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Patterns, correlates, and paternity consequences of extraterritorial foray behavior in the field sparrow (*Spizella pusilla*): an automated telemetry approach

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Abstract

In many territorial species, occasional movements beyond territory boundaries (extraterritorial forays) have been documented in many species. While many explanations for the occurrence of extraterritorial forays have been proposed, a logical and proposed function of extraterritorial forays is to engage in extra-pair copulations with extra-pair mates outside of their territories. We used an automated radio-telemetry system (ARTS) to examine the patterns and correlates of foray behavior of male and female field sparrows (*Spizella pusilla*) and investigated if forays were associated with extra-pair paternity (EPP) and cuckoldry. We found that male and female field sparrows regularly engaged in extraterritorial forays. In males, age and time of foraying (day vs. night) were important factors explaining foray rates (foray/h); older (ASY) males forayed more than younger (SY) males and, while we detected many nocturnal forays, most forays occurred during the day. For females, fertility stage and age appeared to be important in explaining foray rates; older females forayed more during pre-fertile period than fertile and post-fertile periods. Unlike foray rates, the duration of forays (min) was not explained by any of the variables examined. Surprisingly, despite the large number of forays documented (>3500), greater foray rates or duration of forays were not associated with higher probability of EPY for males or females or with cuckoldry in males. Forays may play a role in prospecting and acquiring information about their social and ecological environment, which ultimately may help them to achieve greater reproductive success, but not necessarily in the form of EPP.

Significance statement

Despite many territorial species are known to conduct extraterritorial forays (movements beyond their territory), very little is known about this behavior. We used an automated radio-telemetry system (ARTS) to examine the patterns, correlates, and paternity consequences of extraterritorial foray behavior in male and female field sparrows (*Spizella pusilla*). We documented more than 3500 forays and found that both male and female field sparrows regularly engaged in extraterritorial forays; however, different factors explain their foray rates (age, time of foraying (day vs. night), and fertility stage) but not the duration of forays. Surprisingly, greater foray rates or duration of forays were not associated with higher probability of EPY in males or females or with cuckoldry in males. Rather than exclusively acquiring extra-pair matings, forays likely serve multiple purposes, such as prospecting and acquiring information about their social and ecological environment, which ultimately may help individuals achieve greater reproductive success.

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Introduction

Most breeding birds are territorial, i.e., within a defined area, they monopolize and defend resources such as food, nesting sites, or access to mates, in order to survive and successfully reproduce (Brown 1964, 1969). Movements beyond territory boundaries (extraterritorial forays) however have been documented in many territorial species (Neudorf et al. 1997; Stutchbury et al. 2005; Chiver et al. 2008). Many socially monogamous birds are known to engage in extra-pair paternity (EPP); therefore, a logical and proposed function of extraterritorial forays (hereafter forays) is to engage in extra-pair copulations (EPC) with extra-pair mates settled away from their territories (Griffith et al. 2002; Westneat and Stewart 2003). While not mutually exclusive, other potential explanations for the occurrence of forays are to gather additional food outside their territories (Neudorf et al. 1997; Humbird and Neudorf 2008) and prospect for future dispersal, and breeding sites (Danchin et al. 2001; Pärt and Doligez 2003; Doligez et al. 2004). Despite these reasonable explanations, the relationship among forays and EPP are still in question. While some researchers have found that foray rates (foray/h) and the time spent off territory correlates with higher probability of obtaining extra-pair young (e.g., male reed buntings, *Emberiza schoeniclus*, Kleven et al. 2006; female hooded warblers, *Wilsonia citrina*, Chiver et al. 2008; male and female great tits, *Parus major*, Patrick et al. 2012), others have found a weak or non-existent relationship among foray behavior and EPP (e.g., male hooded warblers, Stutchbury et al. 2005; male American redstarts, *Setophaga ruticila*, Churchill and Hannon 2010). Conceivably, our limited ability to track birds and accurately describe these subtle and relatively rare behaviors is biasing our understanding of the patterns and correlates of foray behavior in birds and consequently, our view regarding the function of forays.

The most widely used approach for studying extraterritorial foray behaviors is tracking songbirds via manual radio-telemetry (e.g., Stutchbury et al. 2005; Kleven et al. 2006; 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 foraying individuals is generally <20 h, 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; Evans et al. 2008). 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 foraying behavior and at worst 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).

The relative use of forays and its related costs and benefits, however, may depend on numerous factors, such as sex, age, and body condition (Westneat and Stewart 2003). For instance, empirical data suggest that foraying may be an effective tactic for older males to acquire extra-pair mates (Weatherhead and Boag 1995; Stutchbury et al. 2005; Kleven et al. 2006), while younger males may stay in their territory and guard their female (Evans et al. 2008). The trade-off between the costs and benefits of foraying (in the form of mate guarding and cuckoldry) is one explanation of this pattern (Birkhead and Møller 1992). Forays allow males to acquire extra-pair mates, but during forays, they reduce mate guarding, resulting in an increased risk of cuckoldry (Westneat 1988; Sherman and Morton 1988). The risk of cuckoldry may differ between males of different age; older males are less often cuckolded than low-quality males possibly due to female preference for older males or traits that correlate with age and social dominance (Hoeschele et al. 2010) and/or because young males may be less experienced at assuring paternity by mate guarding (Weatherhead and Boag 1995). The difference in the likelihood of cuckoldry between individual males, therefore, predicts more foraying effort on older males than younger males.

Like males, females may use forays to search for extra-pair copulations in addition to or in lieu of accepting solicitations from males intruding on their mate's territories (Kempenaers et al. 1997; Double and Cockburn 2008). Females searching for extra-pair matings via forays may improve a female's probability of locating "preferred" mates in the population, potentially of high-quality (Mays and Hill 2004), or increasing genetic diversity of her brood (Arnold and Duvall 1994; Yasui 1998, 2001). A female's ability to balance costs and benefits of foraying during reproductive activities, variation in female motivation and ability to invest in mate searching may vary depending on age (Jennions and Petrie 1997; Duval and Kappor 2015), potentially leading to differences in foraying behavior. In this scenario, female age is predicted to influence whether or not a female forays, how often and for how long she forays (Kempenaers and Dhondt 1993; Kleven et al. 2006; Chiver et al. 2008).

