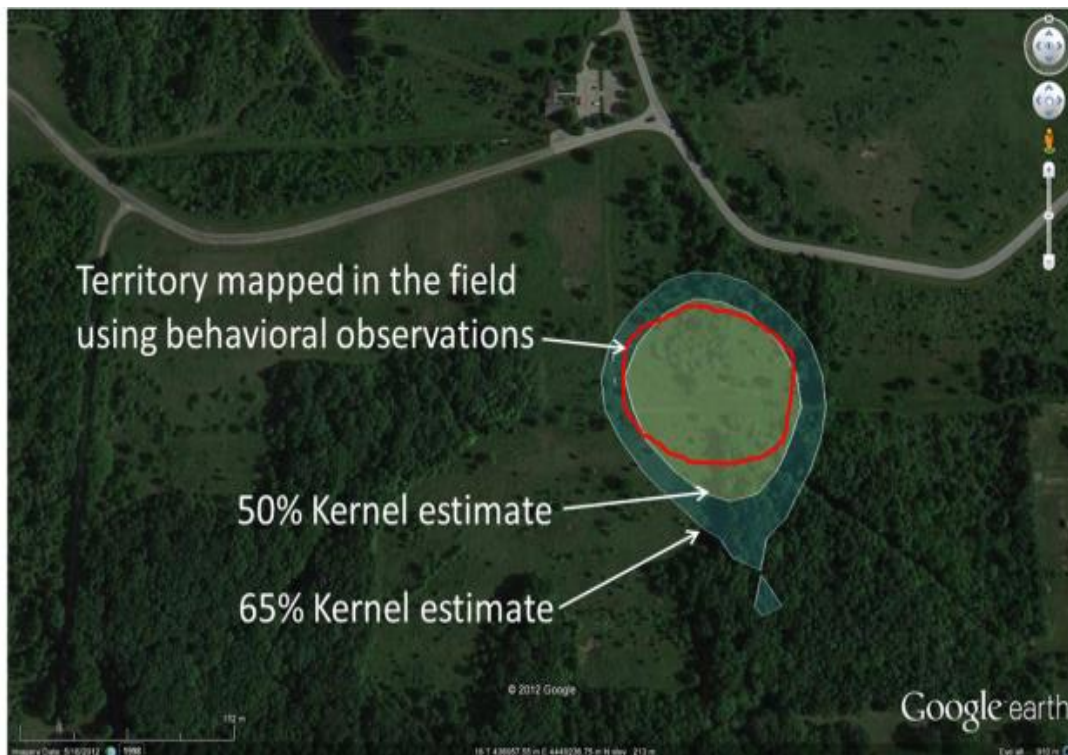


Figure 4.2. Utilization distributions (UD) of a male Field Sparrow (*Spizella pusilla*). 50% Kernel estimate circled in light green color and 65% Kernel estimates are circled in light blue color. Circled in red represents the territory mapped in the field using behavioral observations.

