

Original Article

Who initiates extrapair mating in song sparrows?

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Extrapair paternity (EPP) is a common feature of many mating systems. Although molecular methods have made it possible to document the rate of EPP across numerous taxa, we still lack an understanding of how and why EPP happens. Behavioral data on mating interactions are needed to answer this question. We employed radiotelemetry to follow the movement patterns of tagged song sparrows (*Melospiza melodia*) during their nesting cycle. We found that females and males commonly forayed onto neighboring territories in the prefertile period, frequently together. In the fertile period, however, the foray rate dropped significantly, and females largely stayed on their own territories. Concurrently in the fertile period, both the time mates spent in proximity and intrusion rates on their territories increased compared with the prefertile period. After the female started laying eggs, proximity of the mates to one another declined again, and some males started to foray onto neighboring territories, in most cases into territories where there was a fertile female. Thus, females do not seem to seek out particular males for extrapair copulations (EPCs) in their fertile period, but rather it is the males who actively seek extrapair mating. Males therefore face a trade-off between ensuring paternity at home and pursuing copulations elsewhere. Agonistic interactions between extrapair males and females were almost entirely absent, suggesting that males do not force females into copulations. Therefore, in song sparrows, males have to initiate EPCs by seeking out fertile females, suggesting that males probably drive the pattern of EPP in our population. *Key words*: extrapair paternity, radiotelemetry, sexual conflict, sexual selection, song sparrows. [*Behav Ecol*]

INTRODUCTION

In many species, there is a discrepancy between the social (or apparent) and genetic mating systems. This discrepancy is especially prevalent in the birds: Social monogamy with biparental care is the most common mating system, with over 80% of birds exhibiting this pattern (Cockburn 2006), yet, molecular methods have revealed that in most species, typically some young in the nest are sired by an extrapair male, that is, a male other than the female's social mate. This phenomenon, extrapair paternity (EPP), has been the focus of a great number of studies in behavioral ecology, which have documented variation in levels and patterns of EPP (see reviews in Griffith et al. 2002; Westneat and Stewart 2003; Akçay and Roughgarden 2007).

Before the advent of molecular techniques, the nature of mating interactions between females and males was inferred from behavioral observations (e.g., Beecher MD and Beecher IM 1979; Birkhead 1979). However, as molecular methods for determining parentage came into widespread usage, the direction of inference shifted, and behavioral interactions began to be inferred from genetic studies of paternity, generally with the goal of identifying correlates of success in gaining EPP or maintaining paternity in the home nest. As genetic studies started to accumulate, the earlier focus on male

strategies inferred from behavior was replaced with a focus on female strategies inferred from genetic data. Indeed, most researchers have come to assume that EPP is a result of female strategies and that females benefit from EPP (Jennions and Petrie 2000). Under this hypothesis, females can use EPP to trade-up from nonoptimal fertilization partners.

The general expectation that females are driving EPP (in the sense that females have evolved reproductive strategies that enabled them to benefit from EPP) has been called into question, however, by recent reviews and meta-analyses (Westneat and Stewart 2003; Akçay and Roughgarden 2007). In the most comprehensive meta-analysis to date, Akçay and Roughgarden (2007) found that the overall evidence for female benefits from EPP in birds was weak at best.

In principle, there are 3 broad hypotheses for the function of EPP from the female perspective. First, as most commonly believed, EPP may benefit a female either genetically (Jennions and Petrie 2000; Neff and Pitcher 2005; Kempenaers 2007), directly through access to resources (e.g., Gray 1997; Rubenstein 2007), or as a fertility insurance policy (Sheldon 1994). Second, females may be an unwilling player in the mating "game" if they pay a net fitness cost for extrapair copulations (EPCs) (e.g., Arnqvist and Kirkpatrick 2005). Finally, from the female perspective, producing extrapair young or within-pair young might be selectively neutral, with no clear cost or benefits, and they may accept copulations with little discrimination. Under the latter 2 hypotheses, EPP is solely male driven.

From the male perspective, a simple expectation is that males will pursue EPCs whenever possible, as copulations are thought to be cheap. Their pursuit of EPCs may be constrained, however, by a trade-off between insuring paternity at home through

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mate guarding (Beecher MD and Beecher IM 1979; Birkhead 1979; Gowaty et al. 1989) and territory defense (Tobias and Seddon 2000) versus seeking out paternity elsewhere, although the trade-off may be weak or nonexistent if the females are effectively able to overcome attempts at mate guarding.