The patterns of foray behavior in males and females may also vary with body condition. For instance, differences in body condition, as it reflects an individual's energy reserves, are known to influence physical activity in many avian species during mate search, reproductive, dispersal, stopover, and long-distance migration periods (Rintamaki et al. 1995; Deppe et al. 2015; Duval and Kapoor 2015). Therefore, body condition could influence how birds allocate their efforts toward searching for mates outside their territories, potentially influencing foray behavior. Changes in foray patterns in males and females may also occur across their different fertility stages. For instance, male and female song sparrows (*Melospiza melodia*) commonly remain together in the

pre-fertile period, but afterwards males and females tend to foray separately (Akçay et al. 2012). Males tend to foray frequently during the post-fertile periods, as their role in reproductive activities with their mate is reduced (Akçay et al. 2012; Ward et al. 2014). In contrast, females tend to foray more during their fertile stage, and reduce foray effort when they need to attend to their offspring (Neudorf et al. 1997; Stutchbury et al. 2005).

Differences among individuals of different sex, age, or body condition may not only be reflected in the rate of foraying (number of forays/h) or duration of their forays (min), but also when they conduct their forays (Naguib et al. 2001; Roth et al. 2009). For example, older and better condition males may conduct more forays or spent more time during forays during the day because they can selectively intrude into territories of young and lower-condition males and obtain EPCs (Pedersen et al. 2006), while young and lower-condition males may stay in their territories and mate-guard due to their risk of intrusions from males (Westneat 1988; Griffith et al. 2002). Young and lower-condition 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 foraying at night may 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 foraying (Weatherhead et al. 1994) or because at night, there is a higher probability to find potential extra-pair males outside their territories. For instance, some species have been shown to foray before sunrise or nocturnally and seek EPCs (*Malurus cyaneus*, superb-fairy wrens, Double and Cockburn 2000; *Icteria virens*, yellow-breasted chat, Ward et al. 2014).

We used a combination of an automated radio-telemetry system (ARTS) and microsatellite DNA analyses to investigate the patterns and correlates of extraterritorial foray behavior in male and female field sparrows (*Spizella pusilla*) and how this behavior correlates with patterns of extra-pair paternity (EPP) and cuckoldry. First, we quantified foray behavior of field sparrows using ARTS. ARTS allowed us to track male and female field sparrows over 24-h periods across multiple breeding stages and over a large spatial extent (50–60 territories). Specifically, we explored relationships between male and female extraterritorial foray rates (forays/h) and mean duration of forays (min) and age, physical condition (as the residuals from a regression of mass [g] on tarsus length), fertility stage (pre-fertile, fertile and post-fertile) and time of forays (day vs. night). By taking advantage of our high-resolution spatio-temporal data obtained via automated telemetry, we also discuss other potential functions of foray behavior in the field sparrow. Second, we used a microsatellite analysis to estimate the patterns of paternity in our study population and examine whether males that foray more or for longer periods of time have more EPP (outside their nest), and whether females that foray more or for longer periods of time are more likely to

have extra-pair young in their nests. Lastly, we examined whether males that foray more or for longer periods of time are more likely to be cuckolded by their mate.

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; Celis-Murillo et al. 2016a, b). Field sparrows are sexually monomorphic with respect to plumage, but differ slightly in size (Carey et al. 1994); males are usually larger than females. Field sparrows are short-distance migrants, with some individuals remaining 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 few 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 nest building. Both sexes provision 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 1st to July 31st of 2012 to 2014, we studied male and female field sparrows at 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 3–6 field sparrow males established territories in each of these grassland patches and formed clumped aggregations of territories separated by forest patches (hereafter "neighborhoods"). Each year, at the beginning of the season, and over the course of multiple visits (36–48 visits), we used spot-mapping (6–8 points per male per visit) to locate territorial males and behavioral observations of their dawn singing, counter-singing with their neighbors, or engaging in boundary disputes during the day. This facilitated the delineation of each male's territory boundary in a map and aerial pictures and helped to delineate the territories of 50–60 territorial males distributed across 10 different neighborhoods of varying sizes (2–8 ha). We captured male and female birds using targeted mist netting, and banded sparrows with uniquely numbered USGS aluminum and colored plastic leg bands. Age (when possible), sex, tarsus length [mm], and mass [g] were recorded for all individuals. We estimated age as "second year" (SY, birds that were in

their first breeding season) and "after second year" (ASY) by following Pyle (1997). Because most field sparrows start mating and nesting shortly after their arrival to their breeding grounds, we were able to reliably determine sex for individuals by observing cloacal protuberance in males and brood patches in females. We confirmed sex designations with subsequent behavioral observations (e.g., monitoring incubation and song). For adults and nestlings, we collected 30 μl of blood via brachial venipuncture for paternity analyses. We banded nestlings and collected a blood sample at 5 days of age. Blood was stored in Queen's lysis buffer (Seutin et al. 1991) and was kept in the lab at ambient temperatures. We used DNeasy Blood kit (Qiagen, Valencia, CA, USA) to extract DNA from blood samples. Sparrows were fitted with radio-transmitters weighting 0.5 to 0.6 g (JDJC corp, Fisher, IL). This represented ~5% of birds' average weight (12 g). Transmitters were glued on birds' backs following Raim (1978). This method allowed the transmitters to fall off approximately by the end of the field season, potentially reducing stress and physiological impacts on birds. It was not possible to record data blind because our study involved focal animals in the field.

We conducted behavioral observations and visited territories every 3 days to monitor pairing and reproductive status. Birds were classified as paired but not nesting, building a nest, laying eggs, incubating eggs, nestlings, and fledglings. To minimize error in assigning reproductive stages, we later combined reproductive stages into more conservative periods following Akçay et al. (2012); pre-fertile period (paired but not nesting, and initial 4 days of building nest), fertile period (4 days before the first egg is laid and the period of laying eggs), and post-fertile period (incubating, feeding nestlings, and caring for fledglings). In addition to monitoring pairing

status and reproductive behaviors across the season, we monitored territory ownership and establishment for each individual throughout the season. Based on our observations, the ownership of territories did not change throughout the season. In our study, we only observed two individuals per year switching territories to a different neighborhood, and these individuals were omitted from analyses.