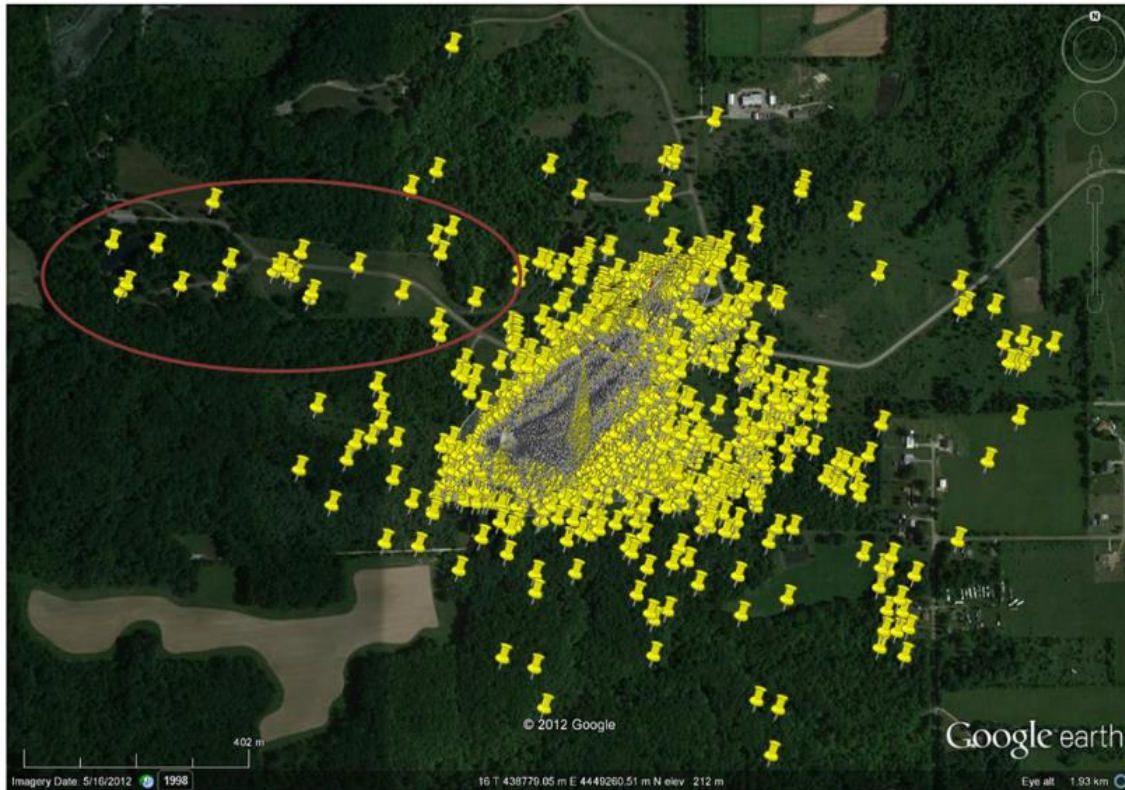


Figure 4.3. A total of 8105 locations from a single female Field Sparrow (*Spizella pusilla*) from 6/6/12 to 6/19/12. Locations were obtained using automated telemetry. Locations circled in red show a long-distance foray (600 m) conducted at 15:00 hrs. on 6/17/12.

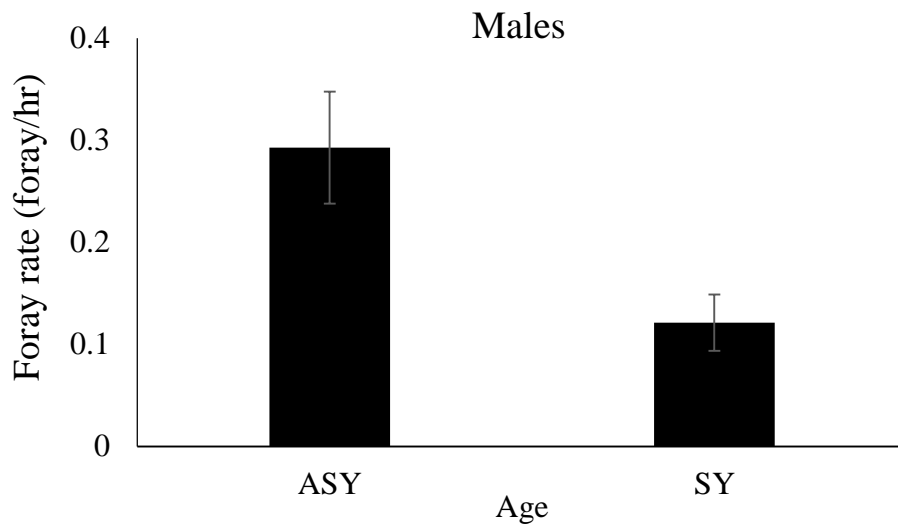


Figure 4.4. Mean foray rate (foray per hour) and SE ( $\pm$ ) by after second year (ASY) and second year (SY) male Field Sparrows (*Spizella pusilla*). Data are from 26 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014.

