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Extrapair paternity in the swamp sparrow, *Melospiza georgiana*: male access or female preference?

**Brian J. Olsen · Russell Greenberg ·
Robert C. Fleischer · Jeffrey R. Walters**

Abstract Over the past two decades, the combination of molecular and field methods has revealed considerable variation in the level of extrapair fertilizations among socially monogamous birds. Models predicting extrapair young range in scale from a single population to multiple Orders, and there is no single, unifying theory for these reproductive tactics. We investigated proximate explanations of extrapair fertilizations in two subspecies of the swamp sparrow, *Melospiza georgiana georgiana* and *Melospiza georgiana nigrescens*, across a range of social and environmental conditions. The presence of extrapair young was best predicted by the size of two male plumage badges (one correlated with parental care and one with territorial aggression) relative to the badge size of their immediate neighbors, the interaction of these two measures, mean territory size, and the maximum size of the aggression badge among neighbors. The size of the male's parental care badge (relative to neighbors) was negatively correlated with the probability of lost paternity. The relative size of the aggression badge was positively correlated with the presence of extrapair young when the parental care badge was small and negatively correlated when the badge was large. Controlling for these crown measures, males with larger territories were less likely to suffer losses in paternity. There was no effect of breeding density, breeding synchrony, their interaction, subspecies, or weather during the fertile period on the presence of extrapair young. These results suggest that female preference for males that provide more parental care (or preference for genes that convey this trait) plays a dominant role in extrapair interactions among swamp sparrows. Models based on female assessments of relative mate quality offer a promising explanation of patterns in extrapair fertilizations among bird species.

Keywords Relative male quality · Good genes · Sexy son · Breeding synchrony · Breeding density · Sexual dimorphism · Sexual dichromatism

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B. J. Olsen · R. Greenberg
Smithsonian Migratory Bird Center, National Zoological Park,
Washington, DC 20008, USA

B. J. Olsen · J. R. Walters
Department of Biological Sciences,
Virginia Polytechnic Institute and State University,
Blacksburg, VA 24061, USA

R. C. Fleischer
Genetics Program,
National Museum of Natural History & National Zoological Park,
Smithsonian Institution,
Washington, DC 20008, USA

B. J. Olsen (✉)
School of Biology & Ecology, University of Maine,
Orono, ME 04469, USA
e-mail: brian.olsen@umit.maine.edu

Introduction

Despite two decades of research exploring the discrepancies between genetic and social mating systems and a number of synthesizing reviews, there is no unifying explanation of patterns in extrapair parentage among avian mating systems (Griffith et al. 2002; Westneat and Stewart 2003; Neudorf 2004). Although most of the interspecific variation in extrapair fertilization (EPF) is explained by phylogeny and fundamental life history traits at the level of the Family or higher (Møller and Birkhead 1993a; Fleischer 1996; Bennett and Owens 2002; Griffith et al. 2002), the proximate mechanisms that lead to this pattern must ultimately operate

among an individual, its social mate, and an extrapair mate (Westneat and Stewart 2003). While no consensus has been reached about their relative importance, a number of factors have been hypothesized to explain variation in EPF frequency within and between populations, including breeding synchrony (Emlen and Oring 1977; Stutchbury and Morton 1995), mate quality (Møller 1988; Petrie and Lipsitch 1994), territorial density (Møller and Birkhead 1993b), and appropriate weather (moderate temperature and lack of precipitation) for extra-territorial forays (Bouwman and Komdeur 2006). In general, these hypothesized factors include features of the social or biophysical environment that affect either the ability of females to assess males during their fertile period, the ability of males to prevent extrapair copulations (EPCs) with their social mate, or the ability of males and females to pursue EPCs (Westneat and Stewart 2003). It remains unclear whether males or females control EPCs and which social and environmental cues reliably predict EPFs.