A significant problem in studying extrapair mating is that EPP can be easily detected in molecular studies, but the actual copulations are very hard to observe directly, which is the reason why behavioral studies of reproductive strategies have not kept up with genetic studies. One way to deal with this problem is to use radiotelemetry to track male and female movement patterns (e.g., Neudorf et al. 1997; Double and Cockburn 2000; Woolfenden et al. 2005; Pedersen et al. 2006), which can elucidate female and male strategies and potentially identify trade-offs they face. For instance, in some studies, females have been found to make targeted forays onto other males' territories in their fertile period (e.g., Neudorf et al. 1997; Chiver et al. 2008), which may indicate female pursuit of extrapair mating.

Most radio-tracking studies to date, however, have focused on either the male or the female but not both. Only 2 studies that we are aware of tracked both members of the pair (Pedersen et al. 2006; Evans et al. 2008) and in only one of these was there an independent observer for each bird so that both could be tracked reliably. In this last study, Evans et al. (2008) found that while female wood thrushes showed increased rates of forays in the fertile period, they were frequently accompanied on these forays by their mates, which may have reduced their opportunity for EPCs. Another problem of previous radio-tracking studies is that they usually have compared the foray behavior of females during the fertile period with foray behavior during the incubation period. During incubation, females are likely to be closely tied to the nest, which alone may explain any changes in their movement patterns.

We employed radiotelemetry to study extrapair mating in the song sparrow, *Melospiza melodia*. The song sparrow is a socially monogamous North American songbird. Males in our population defend all-purpose territories throughout the year to the exclusion of other males, and almost all males are socially monogamous. A previous study in our population found that 24% of offspring resulted from extrapair fertilizations and 36% of the nests had at least one extrapair young (Hill et al. 2011). Extrapair sires were almost always nearby neighbors (Hill et al. 2011; see also Sardell et al. 2010). In pairwise comparisons of extrapair sires with the males they cuckolded, Hill et al. (2011) found no significant effect of song repertoire size, song sharing (a trait that correlates with territory tenure, Beecher et al. 2000), male age, relatedness to the female, or heterozygosity of the males. These results cast doubt on the assumption that females are actively choosing extrapair males.

In the current study, we sought to shed some light on whether EPP is driven by male strategies, female strategies, or both. We fitted both members of song sparrows pairs with radio transmitters and followed their movement patterns during pre-fertile, fertile, and post-fertile (incubation) periods with the aim of determining where EPCs happen and whether males face a trade-off between protecting paternity at home and gaining it elsewhere.

MATERIALS AND METHODS

Study site, subjects, and field methods

The study was conducted in 2008 and 2009 in Discovery Park, Seattle, where our laboratory has studied song sparrows since 1986. The study area consists of approximately 150 territories held by banded males each year. For the current study, we selected an area comprising about 35 territories each year

where we banded all males and females. This area included all the subjects and their immediate and once-removed neighbors. We caught males and females using mist nets and Potter traps starting in January for banding and later for fitting radio transmitters. All tagged subjects were already banded and known to be exhibiting pair behavior at the time of tagging. We tagged 10 pairs in 2008 and 11 pairs in 2009. We tagged an additional 2 pairs in 2011 specifically for the specific goal of gaining information on possible predawn movement patterns of the female. We waited at least 24 h to begin radio tracking after we tagged the second member of the pair.

Because the birds in our population become territorial before nesting starts, we were able to gather data in the pre-fertile period. To this end, we tagged the subjects between March 6–9 in 2008, April 4–10 in 2009, and on April 2 in 2011. We aimed to replace the transmitters when their batteries ran out, if the pair had not started nesting yet. Early spring in both 2008 and 2009 was characterized by a La Nina pattern which leads to colder and wetter than normal weather in the Pacific Northwest and has been shown to delay the first breeding attempt of song sparrows in this area (Wilson and Arcese 2003). Consequently, in 2008, we were able to collect data on the fertile periods of only 2 females. In 2009, we delayed tagging the birds and were able to collect data on fertile periods of most tagged females (see Table 1). In 2011, we collected data from pre-fertile period of 2 females.