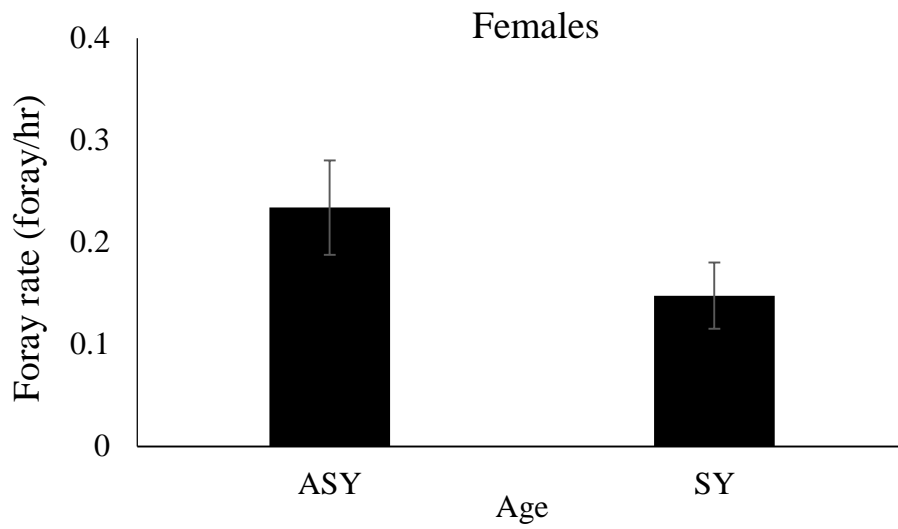


Figure 4.5. Mean foray rate (foray per hour) and SE ( $\pm$ ) by after second year (ASY) and second year (SY) female Field Sparrows (*Spizella pusilla*). Data are from 22 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014.

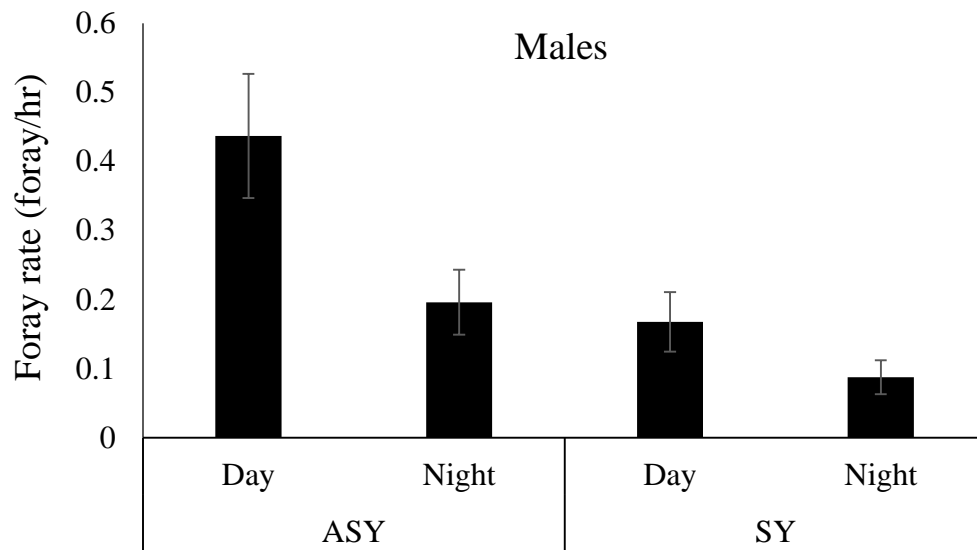


Figure 4.6. Mean foray rate (foray per hour) and SE ( $\pm$ ) at day and night by after second year (ASY) and second year (SY) male Field Sparrows (*Spizella pusilla*). Data are from 26 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014.