Phylogenetically controlled, inter-population comparisons are necessary to develop a generalizable proximate model of extrapair paternity. We tested a suite of hypothesized proximate mechanisms for EPF in two subspecies of the swamp sparrow: the tidal marsh endemic, *Melospiza georgiana nigrescens*, and the inland, freshwater-breeding *Melospiza georgiana georgiana*. Swamp sparrows are socially monogamous and both males and females feed young, although only females brood nestlings and incubate eggs (Mowbray 1997). Mate-guarding in the species, although present, is loose (males guard at distances of several meters from the female or greater), occurs only sporadically, and has not been observed in all individuals or consistently within a single individual among multiple

nesting attempts (pers. obs.). Extra-territorial forays by single birds of either sex are not uncommon (pers. obs.). Within and between the environments of these two subspecies, there exist wide ranges of abiotic conditions (e.g., tides, salinity, nutrients, and climate), which result in large variation in breeding densities and synchrony in the sparrows. Although in general inland territories are denser and breeding is more synchronous, the range of values from both subspecies broadly overlap one another. This variation in a suite of potentially influential variables (Table 1) offers a unique opportunity to distinguish which among them influence the frequency of EPF.

Unusually appropriate plumage characteristics in this species allow us to infer whether the occurrence of EPC is controlled by the male or the female. The breeding season crowns of these sparrows are largely sexually dichromatic (Greenberg 1988). Most breeding males possess rusty caps and black forehead patches that are acquired before the breeding season, lost soon thereafter, and vary in size in a manner unrelated to age (Mowbray 1997; Olsen 2007). Such seasonally acquired, sexually dimorphic plumage characteristics are usually signals that reflect male quality relative to either male–male interactions or female choice (Mulder and Magrath 1994; Örnborg et al. 2002; McGraw 2003). In our populations, male forehead size and blackness is positively correlated with territory quality and the intensity of territorial aggression, and cap size and rustiness is positively correlated with the proportion of nestling provisioning supplied by the male (Olsen 2007). Females might therefore prefer rusty-capped males (given similar territory quality) because they are better providers, and they certainly risk the largest retaliation in terms of lost parental care from such males if they pursue EPCs. The most

Table 1 Ranges and means of the candidate predictor variables for extrapair fertilization in swamp sparrows

Candidate predictor	Minimum	Maximum	Mean	Standard error
Territory area (ha)	0.01	0.95	0.19	0.03
Territory density (neighboring males/0.7 ha[a])	2	29	10.3	0.7
2-day breeding synchrony (% females)	0	87.5	38.0	3.3
5-day breeding synchrony (% females)	0	100	50.4	3.6
Mean high daily temperatures during the 2-day fertile period (°C)	15.8	35.1	24.8	0.6
Mean high daily temperatures during the 5-day fertile period (°C)	17.0	35.1	24.8	0.5
Mean low daily temperatures during the 2-day fertile period (°C)	4.9	22.0	13.1	0.6
Mean low daily temperatures during the 5-day fertile period (°C)	5.6	21.8	13.1	0.6
Mean precipitation during the 2-day fertile period	0	1.0	0.5	0.05
Mean precipitation during the 5-day fertile period	0	1.0	0.5	0.03
Length of focal male rusty cap (mm)	7.6	18.7	13.8	0.3
Length of focal male black forehead (mm)	4.0	10.5	6.2	0.2
Length of the longest male cap patch among neighbors (mm)	10.5	18.7	16.2	0.2
Length of the shortest male cap patch among neighbors (mm)	6.6	15.5	10.4	0.3
Length of the longest male forehead patch among neighbors (mm)	5.3	10.5	7.5	0.2
Length of the shortest male forehead patch among neighbors (mm)	2.8	9.1	5.2	0.1

[a] Area that is inscribed by a circle with twice the diameter of a mean territory (mean territory diameter=47.65 m).

aggressive males with the largest black forehead patches, on the other hand, should better prevent territorial intrusions of neighboring males and better prevent female forays into neighboring territories. We do not know which type of male females prefer, so if males with large forehead patches (relative to either the population as a whole or to neighboring males) suffer the lowest losses in paternity, it could be because males control EPC or because females control EPC and prefer aggressive males. But if rusty-capped males (especially those with larger caps relative to neighbors) should suffer the lowest losses in paternity, it would imply that females control EPC.