Automated radio-telemetry and tracking birds

We 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 m apart and strategically placed in the study area to collect data from each radio-tagged bird of study (Fig. 1). The height of towers was 12–14 m. We connected each ARU to an array of six three-element Yagi antennas (Nighthawk model— JDJC Corp., Fisher, IL) attached to the top of towers. We positioned the six Yagi antennas 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 (~29 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. Custom scripts developed in R 2.15.2 software (R Development Core Team 2008) were used to estimate the locations of each bird via triangulation based on detection records collected from multiple receiving units (Ward et al. 2013, scripts available at http://ward.nres.illinois.edu/). As in previous studies (Ward et al. 2013, 2014), we used thresholds for signal strength, noise, and pulse width to remove potential locations

Fig. 1 Automated radio-telemetry system (ARTS). Representation of four automated radio-telemetry towers triangulating signals to obtain a bird location in Kennekuk Cove County Park, IL, USA. Polygons in *white* represent territories of male field sparrows
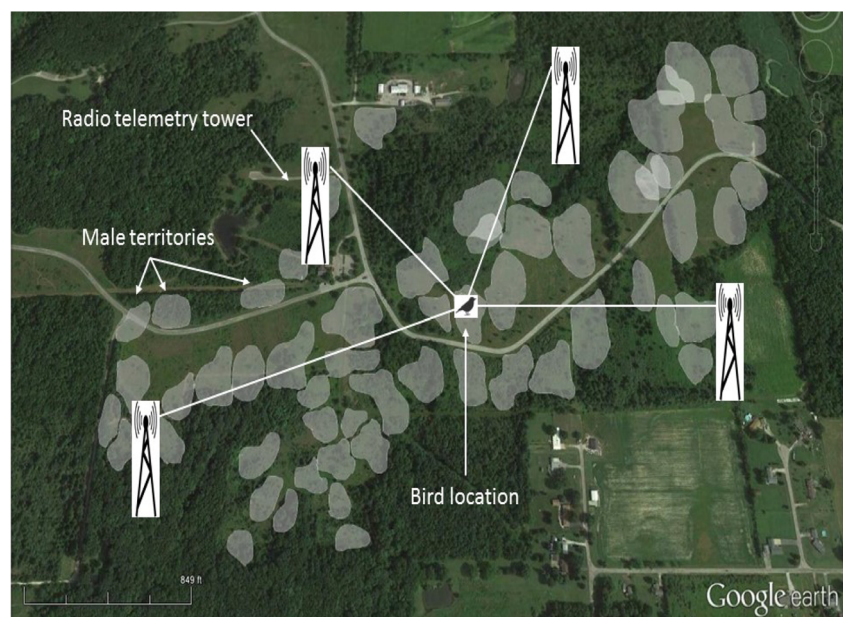
caused by multipath effects (signals bouncing off manmade objects or spurious radio signals). After applying filters and removing spurious data, we estimated X and Y coordinates for each intersection of signals and used the harmonic mean of the X and Y values for each coordinate to estimate location. We plotted the locations of birds in Google Earth 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 our 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 ± 12.6 m (mean difference of a radio transmitter attached to a tree and where the ARTS estimated the location of the radio transmitter).

Forays in other species have been identified by visually watching focal individuals leave their territories (Kleven et al. 2006; Dalziell and Cockburn 2008; Barron et al. 2015). However, we took a different approach and determined which utilization distribution (UD) best matched the territories of males. UDs are the relative frequency distributions of an animal's occurrence in space and time (Keating and Cherry 2009). We estimated each individual's UD from 20 to 95% by units of 5%. We estimated UDs using the dynamic Brownian bridge estimators in the R package "move" (Kranstauber et al. 2012). The contribution of each location was smoothed out to from a kernel estimate (polygon) (Silverman 1986). The data on UDs showed that 50–55% kernel estimates matched well in size and shape to the territories of the field sparrows delineated by our behavioral observations. We then used a conservative approach to identify forays. First, we used 60% UD as the individual's territory (Fig. 2). Even though the 60% UD was slightly larger than the mapped territory, it allowed us to account for some of the error inherent in the ARTS. Communication radios, lightning strikes, and aircraft under certain situations can create signals that meet all the filters used in this study. Many of these very short forays were also biologically questionable (e.g., a foray in an inappropriate habitat hundreds of meters away from a territory for a period of less than a minute). Thus, we defined forays as three consecutive locations outside of an individual's 60% UD, and each foray ended when the individual returned to within the 60% UD (Fig. 3). We collected data on 62 field sparrows but due to transmitters falling off and transmitter failure, we only analyzed data from 46 individuals all of which had at least 228 locations. Once we quantified forays for each bird, we estimated foray rates (forays per hour) and mean duration (minutes) of forays for each individual bird.

Extra-pair paternity analyses

To determine paternity, we 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) (Online resources, S1). We searched for cross-amplification of each locus for field sparrows first on a temperature gradient. Once we identified an optimal annealing temperature, we checked for allelic polymorphisms for each locus. PCR reaction conditions and cycles were variable by locus and are described in detail in the online supplement (Online resources, S2)

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)]. All individuals ($n = 424$) were genotyped at more than four loci and the majority (> 99%) were genotyped at all seven loci (Online resource, S1). Allelic diversity ranged from four to 36 alleles and no locus deviated