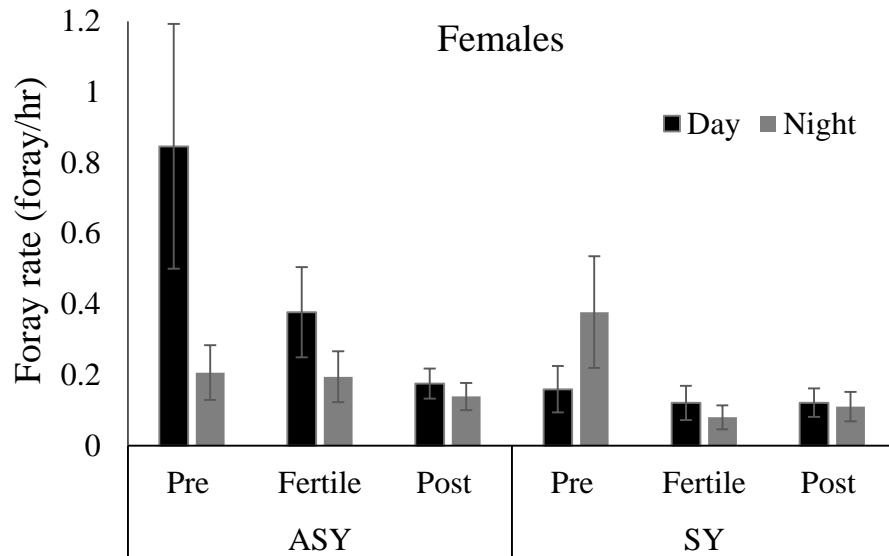


Figure 4.7. Mean foray rate (foray per hour) and SE ( $\pm$ ) of female Field Sparrows (*Spizella pusilla*) at day and night by after second year (ASY) and second year (SY) birds and across fertility stages. Pre = prefertile stage, Fertile= fertile stage and Post=postfertile stage. Data are from 22 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014.

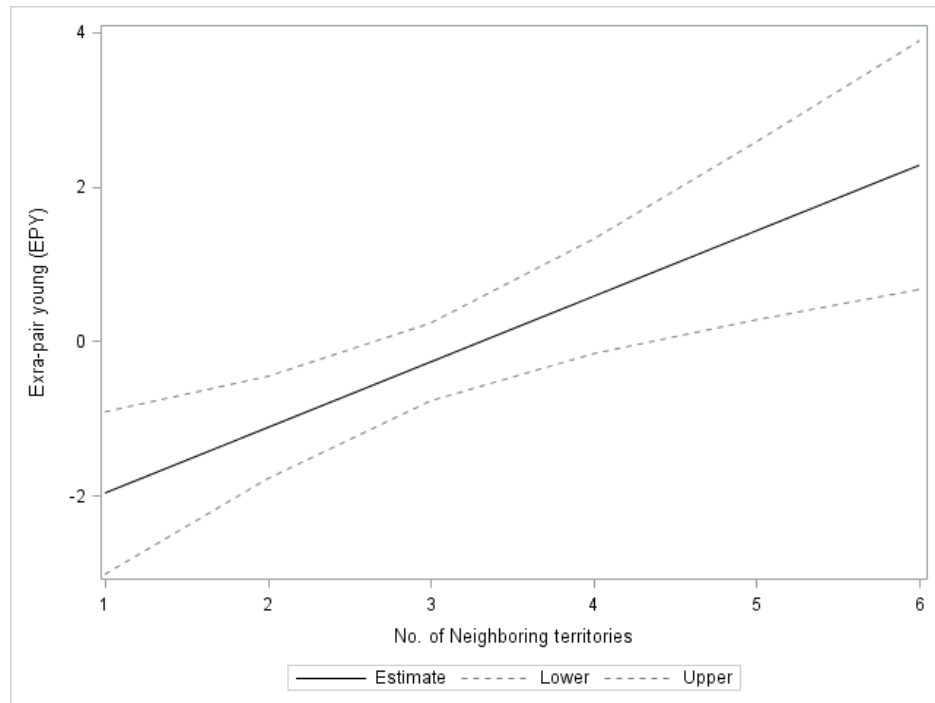


Figure 4.8. Probability scale of female extra-pair young in the nest and the number of neighboring territorial males. Predicted probabilities presented ( $\pm$  95% C.I.) from a logistic regression with a binomial response (n = 54 females).

**TABLES**

Table 4.1. Comparison of candidate models predicting the foray rate (forays/hr) in males of Field Sparrow, *Spizella pusilla*. Models were ranked based on Akaike’s Information Criterion (AIC).  $K$  is the number of model parameters and  $\Delta AIC_c$  is the difference in AIC from the top model. Data are from 26 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014. \* = denotes interactive effects among variables. + = denotes additive effects among variables.