Radiotelemetry

We fitted subjects with small radio transmitters (BD-2N; Holohil Systems Ltd, Carp, ON, Canada) using a loop harness (Rappole and Tipton 1991). The transmitters on males weighed approximately 1.0 g, and those on females weighed approximately 0.75 g, owing to a smaller battery. Subjects were radio tracked with radio receivers (Communication Specialists, R-1000) connected to a 3 element Yagi-antenna.

Two observers followed each pair for 1-h sessions (or longer if a foray was in progress). One of the observers followed the male and the other observer followed the female from a safe distance (usually about 20 m) to avoid interfering with their activities. The observer following the male also recorded the whole observation session with a Marantz PMD660 solid state recorder and Sennheiser ME66/K6 shotgun microphone. The observer following the female was responsible for taking notes on behavior (see below). Each observer was also equipped with a walkie-talkie to communicate in case the focal birds were away from each other. The exception to this was predawn tracking in 2011 where pairs were followed by a single observer with priority given to the female if the pair split up.

We followed each pair as frequently as possible and at least once every other day at different times of the day. In 2008 and 2009, radio tracking was carried out between 0530 and 1400 h with most of the sessions between 0700 and 1400 h. Predawn radio tracking in 2011 was started an hour before civil dawn and continued until 30 min after dawn.

The observer following the female took notes on a datasheet throughout the session and marked the locations of the birds on a large-scale map centered on focal pair's territory. To facilitate the reporting of locations, we flagged prominent landmarks (such as large stumps or fallen trees) and indicated these on the maps. We noted the behavior and the location of the birds every 5 min or with each movement larger than 5 m. We noted the distance between the members of the focal pair using 3 categories: <5, 5–15, and >15 m. Because the birds were not always visible, it was frequently not possible to ascertain who initiated flights when birds moved in the same direction.

We also noted vocal behaviors of the male (chirps and song) and the female (chirps, growls, and chitters), solicitation

Table 1
Duration of radio-tracking sessions (minutes)

Year	Pair (male–female)	Prefertile	Fertile (nest building/egg laying)	Incubation	Total	Notes
2008	cgam–yopm	1031	55 (0/55)	41	1182	
2008	cmar–ayom	1331	636 (636/0)	0	1967	
2008	worm–pmaa	748	0	0	748	
2009	bgmy–ozom	447	236 (157/79)	57	976	
2009	camy–ayam	433	286 (166/120)	60	1065	
2009	gypm–iman	398	322 (240/82)	0	1042	
2009	hbam–iism	574	363 (247/116)	0	1300	
2009	mawy–mpzi	566	330 (270/60)	135	1361	
2009	smac–camr	362	238 (178/60)	60	898	
2009	wpmr–yrms	696	240 (240/0)	0	1176	
2009	yssm–chmc	305	226 (166/60)	60	817	
2009	zzom–grmb	633	365 (305/60)	60	1423	
	Total	7524	3297 (2605/692)	473	13 955	
2008	wwma–hybm				605	Male predated
2008	mawa–zjzm				60	Male predated
2008	ymob–sbim				188	Male predated
2008	cmpp–osim				239	Male predated
2008	gbmy–szzm				0	Male and female predated
2008	mopy–rbjm				1376	Nest failure before we could locate the nest
2008	mybw–aigm				1757	Nest failure before we could locate the nest
2009	cabm–corm				178	Male predated
2009	bomi–scmz				505	Divorced
Grand total					18 863	

We did not include data from the subjects in the second half of the list as there were no first-egg dates for these due to the reasons noted.

displays by the female, actual copulations, pounces (in which a male flies directly up to a female as if to attack and flies away subsequently while giving a flight song; in most cases, there are no actual contacts), chases, and fights. We used chases in which the focal male chased a conspecific bird off his territory as a measure of intrusion pressure.

Forays

Song sparrow territories can be ascertained with an accuracy of a couple of meters by observing singing posts and boundary disputes. In our population, territories tend to be dense and continuous, interrupted only by occasional open areas, such as parking lots or meadows. Therefore, we defined forays as any movements that took the focal bird more than 5 m across their boundary, as these were unambiguously in the territory of a neighbor. In cases where the boundary was a road or trail, we did not count movements on the road or trail as forays and considered movements forays only if the focal birds moved 5 m past the road or trail. Similarly, we did not count trips into open and nondefended areas directly adjacent to the bird's own territory as forays. When a neighbor to our subjects disappeared, his territory was divided up between his neighbors and the new boundaries were established typically within a couple days; we did not count movements across the disputed new boundary as forays unless the movements took the birds across the former boundaries.