Fig. 2 Utilization distributions (UD) of a male field sparrow (*Spizella pusilla*). 50% Kernel estimate shown in *light green color* and 60% Kernel estimates circled in *white color*. Circled in *red* represents the territory mapped in the field using behavioral observations
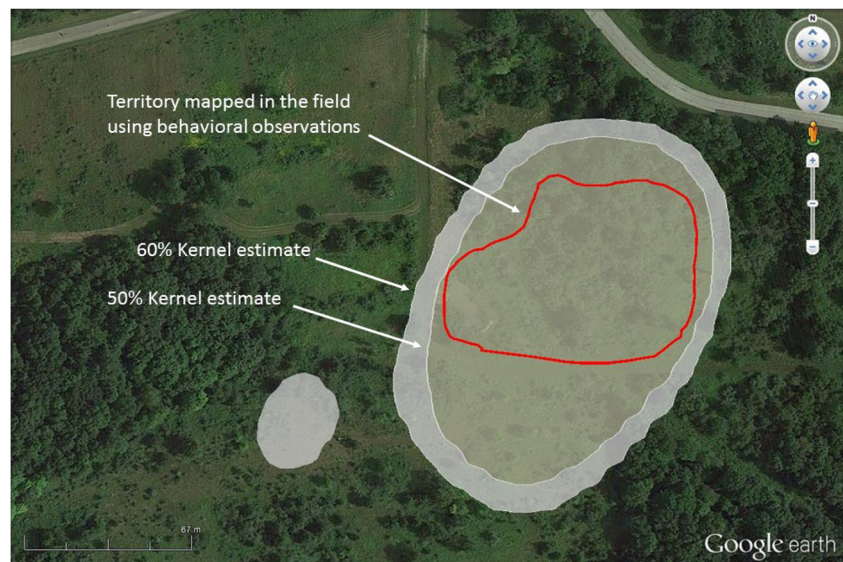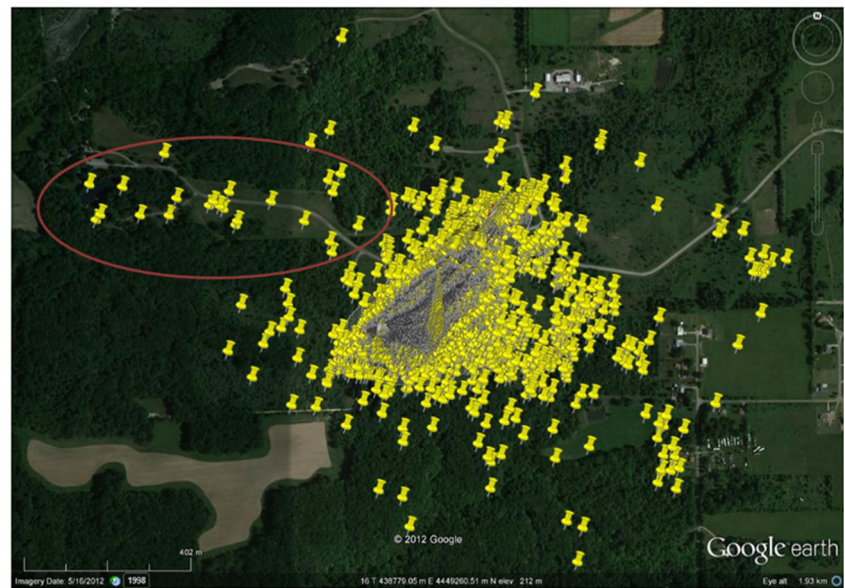
Fig. 3 A total of 8105 locations from a single female field sparrow (*Spizella pusilla*) from 6 to 9 June, 2012. Locations were obtained using automated telemetry. Locations circled in red show a long-distance foray (600 m) conducted at 15:00 h. on 17 June, 2012

significantly from Hardy-Weinberg equilibrium ($p > 0.05$) nor did any loci show evidence of linkage disequilibrium. The frequency of null alleles from all but one locus (Sw09) ranged from 0.003 to 0.051, which is considered rare, and should not cause sufficient concern for paternity analyses (Dakin and Avise 2004). Because locus Sw09 had a relatively high (0.10) frequency of null alleles, we conducted our parentage analyses with and without this locus. The analyses did not differ in the identity of parents assigned to offspring so we included it in our analyses to maximize the potential to identify sires genetically. Because genotyping in this type of project is seldom 100% accurate, we reran 20% of samples to obtain an empirical measure of genotyping error (0.02) and used this rate with a 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, we performed a simulation of 10,000 tests based on adult genotype frequencies using a genotyping error rate of 0.02 and assuming we sampled 75% of the candidate mothers and 90% of the candidate fathers. Our assumptions for the portion of males and females that were sampled were based on field observations. We used parentage assignments with ≥95% confidence, as determined by the likelihood-odds ratios (Kalinowski et al. 2007).

Statistical analyses

Extraterritorial foray behavior We examined males and females separately because we expected males and females to differ in foraying behavior. We used generalized linear mixed models (GLMM, GLIMMIX procedure, SAS 9.3) with a

negative binomial distribution and a log link function (Littell et al. 2006) to examine the factors influencing foray rates (forays/h.) and the average duration of forays (min) in male and female field sparrows. We used a negative binomial distribution to account for potential overdispersion of our data. We treated number of forays with a number of hours tracked as an offset and mean duration of forays (in minutes), as two different response variables and age, physical condition, as the residuals from a regression of mass [g] on tarsus length [mm], time of day (day or night), fertility stage (pre-fertile, fertile or post-fertile), ordinal date, year, and interactive combinations of these variables as fixed effects. We treated bird identity as a random effect to account for repeated sampling of individuals within years (i.e., during multiple fertility stages and during both day and night) and the tracking of one individual in two separate years. Prior to fitting models, we examined correlations among all variables and excluded variables that were highly correlated ($|r| > 0.50$). We evaluated a priori candidate models using Akaike's information criterion adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002; Grueber et al. 2011; Symonds and Mousalli 2011). We considered models within 4 AIC_c of the top model to be competitive, as this represents a conservative inclusion of the most plausible models (Burnham et al. 2010). We also evaluated all models for their inclusion of uninformative parameters (i.e., "pretending variables"; Anderson 2008) by examining model deviance and the inclusion of zero in 85% confidence limits (Arnold 2010). In case of model selection uncertainty, we calculated model-averaged values as well as unconditional 85% confidence intervals for variables contained within competitive models (Burnham and Anderson 2002). We report means ± SE unless otherwise noted.