Model	K	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
Age + Day/Night	4	671.52	0.00	0.651
Age * Day/Night	5	673.66	2.14	0.223
Tarsus + Day/Night	4	676.70	5.18	0.049
Day/Night	3	677.02	5.50	0.042
Fertility Stage + Age * Day/Night	7	677.98	6.46	0.026
Fertility Stage * Day/Night	7	682.25	10.73	0.003
Age	3	682.95	11.43	0.002
Tarsus * Age	4	683.24	11.72	0.002
Julian * Age	4	683.52	12.00	0.002
Fertility Stage + Age	5	687.14	15.62	0.000
Julian * Tarsus	4	688.02	16.50	0.000
Julian	3	688.80	17.28	0.000
Year	3	688.87	17.35	0.000
Fertility Stage * Age	7	690.49	18.97	0.000
Null	2	690.59	19.07	0.000
Tarsus	3	691.38	19.86	0.000
Fertility Stage	4	693.75	22.23	0.000



Table 4.2. Comparison of candidate models predicting the probability of foraging in females of Field Sparrow, *Spizella pusilla*. Models were ranked based on Akaike's Information Criterion (AIC).  $K$  is the number of model parameters and  $\Delta AIC_c$  is the difference in AIC from the top model. Data are from 22 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014. \* = denotes interactive effects among variables. + = denotes additive effects among variables.

Model	K	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
Fertility Stage + Age * Day/Night	7	599.37	0.00	0.49
Fertility Stage + Age	5	600.60	1.23	0.26
Fertility Stage	4	602.53	3.16	0.10
Fertility Stage * Age	7	603.22	3.85	0.07
Fertility Stage * Day/Night	7	605.39	6.02	0.02
Julian * Age	4	606.47	7.10	0.01
Age * Day/Night	4	607.00	7.63	0.01
Julian	3	608.67	9.30	0.00
Age	3	608.80	9.43	0.00
Day/Night	3	608.92	9.55	0.00
Age + Day/Night	4	609.03	9.66	0.00
Null	2	609.12	9.75	0.00
Julian * Tarsus	4	609.58	10.21	0.00
Year	3	610.69	11.32	0.00
Tarsus * Age	4	610.97	11.60	0.00
Tarsus + Day/Night	4	611.10	11.73	0.00
Tarsus	3	611.27	11.90	0.00

## CHAPTER 5

### SUMMARY

A significant amount of research has been conducted on the mating behaviors of birds over the past half century (Trivers 1972, Clutton-Brock 1991, Gross 1996, Brockmann 2001); and with continuing technological advancements for studying avian ecology and genetics, our knowledge of this critical period of the life cycle continues to increase (Emlen and Oring 1977, Thornhill and Alcock 1983, Mobley et al. 2011). The roles of diurnal singing and visual displays figure prominently in our understanding of how birds establish and defend territories through male-male interactions and attract social mates via female choice (Trivers 1972, Emlen and Oring 1977). Other behaviors, such as nocturnal singing (La 2012) and extra-territorial forays (Neudorf et al. 1998, Stutchbury et al. 2005, Ward et al. 2014), and their roles in reproduction have received much less attention, particularly nocturnal singing.

The overarching objective of my research was to explore the function of nocturnal song and extra-territorial foray behavior in the Field Sparrow. My research on nocturnal song, extra-territorial foray behavior, and extra-pair paternity has led to a clearer, more comprehensive understanding of extra-pair mating behavior as a reproductive tactic used by the Field Sparrow. Specifically, I provide evidence supporting the role of nocturnal complex song for announcing presence/availability of extra-pair males to females, either through intruder males vocalizing to females on her territory or through territorial males vocalizing to foraging or neighboring females. Additionally, there is strong evidence that females select extra-pair mates based on their familiarity; all extra-pair sires whose identity could be reliably confirmed and for which I had information on current and previous relationships between the female and extra-pair sires were either current neighbors or previous mates and neighbors. Finally, my findings also are

consistent with the female choice for extra-pair mates coupled with female foray behavior are driving patterns of extra-pair paternity and nocturnal singing behavior.