Finding nests and defining the fertile period

Because knowledge of the first-egg date for the subjects was critical, we supplemented radio-tracking sessions with observations of the females in order to find their nests. This way, for

all tagged subjects, we located the nest while the nest was being built or during egg laying. For most of the neighbors, we estimated the date of the first egg using the same methods, although we found some of these nests mid-incubation, in which case, we estimated the date of first egg from the date the eggs hatched, which happens after about 13 days of incubation (Nice 1943).

For analysis, we defined 3 time periods relative to the date of the first egg laid by the female (Figure 1). The prefertile period encompassed all of the tracking sessions from the first session through 6 days before the first egg. The fertile period was defined as being from 5 days before (day –4) the day of the first egg (day 1) until the day of the penultimate egg (day 2 or 3, depending on whether the final clutch size was 3 or 4). The day of the penultimate egg is assumed to be the last day

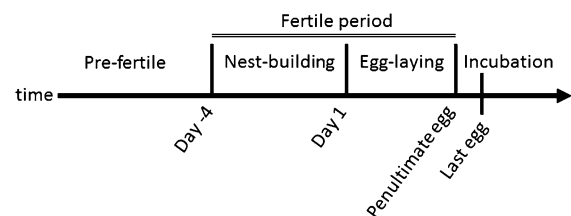


Figure 1

Definitions of the time periods employed in the study. Day 1 was defined as the day of the first egg. Prefertile period extended from the time of tagging to day –4 (5 days before the first egg), nest-building period was from day –4 to day 0 (the day before the first egg), egg-laying period was from day 1 to the day of penultimate egg (day 2 or 3 depending on clutch size), and incubation period started after that. Nest-building and egg-laying periods were considered the fertile period of the female.

on which a new egg can be fertilized. This definition of the fertile period follows the convention used in similar studies (Neudorf et al. 1997; Chiver et al. 2008; Evans et al. 2008). The onset of fertile period is somewhat arbitrary, but it agrees well with experimental studies in wild birds that have showed detrimental effects of aged sperm appearing at 5 days (White et al. 2008). We divided up the fertile period further into nest-building (day -4 to day 0) and egg-laying periods, as a preliminary examination of the data suggested important differences between these 2 periods (see Results). Finally, the postfertile period was defined as starting with the laying of the penultimate egg. Song sparrows usually start incubating the day the penultimate egg is laid (Nice 1943); therefore, we call this period incubation, even though another egg is laid during the period. For this period, we only used observations when the females were not on the nest to determine the time the pairs spent together.

We attempted to get blood samples from nestlings of the subjects; however, because of high rates of nest failure (due to predation and inclement weather), only 3 nests (of 12) were successful. Thus, we were not able to carry out paternity analyses to complement the behavioral observations.

Data analysis

We used Wilcoxon signed-rank tests for comparing each time period with the preceding time period (i.e., prefertile vs. nest building, nest building vs. egg laying, and egg laying vs. incubation). Sample sizes for each test varied accordingly (see Table 1). Analyses were carried out in SPSS 14.0 (SPSS Inc., Chicago, IL). All tests were two tailed.

Ethical note

Of the radio-tagged subjects, half of the 2008 males (5 of 10), one 2008 female, and one 2009 male were depredated. In all cases, in 2008, the evidence on the scene around the radio-tag was consistent with predation by Cooper's hawk (*Accipiter cooperii*). In the same time period (March to mid-May), 5 (of 12) nontagged males also disappeared from their territories immediately surrounding the area with the tagged males. These males were most likely depredated as well, as they were not seen again, and were replaced by their neighbors. Therefore, it is unlikely that radio-tags were responsible for high predation rates.

RESULTS

Copulations

During the study, we observed a total of 87 copulation solicitation displays from the focal females (all within her own territory), but only 8 copulations (from 2 pairs). All copulations were within-pair copulations, and all of them were preceded by a solicitation display by the female (i.e., none of

them were forced). Seven of 8 copulations occurred during the fertile period of the female, and the other occurred on day -6 (2 days before the start date of the fertile period). Females showed a slight increase in solicitation rates during the nest-building period compared with the prefertile period (Figure 3), but the difference was not significant, even after removing one outlier female ($z = 0.70$, $P = 0.40$, $n = 9$).