The two crown characteristics are inversely correlated in the coastal population and uncorrelated in the inland population, resulting in a wide array of crown types with which to test these predictions (Olsen 2007). Furthermore, male crowns from the coastal subspecies show a significantly greater area of black than those among inland males (Greenberg and Droege 1990), likely as a result of stronger intrasexual selection for territorial aggression within the tidal salt marsh (Olsen 2007). Concomitantly, coastal males defend territories more aggressively on average (Olsen 2007). Thus, if males control EPC, we would expect a lower prevalence of EPF in the coastal subspecies due to the difference in time spent defending territories. If females control EPC, on the other hand, there is no reason to expect such a subspecies difference, as male quality should vary relatively to that of neighbors.

With these considerations in mind, we tested for relationships between the presence of EPFs and subspecies, focal male badge size, neighboring males' badge sizes, territory size, local breeding density, breeding synchrony, and ambient air temperature and precipitation during the female's fertile period.

Materials and methods

Study sites and weather variables

We conducted all investigations on four plots, two for each subspecies, from May until August. Populations on coastal plots were studied from 2002 to 2005 on *Spartina* marsh within Delaware state game lands along the Smyrna River (75.5° W, 39.3° N). Inland plots were observed from 2004 to 2005 in minerotrophic fens on the Allegheny Plateau in Western Maryland (79.3° W, 39.6° N).

We obtained daily high and low temperatures and precipitation accumulation from the Maryland/Delaware/ D.C. chapter of the Atlantic Coast Observer Network (ACON 2006). Temperatures and precipitation values for coastal sites were assigned from those recorded at the Bear, DE station (75.6° W, 39.6° N), and inland values were

assigned from the Frostburg, MD station (79.9° W, 39.6° N). We calculated the average temperature (for both daily high temperatures and daily low temperatures) and precipitation (cumulative) during each female's fertile period (for two intervals: 2 and 5 days prior to laying until clutch completion).

Capturing and processing individuals

We attempted to capture all adults via mist-net each season. Adults and nestlings were marked with unique color-band combinations to assist in individual recognition in the field. Blood was drawn from the brachial vein on adults during capture, and nestlings were bled and banded between 5 and 8 days of age. For each captured adult male, we also quantified the size of both the black forehead patch that predicts territorial aggression and the rusty cap patch that predicts parental care (Olsen 2007). Forehead size was measured as the length of the black patch from the proximal end of the culmen to the anterior line of the rusty cap feathers. Cap patch size was measured likewise along the center of the head as the length from the most anterior to the most posterior rusty feather. For both of these measurements, we used a digital caliper accurate to 0.1 mm.

Breeding density and synchrony

Territories were delineated using minimum convex polygons defined by male song-posts throughout the season (May–July). These song-posts are clearly visible above the salt marsh vegetation from a distance greater than a territory width. Males sing from multiple locations every hour and generally use the same song-posts both throughout each day and over the season, with small adjustments as the vegetation changes. Late season song-posts (August) were omitted due to dramatic changes in territory boundaries after some males ceased territorial behavior. We determined the area and centroid of all minimum convex polygons delineating territories using ArcMap 8.3 (ESRI 2002).

Breeding density was defined for each territory polygon by counting the number of territories that fell partially or completely within a distance of two mean territory diameters from the territory centroid (95.3 m=twice the diameter of a circular territory with the mean territory area found across all sites). Studies to date on a variety of passerine songbirds have implicated neighboring or nearby males as the primary extrapair mate rather than floater/non-territorial males or distant birds (e.g., Stutchbury et al. 1994; Langefors et al. 1998; Dickinson 2001; Tobias and Seddon 2002; Mennill et al. 2004; but see Woolfenden et al. 2005). To describe the relative patch size of candidate extrapair males, we identified the neighboring males (those that fell within two territory diameters) with the longest and

shortest cap patches and the longest and shortest forehead patches. Using these values, we also determined the relative sizes of focal males for both the cap and forehead patches: (focal male's patch−the smallest neighboring cap)÷(the size of the range in neighboring values).