Extra-pair paternity We used generalized linear mixed models (GLMM, GLIMMIX procedure, SAS 9.3) with a binomial

distribution and a logit link function (Littell et al. 2006) to examine whether the probability of males obtaining EPY outside their nest increased with foray behavior and whether the probability of being cuckolded (EPY within their nest) increased with foray behavior. We included an interaction between male age and time of day as these were important predictors of foray rate in males. We also examined whether the probability of females obtaining EPY in their nest increased with foray behavior while controlling for female age and fertility period. We treated extra-pair paternity (coded as yes = 1 and no = 0) as the response variable, foray rate (forays/h.) as a fixed effect, and we treated bird identity as a random effect to account for sampling some individuals in more than 1 year. We also examined the influence of foray duration on EPY in males and females and cuckoldry in males using the same framework. We report means ± SE unless otherwise noted.

Results

We banded 567 field sparrows (161 males, 74 females, and 332 nestlings) over the course of the study. We documented foray behavior of 47 radio-tagged adult birds (25 males and 22 females) during 2012–2014. We tracked one male on two consecutive years. Across the study, eight birds were tracked in 2012, 14 birds in 2013, and 26 birds in 2014. We identified 3523 total forays over the 3-year study and tracked birds for 15,209 h (Table 1). We tracked each bird for an average of 317 h (~13 days) and acquired an average of 5394 locations per bird, with a maximum number of locations of 34,033 over the course of 28 days. The average number of forays per hour in males was 0.28 forays/h ± 0.34 SD (range = 0.05–1.89) and for females was 0.25 forays/h ± 0.37 SD (range = 0.01–2.68) (online resources, S3−4). The average duration of male forays was 87.27 min ± 166.10 SD and for females 90.17 min ± 116 min SD (online resources, S5–6).

Foray rates (forays/h.) of males were best explained by one model with an interaction of age (ASY and SY) and time of day (Day_Night). This top model received nearly half the weight of evidence ($\sum w_i = 0.49$) (Table 2). ASY males forayed more than SY males and overall, more forays occurred during the day than at night (Fig. 4). The patterns from this top-ranked model were driven by the main effects of age and time of day, as the interaction effects were not strongly supported (ASY day = 0.12 ± 0.38). However, because this first model was not overwhelmingly supported, and two additional models were ranked within 4 AIC$_c$ of the top model, we generated model-averaged estimates of the variables within our competitive models. The second ranked model, the global model, despite being ranked as competitive ($\sum w_i = 0.38$ and within 4 AIC$_c$ of the top model; Burnham et al. 2010), was driven by the variables of age, day_night and year (age: ASY β = 0.51 ± 0.29; Day_Night: day β = 0.73 ± 0.18; year: 2012 β = 0.41 ± 0.33, 2013 β = 0.90 ± 0.36). The coefficients for

fertility stage, condition and ordinal date were not informative (fertility stage: fertile β = 0.11 ± 0.23, post-fertile β = 0.12 ± 0.23; condition: β = −0.16 ± 0.13; ordinal date: β = 0.001 ± 0.008). The model of year alone was also a predictor of foray rates (year: 2012 β = 0.73 ± 0.0.27, 2013 β = 1.3 ± 0.25; birds forayed more in 2013 (0.46 forays/h ± 0.08) than in 2012 (0.26 forays/h ± 0.05) and 2014 (0.12 forays/h ± 0.02). We found little support for the other models containing fertility stage, ordinal date, condition, or interactions among these variables for influencing foray rates of males (Table 2). In contrast, we found no support for any of the models we tested (age, fertility stage, ordinal date, condition, or interactions among these variables) for influencing foray duration in males; null model was ranked within 4 AIC$_c$ of the top model, suggesting that the models we tested were not competitive (Table 3).

Foray rate (forays/h) of females was best explained by fertility stage; this top model received nearly half the weight of evidence ($\sum w_i = 0.42$; Table 4); females forayed more during the pre-fertile stages than the fertile and post-fertile stages (fertility stage: fertile β = −0.93 ± 0.42; post-fertile β = −0.77 ± 0.40) (Fig. 5). Two additional models, the interaction of fertility stage and age ($\sum w_i = 0.29$; Table 4) and the interaction of fertility stage and time of day ($\sum w_i = 0.10$) were also ranked within 4 AIC$_c$ of the top model; consequently, we generated model-averaged estimates of the variables within our competitive models. The model of the interaction of fertility stage and age, suggested that ASY females foray more than SY females but that the interaction terms were uninformative (fertile ASY β = 0.48 ± 0.57; post-fertile ASY β = −0.25 ± 0.52) (Fig. 5). The model of the interaction among fertility stage and time of day indicated that females foray more during the day than at night, but that the interaction terms were uninformative (fertile day β = 0.28 ± 0.55; post-fertile day β = −0.19 ± 0.49). Model-averaged values, however, suggested that the predominant influence was fertility stage and not time of day (Fig. 5). The additional models, global, condition, day vs. night, ordinal date, age, and interactive models were considered not competitive as they were ranked with ΔAIC$_c$ > 4 (Table 4). Like in males, any of the models we tested (fertility stage, ordinal date, condition, or interactions among these variables) failed to explain foray duration in females; null model was ranked within 4 AIC$_c$ of the top model suggesting that any of the models were competitive (Table 5).

We collected blood samples from 424 birds (143 males, 73 females, and 308 nestlings). We included the microsatellite genotypes of all known territorial adults for maximum-likelihood simulations and estimated the confidence of paternity assignments. We found at least one extra-pair offspring in 40.0% (32/80) of the broods and 9.7% (30/308) of all offspring sampled were sired by an extra-pair male. We identified 92% (24 of 26) of the extra-pair fathers. Four nests had EPY from two extra-pair

Table 1 Extraterritorial forays of radio-tagged male and female field sparrows, *Spizella pusilla*. Data are from 47 birds tracked for 15,209 h in Kennekuk Cove County Park, IL, during 2012–2014. One bird (2340–49144) was tracked over two consecutive years. Twelve birds were paired to another radio-tagged bird, comprising six radio-tagged pairs

Year	Bird	Males Total forays (n)	Males Time tracked (h)	Females Total forays (n)	Females Time tracked (h)
2012	2340–49135	296	625		
	2340–49140	60	510		
	[a]2340–49144	30	269		
	2340–49149	195	629		
	2340–49807	13	46		
	2360–91802	22	129		
	2360–91829	15	73		
	2340–49117			189	497
Totals		631	2281	189	497