Time spent together

Focal males and females spent on average 55.8% of time within 5 m of each other during the prefertile period (Table 2). They increased time spent close during the nest-building period to 68.2% ($z = 2.14$, $P = 0.032$, $n = 10$) and then decreased it during the egg-laying period (47.3%, $z = -2.24$, $P = 0.025$, $n = 8$, Figure 2). The proportion of time spent close declined further during the incubation period but only slightly (46.2%, $z = 0.17$, $P = 0.87$, $n = 7$).

Forays

Females commonly forayed into neighboring territories during the prefertile period but not during the fertile period (Table 2, Figure 2). During the prefertile period, 10 of 12 females made at least one foray outside the territory for a total of 26 forays. On 21 of these forays (80.7%), the females were accompanied by the male, who followed them to the foreign territory. Average foray duration in the prefertile period was 18.52 min (range: 3–75 min). In contrast, only 2 of 10 females forayed outside their territory during fertile period (both forayed during the nest building) for a total number of 3 forays; in 2 of these forays, males followed the females for the whole duration of the foray. All of these 3 forays were short (5, 5, and 4 min long). Mean rates of female forays were 0.17 forays/h in the prefertile period and 0.05 forays/h in the nest-building period ($z = -1.68$, $P = 0.09$, $n = 10$). Females spent 6.41% of their time on average outside their territory during the prefertile period, which dropped to 0.5% of the time during the nest-building period, $z = -2.24$, $P = 0.025$, $n = 10$. No female was observed foraying during the egg-laying or incubation periods. Females almost always forayed into directly neighboring territories, with only 2 exceptions (both in the prefertile period). In one case, a female crossed 3 territories in a quick fashion, and in the other, one female crossed 1 territory.

Eleven of 12 males forayed outside their territories during the prefertile period of their females, spending 4.00% of the time outside the territory, and making on average 0.28 forays/h. Of the 39 forays by males during their mate's prefertile period, 18 were by the male alone. During the nest-building stage of their females, males tended to decrease both time spent off territory (1.51%, $z = -1.96$, $P = 0.05$, $n = 10$) and foray rates (0.10 forays/h, $z = -2.19$, $P = 0.03$, $n = 10$), with only 3 of 10 males foraying at all (Figure 2). Interestingly, during the egg-laying period of their female, some males (3 of 9) showed increased

Table 2

Summary of behavioral data broken down with respect to fertility status of the focal female

	Prefertile ($n = 12$)	Nest building ($n = 10$)	Egg laying ($n = 9$)	Incubation ($n = 7$)
% Time spent <5 m	55.79 (15.92)	68.25 (14.97)	47.33 (19.30)	46.21 (39.48)
% Female off-territory	6.40 (8.71)	0.52 (1.15)	0 (0)	0 (0)
% Male off-territory	4.00 (5.32)	1.51 (2.28)	6.57 (11.33)	8.66 (13.49)
Female forays/h	0.17 (0.16)	0.06 (0.13)	0 (0)	0 (0)
Male forays/h	0.28 (0.26)	0.10 (0.17)	0.70 (1.16)	0.65 (0.97)
Chases by focal male/h	0.11 (0.04)	0.29 (0.09)	0.16 (0.32)	0 (0)
Solicitations by focal female/h	0.59 (1.1)	0.66 (0.52)	0.48 (0.48)	0.29 (0.76)

The numbers are means (standard deviation).