My results support the conclusion that nocturnal complex song functions in male-female communication, specifically the announcement of the presence or availability of extra-pair males to females (either on their territories or neighboring males). This conclusion is consistent with findings from analyses correlating nocturnal singing behavior of resident males with social factors (fertility stage and occurrence of vocalizations by neighbors and intruders) and results of my playback experiment (Chapter 3). While nocturnal singing behavior of residents was correlated with singing behavior of other males in the neighborhood and their social mate's fertility stage (significantly higher during fertile and postfertile stages), resident males did not respond vocally to simulated intruder vocalizations. Rather, females responded to intruder vocalizations by becoming active, and their response was more pronounced during their prefertile and fertile periods. The relationship between singing activity of residents and other males in the neighborhood (neighboring males and intruders) appears to be indirect, reflecting the common response of males to female reproductive status (i.e., fertility). Furthermore, in light of my finding that females select familiar males, especially current neighbors, as extra-pair mates, the higher nocturnal singing activity of residents during both their social mates' fertile and postfertile stages, suggests that they may be responding to the fertility not only of their social mate, but to other females in the neighborhood. Thus, even though a male's social mate is past her fertility stage, other females in the neighborhood may still be fertile, warranting continued nocturnal singing by the resident male. Taff and his colleagues (2014) showed that daytime singing activity in Common Yellowthroats was positively related to the number of fertile females

in the neighborhood on that particular day, showing the importance of characteristics of the neighborhood on reproductive behaviors.

While extra-territorial foray behavior is common among both male and female Field Sparrows, consistent with patterns documented in other species (Pedersen et al. 2006, Evans et al. 2008, Akcay et al. 2012), my research failed to document a strong link between extra-territorial foray behavior and extra-pair matings; the amount of foray behavior does not necessarily result in a greater number of extra-pair offspring. Rather, my data provide strong evidence that extra-pair matings are determined by familiar relationships and occur primarily between neighbors or familiar individuals (previous mates or neighbors). Out of the 21 extra-pair sires whose identity could be determined (i.e., for which I had blood samples from the extra-pair father), 95% were familiar males: 14 were current neighbors, 4 were previous neighbors, 2 were previous social mates, and the remaining individual's previous relationship with the female could not be determined. This predominance of neighboring males as extra-pair sires is consistent with other studies examining extra-pair paternity in songbirds (Stutchbury et al. 2005, Cleasby and Nakagawa 2012). The importance of familiarity in females' choice of extra-pair mates is further supported by the lack of relationship between extra-pair paternity and male quality (indexed as size) and age (Chapter 4). I found no relationship between the number of extra-pair young sired by males and male quality or age, nor did I find a difference in quality between females' social mates and extra-pair mates.

This study provides empirical support for the hypothesis that males and females may construct a social network centered at their territories (in males) or their nests (in females) (Beletsky and Orians 1989, Grabowska-Zhang et al. 2012, Eliassen and Jorgensen 2014). This social network may provide "direct benefits" to females by allowing them to acquire additional

food resources, increased vigilance from predators via alarm calls from neighbors, as well as the benefits of extra-pair paternity (increased genetic diversity in the nest, Arnold and Duvall 1994, Yasui 1998, 2001). It also is possible that building relationships has benefits for future matings; neighbors in one year may make suitable social mates in future years. Social networks in Field Sparrows appear to not be limited to a single breeding season but extend beyond, as individuals not only select extra-pair sires who currently occupy neighboring territories, but also extra-pair mates who were neighbors in previous breeding seasons.

While the amount of extra-territorial forays by females does not appear to determine the probability of having extra-pair young in the nest, females may be using forays to determine the presence and location of familiar males. The increase in female forays during their prefertile and fertile stages is consistent with this conclusion. For four extra-pair matings in which the sire was not a neighboring male and for which I have tracking data for the female, I documented that the females entered the territories of the extra-pair males that ultimately sired offspring in their nest. Of those four extra-pair matings, I simultaneously tracked the extra-pair male, and documented that none of the extra-pair males had visited the territories of the female whose young he sired. While I have a limited sample of tracked pairs, these data provide compelling support that females are a driving patterns of extra-pair paternity in the population through their foray behavior and apparent preference for familiar males.