Year	Bird	Males Total forays (n)	Males Time tracked (h)	Females Total forays (n)	Females Time tracked (h)
2013	[a]2340–49144	147	334		
	2340–49148	103	229		
	2340–49815	345	570		
	2360–9801	94	370		
	2360–91811	231	323		
	2360–91857	248	408		
	2360–91858	148	237		
	2360–91863	11	307		
	2360–91867	79	266		
	2360–91814			24	223
	2360–91862			26	363
	2360–91865			144	469
	2360–91868			51	303
	2360–91870			109	258
Totals		1406	3044	354	1616

Year	Bird	Males Total forays (n)	Males Time tracked (h)	Females Total forays (n)	Females Time tracked (h)
2014	2340–49830	2	27		
	2340–49881	34	190		
	2340–49882	28	125		
	2340–49883	18	112		
	2360–91844	11	182		
	2700–35120	8	42		
	2700–35504	77	588		
	2700–35505	77	700		
	2700–35534	61	499		
	2700–35540	34	721		
	2340–49831			5	18
	2340–49834			79	560
	2340–49837			24	406
	2340–49838			28	279
	2340–49839			23	231
	2340–49847			20	48
	2340–91870			92	242
	2360–91755			8	183
	2700–35502			11	147
	2700–35506			58	479
	2700–35508			13	119
	2700–35530			61	443
	2700–35535			78	646
	2700–35549			15	186
	2700–35550			19	235
	2760–35173			48	363
Totals		350	3186	582	4585

Table 2 Comparison of candidate models predicting foray rate (forays/h) in male field sparrows, *Spizella pusilla*. Models were ranked based on Akaike's information criterion adjusted for small sample sizes (AIC$_c$). K is the number of model parameters and ΔAIC$_c$ is the difference in AIC$_c$ from the top model. w_i is the model weight. Data are from 25 males tracked in Kennekuk Cove County Park, IL, during 2012–2014. × denotes interactive effects among variables

Model	K	AIC$_c$	ΔAIC$_c$	w_i
Age × Day_Night	5	675.50	0.00	0.49
Global model (Age + Day_Night + FertilityStage + Ordinal date + Year)	8	676.14	0.64	0.36
Year	2	679.39	3.89	0.07
Day_Night	2	679.61	4.11	0.06
Age	2	683.60	8.10	0.01
FertilityStage × Day_Night	6	685.08	9.58	0.00
Condition × Day_Night	3	688.16	12.66	0.00
Ordinal date	2	688.47	12.97	0.00
Fertility Stage × Age	6	691.41	15.91	0.00
Null	1	692.64	17.14	0.00
Condition	2	692.92	17.42	0.00
Condition × Age	3	694.67	19.17	0.00
Condition × FertilityStage	3	696.11	20.61	0.00
Fertility Stage	3	696.36	20.86	0.00

fathers. Of the 47 radio-tagged birds (25 males and 22 females), we tracked and for which we estimated foray rates and duration of forays, and we had extra-pair paternity data for 30 (17 males and 13 females).

The probability of obtaining EPP in males and females (in males, outside their nest and in females within their nest) did not increase with foray rate; individuals that forayed more were not more likely to gain EPY (GLMM for males: $n = 18$, $\beta = -0.64 \pm 2.54$, $F_{1,41} = 0.06$, $P = 0.80$; GLMM for females: $n = 13$, $\beta = -1.32 \pm 3.35$, $F_{1,28} = 0.16$, $P = 0.69$). Similarly, the probability of obtaining EPP in males and females did not increase with foray duration; individuals that forayed for longer periods of time were not more likely to gain EPY (GLMM for males: $n = 18$, $\beta = 0.004 \pm 0.008$, $F_{1,41} = 0.27$, $P = 0.60$; GLMM for females: $n = 13$, $\beta = -0.002 \pm 0.009$, $F_{1,28} = 0.08$, $P = 0.78$). Furthermore, the probability of males being cuckolded (finding EPY within their nest) did not increase with foray rate (GLMM for males: $n = 18$, $\beta = -4.12 \pm 7.62$, $F_{1,28} = 0.29$, $P = 0.59$) or duration of forays (GLMM for males: $n = 18$, $\beta = 0.004 \pm 0.01$, $F_{1,28} = 0.15$, $P = 0.70$).

Discussion

With the high spatial and temporal resolution of movement data obtained via automated telemetry, we gained insight into the patterns, correlates, and paternity consequences of extra-territorial foray behavior in the field sparrow. We found that both male and female sparrows regularly engaged in extraterritorial forays and that factors such as age, time of day (day or night), and fertility stage influence foray rates but not duration of forays. Older males forayed more than younger males and, while we detected many nocturnal forays, most forays occurred during the day. These findings are consistent with Kleven et al. (2006) that specifically examined age differences in foray effort and showed that older males of reed bunting (*E. schoeniclus*) foray seven times as frequently as young males. Based on Weatherhead and Boag (1995), older and more experienced males usually have higher success in extra-pair mating because older males are better at exploiting possibilities for EPCs and coercing females. In addition, females may be more likely to accept copulation from older males, as older males tend to have higher pairing success, clutch size, and fledgling success than SY males (Lemon et al. 1992). Although this pattern of older males foraying more than young males is consistent with several previous studies and correlates with patterns of extra-pair mating in socially monogamous birds (reviewed in Griffith et al. 2002), we did not find evidence for rate of forays and foray duration correlating with extra-pair paternity in our system.
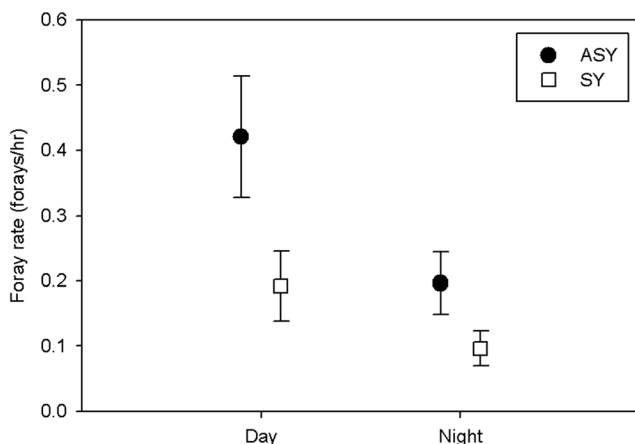