Breeding synchrony was defined for each nesting attempt likewise within this two territory diameter area. We located nests throughout the breeding seasons using the female nest departure call (McDonald and Greenberg 1991), which is a highly efficient means of finding nests in the building, laying, and incubation periods. For each territory, we then determined the percentage of females in the neighboring area whose fertile period (defined at two intervals) overlapped that of the territory's female. Viable, stored sperm has been found in the reproductive tract of female passerines from 2 (Birkhead et al. 1997) to 5 days (Briskie 1994) before the initiation of laying. We therefore calculated the fertile period of all females twice, from either 2 or 5 days before the onset of laying until clutch completion. The fertile period of a neighboring female needed to overlap that of the focal female by only a day to be included in the synchrony count. We used the percentage of neighbors instead of an absolute count of synchronous females to minimize confounding breeding synchrony with territorial density.

Genotyping and parental exclusion

All captured adults and offspring were genotyped at six polymorphic DNA microsatellite loci (Table 2). Five of these were developed for *M. melodia* (Mme2, Mme3, Mme7, Mme8, Mme12: Jeffery et al. 2001) and the last was developed for *M. georgiana* (Mg2we: RC Fleischer, unpublished data). We extracted DNA using a Qiagen Dneasy Tissue Kit following the manufacturer's instruc-

tions for animal tissues. The annealing temperatures and 10 μL PCR mixtures differed by loci (Olsen 2007). We conducted electrophoresis on an ABI 3100 capillary electrophoresis system, sized genotypes with GeneScan 3.7, and scored alleles using Genotyper 2.5 (Applied Biosystems, Inc.). Two base pairs were added to each allele score to account for instrumental differences from published values. Four base pairs were added to Mme8 alleles. Two loci were Z-linked (Mme3 and Mme7), and females were not included in the calculation of allele frequencies for these loci. Mme8 violated the Hardy–Weinberg equilibrium and was subsequently removed from further analysis.

Parental assignment was initially completed using Cervus 2.0 (Marshall et al. 1998). Allele frequencies, the significance of deviations from the Hardy–Weinberg equilibrium, and assignment values simulations were calculated for each plot separately using males only (due to Z-linkage). To capture the most allelic diversity, we combined data from both adult males (sexed by cloacal protuberance) and juvenile males (sexed by heterozygosity at either Mme7 or Mme3) to determine allele frequencies. Coastal samples were 53% and 55% juvenile, and inland samples were 78% and 74% juvenile for Mme3 and Mme7, respectively. Due to the inability to differentiate between juvenile male homozygotes and juvenile females, when testing for deviation from the Hardy–Weinberg equilibrium, we set alpha a priori to 0.15 for homozygote deficiency and 0.0001 for homozygote excess. Single sex parentage (paternity) was assigned at a 95% (strict) confidence level for male offspring with a known, genotyped mother and at an 80% (relaxed) confidence level for those without a genotyped mother. Adult males typed at three or more loci were included as candidates. We then calculated the likelihood of each adult male siring each male offspring

Table 2 Results of genetic analysis for five polymorphic DNA microsatellite loci analyzed in Cervus

Locus	Alleles detected	Males sampled	Heterozygotes	Homozygotes	Exclusion probability (1 parent)	Exclusion probability (2 parents)	Null allele frequency estimate
Among coastal *Melospiza georgiana nigrescens* males							
Mme7[a]	12	210	163	47	0.57	0.72	0.05[b]
Mme3[a]	21	218	150	68	0.63	0.78	0.13[b]
Mg2we	22	218	189	29	0.67	0.81	0.02
Mme2	4	223	101	122	0.11	0.19	0.01
Mme12	5	222	134	88	0.17	0.31	−0.04
Among inland *M. georgiana georgiana* males							
Mme3[a]	11	160	108	52	0.49	0.66	0.10[b]
Mme7[a]	24	182	147	35	0.73	0.84	0.07[b]
Mg2we	23	184	161	23	0.75	0.86	0.03
Mme2	2	184	104	80	0.13	0.19	−0.06
Mme12	4	184	87	97	0.11	0.23	−0.02