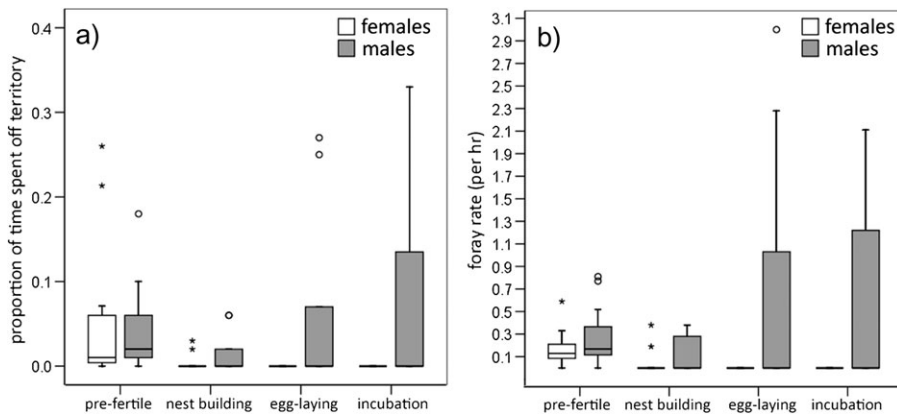


Figure 2
Proportion of time spent off territory (a) and foray rates (b) by females and males. The lines indicate medians, boxes indicate the quartiles, the whiskers 95% confidence intervals, and the asterisk and circles indicate outliers for females and males, respectively.

extraterritorial activity, whereas the remaining males did not foray. Two of these 3 males continued to show increased rates of foraging during the incubation stage, although a fourth male also showed increased foray rates. The overall increase in male foray rates and time spent outside the territory from the nest-building to the egg-laying periods was not statistically significant overall ($z = 1.46$, $P = 0.14$, $n = 8$). The 4 foraging males made 1.38 forays/h during the egg-laying and incubation periods combined, whereas the remaining 5 males did not make any forays during this period. Of the foraging males, 3 of 4 made forays only on territories where the resident female was fertile (Figure 4).

Intrusions and agonistic behaviors

Males faced increased intrusion rates during their mate's nest-building period compared with prefertile periods (0.29 chases/h vs. 0.11 chases/h, $z = 2.38$, $P = 0.02$, $n = 10$, Figure 3). The intrusion rates did not differ between nest-building and egg-laying period (0.17 chases/h, $z = 0.51$, $P = 0.61$, $n = 8$). When we could identify the bird that was chased, in all cases, it was a male from a neighboring territory. All chases ended at the territory boundary. We never saw an intruding male standing his ground after being detected by the resident male during a foray. There was no correlation between solicitation rates of a female and intrusion rates on her territory for either the prefertile or nest-building periods (P 's > 0.20).

In the course of the study, we observed only a single instance of an extrapair male behaving agonistically to a focal female.

Predawn movements

In 2011, we tracked 2 pairs for a total of 9 mornings. Both females were roosting on their territory when radio tracking began each morning. The first movement of the females occurred on average 10 min after civil dawn (range: -1 to 18 min), and we never observed a foray outside of the territory during the radio-tracking period.

DISCUSSION

We found that as the fertility status of the female changed, pair behavior also changed in important ways. First, pairs spent more time close together during the nest-building phase of the female, which also coincided with higher intrusion rates onto their territories by the neighboring males. Song sparrows in our population spend much of their time inside shrubbery, where they cannot be easily followed visually from a distance. This habitat preference means that a male probably needs physical proximity to his mate in order to prevent another male from approaching her (Mays and Ritchison 2004). Interestingly, the increased coordination was incomplete and

was largely restricted to the nest-building stage (as evidenced by the fact that pairs spend significantly less time together during egg-laying compared with nest-building period). A similar pattern has been found in bank swallows where males start following other females than their own mate after she lays the first egg (Beecher MD and Beecher IM 1979). Second, we found that while both males and females forayed outside their territory, both decreased their foray rates once the female entered her fertile period. In fact, females all but stopped foraging, with only 2 females foraging outside their territory and then for only a brief time. We further found that in their forays, females were typically accompanied by their social mates. These forays in the prefertile period most likely were done for foraging purposes. Song sparrows thus contrast with hooded warblers, *Wilsonia citrina* (Neudorf et al. 1997), common yellowthroats, *Geothlypis trichas* (Pedersen et al. 2006), and wood thrushes (Evans et al. 2008), in which females make extensive forays into territories of extrapair males during their fertile period (but not during incubation). A pattern similar to that of song sparrows was found in Acadian flycatchers (Hung et al. 2009), whose females were never observed to foray in either the fertile or incubation periods. Finally, we found that about half of the males showed increased foray rates during the egg-laying and incubation period of their female, whereas the rest did not foray. Most of the male forays