For males, extra-territorial forays may primarily serve a prospecting function. Evidence from other species suggests that prospecting allows males to acquire information on the quality of other territories at the breeding site for use in selecting territories in subsequent years (Eadie and Gauthier 1985, Betts et al. 2008, Pärt et al. 2011). For instance, 75% of nest of Field Sparrow in this population are depredated, and those individuals who experience depredation

events may need to move territories within or between years. Information on the quality of territories will help males to select future territories. Prospecting may also serve to assess the reproductive status (e.g., fertility stage) of females in his neighborhood, as seen in other species (Eadie and Gauthier 1985, Pärt et al. 2011). Given female preference for extra-pair matings with neighbors, males who have information on the fertility status of neighboring females and coordinate their nocturnal vocalizations in relation to the fertility state of neighboring females may be able to increase their number of extra-pair offspring. Thus, proximity to females, rather than male quality, could be key for male's success at acquiring extra-pair paternity. The fact that male foray effort is constant across the breeding season, i.e., is not related to the fertility stage of social mates, is consistent with this conclusion, as there may always be fertile females in the neighborhood, due to lost nests or lost mates. And overall, males forayed more than females, as expected based on their lower investment in parental care compared to that of females (Bateman 1948, Birkhead and Møller 1992).

Regardless of the purpose of forays, individuals appear to foray often. The most likely reason for this is to gain information. The more information an individual can gather, the better informed decisions they can make about where to breed and/or with whom to breed. Isolated patches of habitat may result in birds spending a large amount of time and energy prospecting in far off locations or may restrict birds' access to information, resulting in poorly informed decisions. Isolated patches of habitat also may be avoided. Field Sparrow populations in Illinois have declined over the past half a century (Walk et al. 2010). My research highlights the value of conserving large and well-connected tracks of grasslands and shrublands for Field Sparrows that would facilitate their movement through the landscape.

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## APPENDIX A

Appendix A. Summary statistics of seven microsatellite loci used to determine paternity in field sparrows; n, number of individuals genotyped; N<sub>A</sub>, number of alleles; T, annealing temperature °C; H<sub>O</sub>, observed heterozygosity; H<sub>E</sub>, expected heterozygosity, P<sub>MEX</sub>, probability of maternal exclusion, P<sub>PEX</sub>, probability of paternal exclusion with known mother.

Locus	n	N <sub>A</sub>	T	Allele size range	Het <sub>O</sub>	Het <sub>E</sub>	P <sub>MEX</sub>	P <sub>PEX</sub>	Estimated frequency of null alleles
Sw09 <sup>a</sup>	182	30	58	101-182	0.775	0.949	0.805	0.892	0.100
Sw62 <sup>a</sup>	182	14	53	101-130	0.764	0.846	0.531	0.695	0.051
Sw65 <sup>a</sup>	182	36	65-50 <sup>§</sup>	96-178	0.879	0.944	0.791	0.883	0.033
Sw75 <sup>a</sup>	182	12	58	246-273	0.806	0.826	0.485	0.658	0.015
Mau101 <sup>b</sup>	182	19	65-50 <sup>§</sup>	120-168	0.933	0.915	0.703	0.825	0.012
Mau104 <sup>b</sup>	182	20	57	132-190	0.533	0.545	0.184	0.370	0.003
Mau102 <sup>c</sup>	182	4	60-45 <sup>§</sup>	164-170	0.489	0.529	0.140	0.238	0.038
Total exclusion probability							0.998	0.999	

<sup>a</sup>(Canales-Delgadillo 2010), <sup>b</sup>(Strausberger & Ashley 2001), <sup>c</sup>(Strausberger & Ashley 2003)

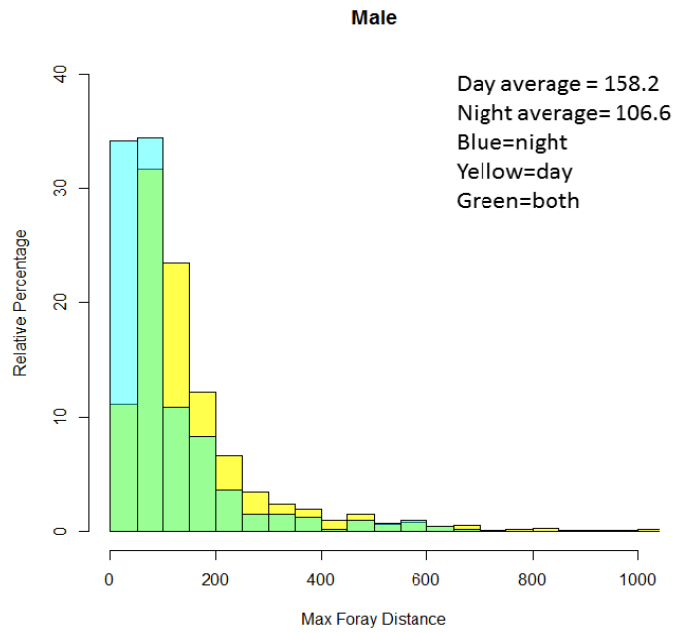
<sup>§</sup>Indicates temperature range for annealing touchdown cycle