[a] Z-linked loci
[b] Alpha set to 0.15 for homozygote deficiency and 0.00 for homozygote excess for Z-linked loci.

using the natural log of the products of the likelihood ratios across all loci. Either the most likely or the second most likely sires were assigned to broods, minimizing the number of males required to explain allelic diversity. This resulted in successful paternal assignment in 81% and 84% of offspring in the two coastal plots and 90% and 86% in the two inland plots using either the strict (genotyped mother) or relaxed (no genotyped mother) delta criterion; 37.8% of all offspring possessed 'Log of the Odds ratio' (LOD) scores over 2.0 (66/118 coastal offspring and 51/191 inland offspring). Mean observed error rates in allele detection probability across all loci were 0.09, 0.17, 0.15, and 0.19 in the two coastal and two inland plots, respectively. The minimum number of required sires for each brood agreed with the results calculated by hand based on Mendelian inheritance. We then recalculated the minimum extrapair sires necessary to explain each full brood including female offspring based on heteromorphic chromosomal (for Z-linked loci) and Mendelian (for other loci) inheritance. We assumed that all broods were produced by a single female (no brood parasitism). Exclusion analysis was conducted on 350 offspring in 113 broods and 97 territories. We made no attempt to assign specific sires to offspring at this stage, as we were not able to sample all candidate males in the populations (89.9% of males were sampled over all plots and years). We calculated the minimum extrapair young possible for 82 broods with two scored candidate parents, 22 broods with four or greater offspring that lacked both scored candidate parents, and nine broods with three or more offspring that lacked a scored territorial male but possessed a scored female. All broods with less than three offspring and no scored parents were excluded from analysis.

Statistical analyses

All statistical tests of the presence or absence of extrapair young were run using a binomial distribution in the Genmod procedure of SAS 9.1.3 (SAS Institute 2005). We tested for predictors of extrapair young within each brood using a repeated-measures logistic regression for nesting attempts within territories. Candidate predictors included territory area, territorial density, breeding synchrony (at either the 2- or 5-day levels), mean daily high temperatures during the fertile period (at either the 2- or 5-day levels), mean daily low temperatures during the fertile period (at either the 2- or 5-day levels), mean precipitation during the fertile period (at either the 2- or 5-day levels), rusty cap length of the focal male, black forehead length of the focal male, the interaction of cap and forehead length, the relative forehead and cap patch sizes of the focal male and their interaction, and both maximum and minimum neighbor cap size, forehead size, and their

interaction. We tested for one additional interaction effect based on previous findings: breeding synchrony by territorial density (Thusius et al. 2001). Candidate blocking effects included year within site, subspecies, and Julian date. Given the sample size, we selected top performing models from those with less than seven predictors to avoid overfitting the data. Fertile period length was considered to be either 2 or 5 days, so we tested no model with variables calculated over both intervals. Model selection was based on AICc, and models with ΔAICc scores <2.0 were considered equivalent. We tested for positive correlations between male body size (measured using tarsus length) and crown measurements with two, one-tailed regressions. All means reported are ± standard error (SE).