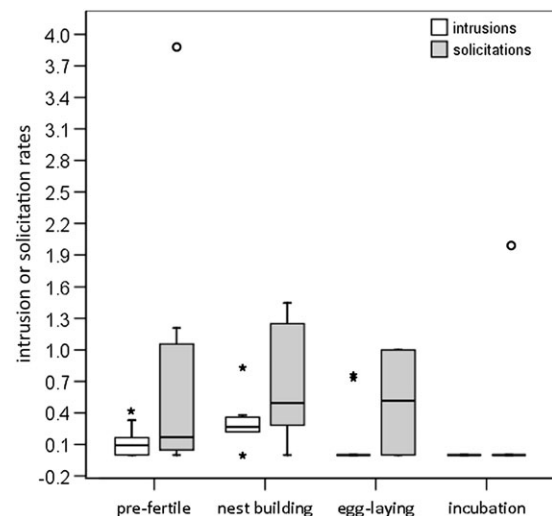


Figure 3
Intrusion and solicitation rates. Boxplots as in Figure 2, except that asterisks and circles indicate outliers for the intrusion and solicitation rates, respectively.

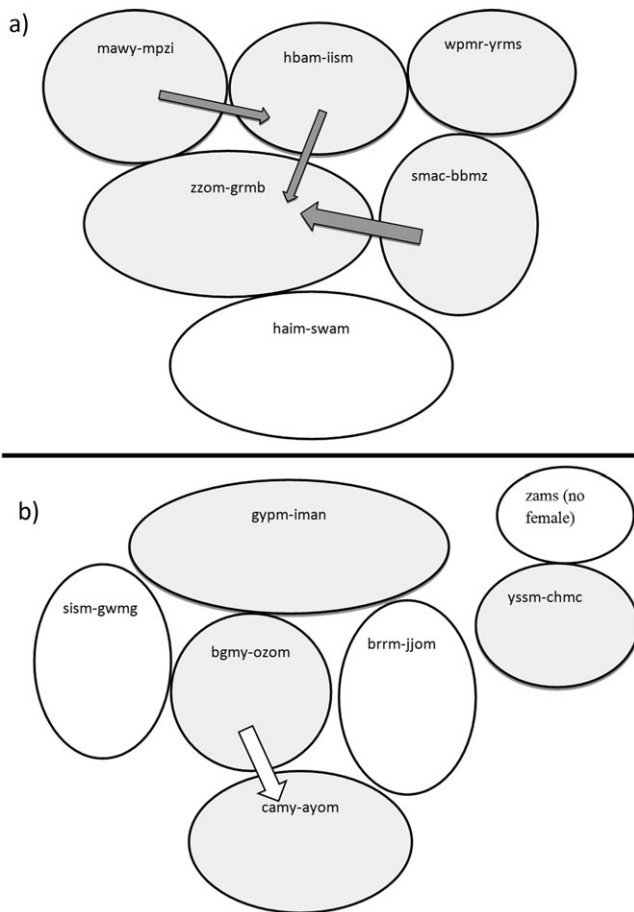


Figure 4

Schematics of 2 neighborhoods (a, b) where the tagged birds lived in 2009. Shaded territories, are where the pair was tagged (male–female). The shaded arrows denote single-male forays into neighboring territories when the female on that territory was fertile. The open arrow denotes that the female was not fertile during the single-male forays. The thickness of the arrow is correlated with foray rate.

in these periods (all forays made by 3 of the 4 males) were made to territories where the resident female was fertile at the time (Figure 4). Due to small sample size, we were not able to determine statistically whether these males forayed into territories with fertile females more often than expected by chance. Nonetheless, it is clear that a portion of the males make forays into other territories at a rather high rate (more than 1 foray an hour), at a time when many females are fertile, suggesting that they are very likely encountering opportunities for EPCs.

Therefore, our results indicate that in song sparrows, critical EPCs (i.e., EPCs occurring during the female’s fertile period) most likely happen on the female’s territory. This finding provides evidence against 2 scenarios about how EPCs happen in song sparrows. First, female song sparrows do not seem to seek out particular extrapair males by foraying onto their territories. One caveat to this conclusion is that our sampling of very early hours of the day was incomplete, although the data we collected in 2011 suggest that females do not exhibit increased foray behavior before dawn. Therefore, while we cannot strictly rule out targeted predawn forays by females during the fertile period as has been found in the superb fairy wren, *Malurus cyaneus* (Double and Cockburn 2000), our evidence argues against this possibility. In the superb fairy-wren, fe-

males visit “hidden leks” with multiple males displaying in proximity before dawn (Cockburn et al. 2009). Unlike the fairy-wrens, however, song sparrows lack a distinct dawn display, and therefore, predawn forays as seen in the fairy-wrens are very unlikely (Pedersen et al. 2006, also failed to detect any predawn forays despite extensive sampling in common yellowthroats).