Fig. 4 Model-averaged predicted estimates of foray rate (foray per h) and SE (±) at day and night by after second year (ASY) and second year (SY) male field sparrows (*Spizella pusilla*). Data are from 25 males tracked in Kennekuk Cove County Park, IL, during 2012–2014

Table 3 Comparison of candidate models predicting mean duration of forays (min) in male field sparrows, *Spizella pusilla*. Models were ranked based on Akaike's information criterion adjusted for small sample sizes (AIC$_c$). K is the number of model parameters and ΔAIC$_c$ is the difference in AIC$_c$ from the top model. w_i is the model weight. Data are from 25 males tracked in Kennekuk Cove County Park, Illinois during 2012–2014. × = denotes interactive effects among variables

Model	K	AIC$_c$	ΔAIC$_c$	w_i
Day_Night	2	948.10	0.00	0.271
Null	1	949.20	1.10	0.157
Age	2	949.28	1.18	0.150
Condition	2	950.05	1.95	0.102
Age × Day_Night	5	950.57	2.47	0.079
Condition × Age	3	950.62	2.52	0.077
Condition × FertilityStage	3	951.50	3.40	0.050
FertilityStage × Age	6	951.70	3.60	0.045
Condition × Day_Night	3	952.27	4.17	0.034
FertilityStage	3	953.40	5.30	0.019
FertilityStage × Day_Night	6	954.08	5.98	0.014
Year	2	958.82	10.72	0.001
Ordinal date	2	959.36	11.26	0.001
Global model (Age + Day_Night + FertilityStage + Ordinal date + Year)	8	961.26	13.16	0.000

For females, fertility stage and age appeared to be an important factor explaining foray rates; females forayed more during the pre-fertile period than the fertile and post-fertile periods and overall, ASY females forayed more than SY females. The pattern of foraying more during the pre-fertile period is consistent with studies of foray behavior in other species (song sparrows, Açkay et al. 2012; yellow-breasted chat, Ward et al. 2014). However, while in some species female forays stop after fertile periods (song sparrow, Açkay et al. 2012), our female sparrows, although less frequently, forayed throughout all fertility stages, including post-fertile stages, suggesting that seeking EPCs and acquiring EPPs may not be the only reason for foraying.

Male field sparrows forayed most often during the day and less often at night. Although this was not surprising, the fact that our field sparrows forayed greater than expected at night was interesting, especially given that field sparrows are primarily diurnal (Carey et al. 1994). Nocturnal activity (singing) in field sparrows, although rare, has been documented in our system; territorial mated males tend to vocalize at night throughout the breeding season, potentially advertising their location and willingness to copulate (Celis-Murillo et al. 2016a, b). These observations, therefore, reveal that field sparrows may employ both a passive (advertise) and active approach (foray) to seek and/or attract extra-pair mates, even at night.

Despite documenting >3500 forays, we failed to find a link between the foray rate or duration of forays and extra-pair paternity (in the form of EPY) in males and females. Furthermore, we failed to document a link between foray rate or duration of forays and cuckoldry in males. It is possible, however, that despite birds

Table 4 Comparison of candidate models predicting foray rate (forays/h) in female field sparrows, *Spizella pusilla*. Models were ranked based on Akaike's information criterion adjusted for small sample sizes (AIC$_c$). K is the number of model parameters and ΔAIC$_c$ is the difference in AIC$_c$ from the top model. w_i is the model weight. Data are from 22 females tracked in Kennekuk Cove County Park, IL, during the years 2012–2014. × denotes interactive effects among variables

| Model	K	AIC$_c$	ΔAIC$_c$	w_i
FertilityStage	3	602.53	0.00	0.42
FertilityStage × Age	6	603.22	0.69	0.30
FertilityStage × Day_Night	6	605.39	2.86	0.10
Global model (Age + Day_Night + FertilityStage + Ordinal date + Year)	8	607.04	4.51	0.04
Age × Day_Night	4	607.05	4.52	0.04
Ordinal date	2	608.67	6.14	0.02
Age	2	608.80	6.27	0.02
Day_Night	2	608.92	6.39	0.02
Null	1	609.12	6.59	0.02
Condition × FertilityStage	3	610.53	8.00	0.01
Condition	2	611.07	8.54	0.01
Year	2	612.24	9.71	0.00
Condition × Day_Night	3	613.14	10.61	0.00
Condition ×Age	3	613.26	10.70	0.00
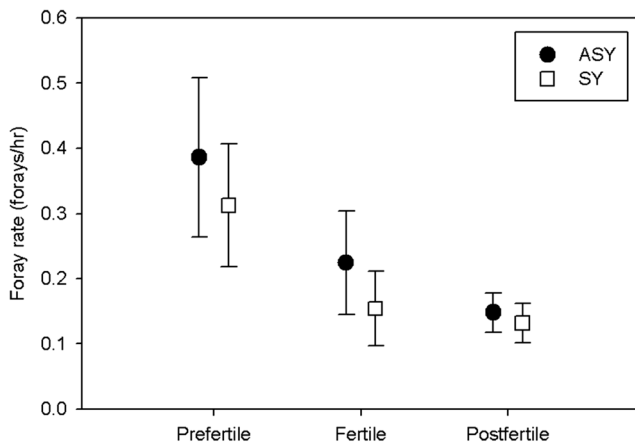
Fig. 5 Model-averaged predicted estimates of foray rate (forays per hour) and SE (±) of after second year (ASY) and second year (SY) female field sparrows (*Spizella pusilla*) and across fertility stages. Data are from 22 females tracked in Kennekuk Cove County Park, IL, during 2012–2014

using forays to seek extra-pair mates they could be copulating frequently on forays. Thus, a correlation among foray effort and measurable EPYs could be difficult to obtain. This is consistent with many experimental studies that have shown that the occurrence of EPCs in nature is usually much greater than the observed number of EPY (Hunter et al. 1992; Fossøy et al. 2006) and that even females having no EPY may still be sexually promiscuous (Fossøy et al. 2006). Additionally, Sellaeg (2014), using a mathematical model, showed that while there might be a large number of EPCs in a population, the proportion of nests with EPY can be very small, making very difficult for investigators to find an effect of forays on EPP. EPCs could increase with more foray behavior of males and/or females; however, in our study we could not document the frequency of EPCs. Alternatively, it

might be that just a few forays are necessary for an extra-pair fertilization to occur and consequently, the overall relationship between foray rate and/or duration and EPY or cuckoldry is normally weak.