Results

For 241 coastal and 184 inland males, we found an average of 12.8 alleles for our five loci (Table 2), which gave us high power of exclusion for broods with one (coastal=0.96, inland=0.97) or two (coastal=0.993, inland=0.995) genotyped parents. Extrapair males sired 20.9% of offspring (31/149 coastal and 42/201 inland offspring), and extrapair young occurred in 41.6% of broods (21/54 coastal and 26/59 inland). These levels are similar to the average of other Emberizid sparrows reported in the literature (24.1% of offspring, 41.0% of broods: Griffith et al. 2002). The complete dataset (where all data had been adequately gathered on all adult males and territories) included 235 offspring from 63 broods in 52 territories (with a maximum of two attempts per territory). There was no difference by subspecies alone ($n=52$, $\chi^2_{1,\,61}=0.02$, $P=0.89$).

The highest ranked model explaining the presence of extrapair young included male cap size relative to neighbor caps ($n=52$, $\chi^2_{1,\,57}=3.9$, $P=0.05$), relative male forehead size ($\chi^2_{1,\,57}=9.5$, $P=0.002$), their interaction ($\chi^2_{1,\,57}=6.6$, $P=0.01$), territory area ($\chi^2_{1,\,57}=6.9$, $P=0.009$), and the largest neighboring forehead size ($\chi^2_{1,\,57}=4.3$, $P=0.04$). Nine additional models were equivalent to this model (ΔAICc<2.0), each of which included the five variables from the highest ranked model plus an additional variable that was never significant. These next nine models included the effects of the smallest neighbor cap patch size (ΔAICc=0.3, $\chi^2_{1,\,56}=1.8$, $P=0.18$), the interaction of the smallest neighbor cap patch with the largest neighbor forehead patch size (ΔAICc=0.8, $\chi^2_{1,\,56}=1.5$, $P=0.22$), territory density (ΔAICc=0.8, $\chi^2_{1,\,56}=0.6$, $P=0.44$), the interaction of territory density and breeding synchrony at the 5-day fertility length (ΔAICc=0.9, $\chi^2_{1,\,56}=1.5$, $P=0.23$), mean daily maximum temperatures during the fertile period at the 5-day level (ΔAICc=1.0, $\chi^2_{1,\,56}=0.9$, $P=0.34$), subspecies (ΔAICc=1.0, $\chi^2_{1,\,56}=1.2$, $P=0.27$), focal male cap size

Fig. 1 The relationship between forehead patch size and the percentage of nests with extrapair young for focal swamp sparrow males of varying cap patch sizes. **a** Males with the smallest cap sizes among their neighborhoods ($N=1, 3, 5, 3$; points from left to right); **b** males with cap sizes in the lower 50% of their neighborhoods ($N=2, 1, 5, 2$); **c** males with cap sizes in the upper 50% of their neighborhoods ($N=8, 9, 10, 3$); **d** males with the largest cap sizes in their neighborhoods ($N=3, 6, 1, 2$)
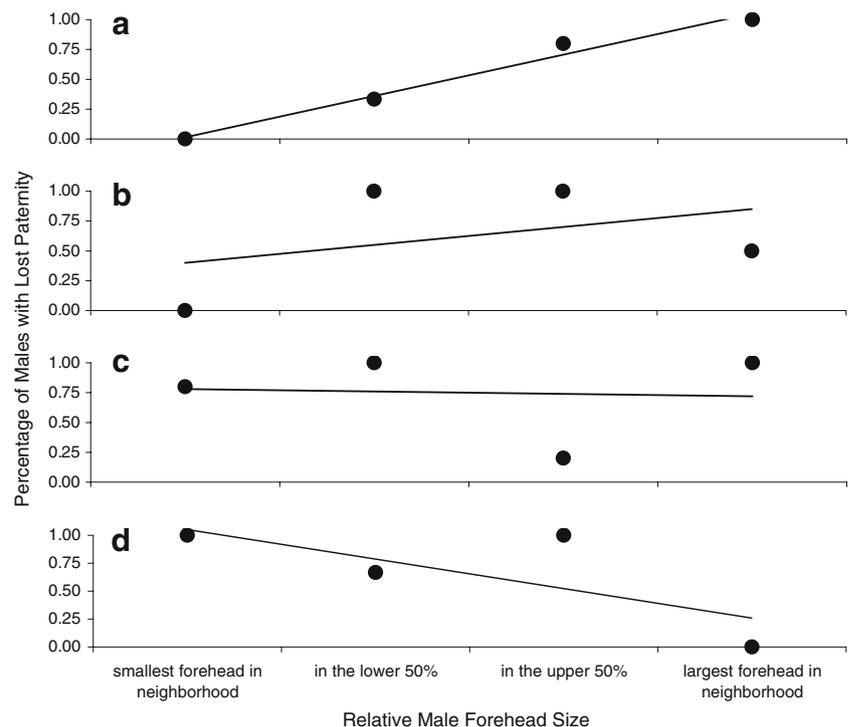
($\Delta AICc=1.8$, $\chi^2_{1,\ 56}=0.6$, $P=0.46$), or mean daily minimum temperatures during the fertile period at the 2-day ($\Delta AICc=1.8$, $\chi^2_{1,\ 56}=0.4$, $P=0.51$) and 5-day levels ($\Delta AICc=0.7$, $\chi^2_{1,\ 56}=1.6$, $P=0.21$).