Second, aggressive interactions between extrapair males and females were almost entirely absent. This finding makes sense because if females stay on their own territory when they are fertile, males cannot easily harass them into copulations; intruding males face eviction as soon as they are detected by the resident male. A female not willing to copulate therefore has only to recruit her mate to chase off the harassing male. In more than 300 h of radio tracking, we witnessed only a single case of an intruding male behaving aggressively to a neighboring female on her own territory; this male was evicted by the resident male within seconds. Since females spend almost all their time on their own territories when fertile and while there, seem to be almost immune from forced copulation attempts by intruders, forced EPCs cannot account for the high rate of EPP observed in our population (Hill et al. 2011).

Nonetheless, the fact that females stayed “home” during the period of their peak fertility despite commonly foraying out of the territory in their pre-fertile period suggests that there may indeed be potential for sexual conflict between females and extrapair males (Arnqvist and Kirkpatrick 2005). It is easy to speculate that staying home may be a female strategy to avoid unwanted EPCs, but it should be noted that we never saw a resident male harassing a visiting female during her forays in her pre-fertile period, whereas resident males readily chased intruding males. In any case, if females are not pursuing EPCs and can avoid forced copulation, why do they nonetheless mate often enough with intruding males to produce an EPP rate of 24%?

There are multiple hypotheses about female strategies leading to EPP. First, even if they do not leave their territory during the fertile period, females may exert mate choice by selectively accepting copulations from certain males only. Females also might use cryptic mate choice after copulation for biasing paternity toward preferred partners (Griffith 2009). Note, however, that a genetic study of our population failed to show any correlate of female choice of extrapair partners (Hill et al. 2011). A simpler alternative is that females might simply be indifferent to the identity of fertilization partners (“any dude will do” hypothesis, Hill et al. 2011). This hypothesis is consistent with the expectation that there should be low heritability of fitness, as indeed is found sometimes (e.g., Kruuk et al. 2000) or that selection for indirect benefits should be relatively weak (Qvarnström et al. 2006). Nevertheless, such indiscriminate polyandry may still be beneficial to the female as an insurance policy against occasional infertility (Sheldon 1994). If infertility is relatively rare, females may not be under selection to seek out EPCs but might nevertheless accept any that come their way.

If the female side of the equation does not have a clear positive or negative sign at least with respect to the identity of extrapair partners, the pattern of EPP would seem to be most heavily dependent on the strategy of the male, who apparently can prevent any advances from extrapair males by spending time close to his mate, and chasing off intruders. A male, however, faces a trade-off while guarding his female, since staying home and coordinating with his mate means that he is unlikely to encounter other extrapair females himself, given that fertile females stay on their own territories. Such a trade-off predicts that most paternity will be exchanged among males that pursue EPCs outside their territory for some of the time. In an earlier study, in our population, we indeed

discovered that males who gained paternity in other nests tended to lose paternity in their own nests and that this subset of males tended to be older than those who neither lost nor gained paternity (Hill et al. 2011). In the current study, all of the males who showed increased foraging activity during egg laying and incubation were older than 2 years. The males in their first breeding season in our sample ($n = 3$) did not foray once their females were fertile, although the small sample size precludes strong conclusions.

The behavioral results of the present study, when taken with the earlier molecular results on this population, indicate that song sparrow females in our population do not foray onto other territories to initiate copulations but apparently accept EPCs on their own territory. Thus, song sparrow females may play a role in affecting the outcome of extrapair mating by selectively accepting copulations from only certain intruding males or through postcopulatory selection of sperm, although direct evidence for this inference is lacking in the genetic data. In any case, males have to make the first move, suggesting that the pattern of EPP seen in our population is probably driven to a large extent by a male strategy of balancing a trade-off between protecting paternity by guarding his mate at home and gaining paternity by mating with females on nearby territories.

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