Regardless of the purpose of forays, individuals appear to foray often. An alternative and not mutually exclusive explanation for the lack of relationship between forays and EPP is that forays may also serve for prospecting and acquiring information about their social (conspecific and heterospecific neighbors) and ecological environment (potential new territories, nesting sites, habitats, predators) (Dale et al. 1990; Pärt 1995; Giraldeu 1997; Pärt et al. 2011). For instance, prospecting in males may allow them to obtain information that could enhance their future breeding success (Doligez et al. 1994; Schjørring et al. 1999). The finding that male foray activity is constant across the breeding season rather than peaking during fertile periods of social mates or neighbors supports the idea that forays may serve many functions, including prospecting. Like males, females may foray to gather public information about future breeding habitat and for nest site selection (Eadie and Gauthier 1985; Betts et al. 2008; Pärt et al. 2011) and to assess potential males for future breeding attempts (Stutchbury et al. 1997). The increase in female forays during their pre-fertile and fertile stages is consistent with this conclusion. In some species, prospecting behavior is directly linked to the choice of a future breeding territory (Schjørring et al. 1999; Doligez et al. 2004). For example, up to 79% of northern wheatears (*Oenanthe oenanthe*) establish territories at their previous year's prospecting sites (Pärt et al. 2011). Similarly, cavity-nesting ducks (common goldeneyes, *Bucephala clangula*, and barrow's goldenyes, *Bucephala islandica*) search for nest sites at the end of the summer, in preparation for next breeding season (Eadie and

Table 5 Comparison of candidate models predicting mean duration of forays (min) in female field sparrows, *Spizella pusilla*. Models were ranked based on Akaike's information criterion adjusted for small sample sizes (AIC$_c$). K is the number of model parameters and ΔAIC$_c$ is the difference in AIC$_c$ from the top model. w_i is the model weight. Data are from 22 females tracked in Kennekuk Cove County Park, Illinois during the years 2012–2014. × denotes interactive effects among variables

Model	K	AIC$_c$	ΔAIC$_c$	w_i
FertilityStage × Day_Night	6	939.77	0.00	0.414
Day_Night	2	941.67	1.90	0.160
Age × Day_Night	5	941.91	2.14	0.142
Global model (Age + Day_Night + FertilityStage + Ordinal date + Year)	8	942.74	2.97	0.094
Null	1	943.03	3.26	0.081
Age	2	944.04	4.27	0.049
FertilityStage	3	946.21	6.44	0.017
Year	2	947.18	7.41	0.010
FertilityStage × Age	6	947.55	7.78	0.008
Condition × Day_Night	3	947.85	8.08	0.007
Ordinal date	2	947.95	8.18	0.007
Condition	2	948.22	8.45	0.006
Condition × Age	3	950.13	10.36	0.002
Condition × FertilityStage	3	951.53	11.76	0.001

Gauthier 1985). Foray behavior may help individuals gather social and ecological information allowing them to make informed decisions about where and/or with whom to breed in subsequent breeding attempts, within the same year (e.g., if a nest is depredated, or in cases of divorce or mate death) or in subsequent years.

Another alternative function of foraying is for foraging. Açkay et al. (2012), by simultaneously tracking paired male and female song sparrows, showed that females forayed more in the pre-fertile period, and suggested that these forays were for foraging, especially as most forays during the pre-fertile period were accompanied by their social mate. We conducted daily behavioral observations and described male-male and male-female interactions of birds within and outside their territories; however, we never observed birds foraging outside their territories. In the few cases where we saw males intruding into neighboring territories, intruders approached females in their territories and their mates showed aggressive behavior toward the intruder, but intruders were never seen foraging. Similar to our observations, other studies have also reported that territorial birds are rarely seen foraging outside of their territories (Yezerinac and Weatherhead 1997; Pitcher and Stutchbury 2000). In addition, Humbird and Neudorf (2008) experimentally tested if supplemented female northern cardinals (*Cardinalis cardinalis*) decreased their foraying effort. They found that supplemented females make more forays and spend more time off territory than unsupplemented females but suggested that forays may not have a role in foraging. Furthermore, if forays are related to foraging, females would be predicted to foray more during the post-fertile stages. In our study, however, females forayed more during pre-fertile and fertile stages than post-fertile stages. Although we cannot rule out foraging as a reason for foraying, we believe that other factors were more important. When we informally examined the spatial patterns of movements of individual birds, we did not see a clear spatial pattern of forays by individual birds, i.e., forays did not appear to be directed specifically at one or few particular territories or neighborhoods. Instead, forays appeared to be in random directions as if birds were prospecting (AC-M unpubl. data). For many species, visiting other patches or other neighborhoods can allow birds to gather information on potential mates in case their mates abandon the pair (Maness and Anderson 2008), local patch quality for potential nest sites (Eadie and Gauthier 1985; Doligez et al. 2004) and even nesting success of conspecifics (Schuett et al. 2012).

Overall, our findings suggest that extraterritorial forays are common in male and female of field sparrows; however, there is not a direct relationship of male and female foray rates and foray duration with extra-pair paternity or a direct relationship among male foray rates and foray duration and cuckoldry. While forays likely serves some function in acquiring EPCs and extra-pair matings, foray behavior may also have a major role in prospecting and gaining public information regarding their social and ecological environment, which ultimately may help them to achieve higher reproductive success but not necessarily in the form of EPP.

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