The effect of relative cap patch size was positive, such that larger patches relative to neighboring males resulted in lower probabilities of lost paternity. However, there was an interaction between the cap and forehead patch sizes, such that increasing forehead patch size decreased the probability of lost paternity at high sizes of the cap patch but increased the probability at low sizes of the cap patch (Fig. 1). Furthermore, there was a tradeoff between the size of the cap and forehead patches among cuckolded males, while the relative size of the cap and forehead patches were not correlated in males without extrapair young (Fig. 2). Male body size was not positively correlated with either the cap patch size ($n=45$, $r^2=0.07$, $t_{1,\ 43}=-1.8$, $P=0.96$) or the forehead patch size ($n=45$, $r^2<0.01$, $t_{1,\ 43}=0.02$, $P=0.49$).

The absolute size of the rusty cap patch was smaller on average for cuckolded males (13.3 ± 0.5 mm) than for males without extrapair young (14.2 ± 0.3 mm). For cuckolded males, the rusty cap patch was closer in size to the smallest cap patch of neighbors ($22.9\pm22.4\%$ of the difference between the largest and smallest cap patches), while the cap patch size was closer to the largest cap patch ($66.0\pm7.7\%$) for males that did not tend extrapair young (Fig. 3). The absolute size of the black forehead patch, on the other hand, was larger in males that lost paternity (6.5 ± 0.3 mm) than in males that sired all the young in their nests (6.0 ± 0.2 mm).

This difference was also present in the measurement of relative size. For cuckolded males the forehead patch was nearer in size to the largest neighboring patch ($89.9\pm25.9\%$ of the difference between the largest and smallest forehead patches), even though the average largest forehead patch of
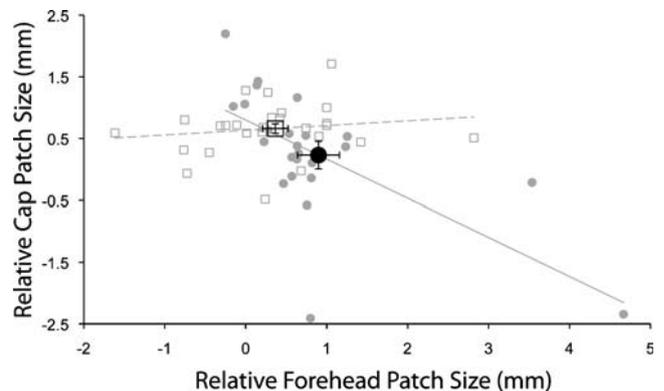