## APPENDIX B

Appendix B. Extraterritorial forays of radio-tagged male and female Field Sparrows, *Spizella pusilla*. Data are from 62 birds tracked for 20,395 hours in Kennekuk Cove County Park, Illinois during the years 2012-2014. Out of these 26 birds, 18 birds were paired to another radio-tagged bird, comprising 9 total pairs.

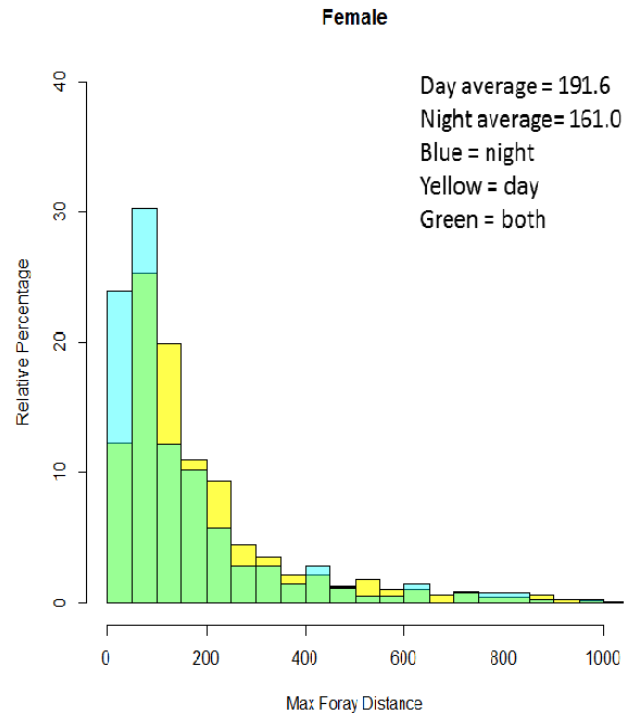
		Males		Females				Males		Females				Males		Females	
Year	Bird ID	Total forays (N)	Time tracked (h)	Total forays (N)	Time tracked (h)	Year	Bird ID	Total forays (N)	Time tracked (h)	Total forays (N)	Time tracked (h)	Year	Bird ID	Total forays (N)	Time tracked (h)	Total forays (N)	Time tracked (h)
2012	2n2	30	269			2013	11A	157	265	94	325	2014	A1			20	48
	2n4	13	46				2C	147	334	24	223		A2	11	182		
	2n-4	60	510				2D	103	229				A6			78	646
	2n5	38	333				2E	248	408				A8	18	112	19	235
	2s1	33	198				2G	148	237				A9	34	721	15	186
	2s3	167	695				2H	72	235				B1			5	18
	5nw1	296	625				4A	206	255				B3	28	125		
	5nw2	195	629				5H			51	303		B4			11	147
	5se1			189	497		5I			109	258		B5	34	190		
	5se2	322	538				5L	345	570				B7			8	183
	7se3	22	129				7A	231	323				C1			61	443
	7sw1	135	476				7B	122	142				C11			92	242
	7sw4	15	73				7D	44	234				C13			32	279
							7E	261	229				C14	154	1288		
					7F	108	279	155	469	C5			48	363			
					7G	94	370			C6			28	231			
					7M	79	266			C9			86	502			
					9A	11	307			D1	2	27	79	560			
					9C	142	375	26	363	D10	61	499	51	481			
										D5			58	479			
										D7	8	42	20	149			
Totals		1326	4521	189	497			2518	5058	459	1941			350	3186	711	5192

## APPENDIX C



Appendix C. Relative percentage of foray distance at day, night and both by male Field Sparrows, *Spizella pusilla*. Data are from 26 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014.

## APPENDIX D



Appendix D. Relative percentage of foray distance at day, night and both by females of Field Sparrow, *Spizella pusilla*. Data are from 22 birds tracked in Kennekuk Cove County Park, Illinois during the years 2012-2014.