Fig. 2 The relative size of the rusty cap patch and the black forehead patch on the crown of swamp sparrow males with nests that included (*filled circles* and *solid regression line*; $N=27$) or did not include (*open squares* and *dashed regression line*; $N=36$) extrapair young. Point values were calculated by: (size of male plumage patch−size of smallest patch among neighbors)÷range of values among neighbors. Negative values indicate males with smaller plumage patch than all recorded neighbors, and values greater than one indicate males with the largest patch among neighbors. Means of each group (±SE) are indicated with the *larger symbols of the same shape*. Results from Olsen (2007) indicate that rustiness in the cap is positively correlated with parental care and black in the forehead patch is positively correlated with territorial aggression in male swamp sparrows
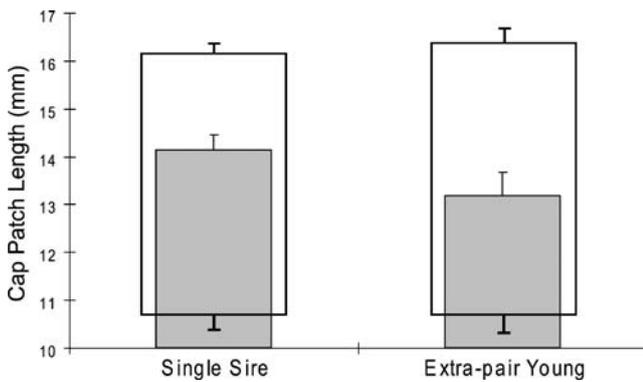
Fig. 3 A comparison of the rusty cap patch size of focal male swamp sparrows versus neighboring males within a distance of two mean territory diameters. The *gray bars* indicate the mean cap patch length (+SE) for the nests of focal males that did ($N=27$) or did not ($N=36$) include extrapair young. The *solid, open rectangles* indicate the cap patch lengths of neighboring males in each of these two scenarios. The *top* and *bottom of the solid-lined rectangles* indicate the mean length (±SE) of the largest and smallest neighboring rusty cap patches, respectively

neighboring males in these neighborhoods (7.7±0.2 mm) was significantly larger than it was in neighborhoods where the focal male sired all young in its nest (7.4±0.2 mm). Males that did not lose paternity had forehead patches nearer in size to their smallest neighboring forehead patch (36.6±15.7%), despite the lower maximum forehead sizes in these neighborhoods (Fig. 4). Of the males with the smallest forehead patch in their neighborhood, 28.6% (4/14 males) lost paternity (with an average relative cap patch size of 74.7±13.7% of the range in neighboring cap sizes), whereas 66.7% of males (8/12) with the smallest cap patch in their community suffered such losses (with average relative forehead size of 139.2±52.4%). Finally, males tending nests with extrapair young also defended smaller territories (0.12± 0.03 ha) than males that did not (0.24±0.04 ha).

AICc model selection made it clear that models defining male crown characteristics relative to their neighbors performed better than those that did not. Despite high model significance, models including only absolute measures of the focal male and/or neighboring male crown characteristics did not explain losses in paternity as well as models with male crown characteristics defined relative to the social environment of focal males. For example, all of the following models performed less well than the highest ranked model, despite high model significance: the model that included the two absolute crown patch sizes of focal males, their interaction, and territory size ($\Delta AICc=11.5$, for all independent variables $P<0.03$), the model with absolute neighbor forehead (maximum) and cap (minimum) patch sizes, their interaction, and territory area ($\Delta AICc=26.1$, for all independent variables $P<0.10$), and the model with absolute values of focal male crown patches, their

interaction, the absolute values of neighbor crown values, their interaction, and territory area ($\Delta AICc=5.4$, for all independent variables $P<0.06$).

The highest ranked model was not improved by the addition of any additional single candidate variable. Excluding the nine models already described that were equivalent, this includes no significant additional effect of breeding synchrony at the 2-day ($\Delta AICc=2.2$, $\chi^2_{1,\ 56}=$ 0.03, $P=0.86$) or 5-day levels ($\Delta AICc=2.1$, $\chi^2_{1,\ 56}=0.1$, $P=0.71$), the interaction of breeding density and synchrony at the 2-day level ($\Delta AICc=2.1$, $\chi^2_{1,\ 56}=0.3$, $P=0.59$), mean daily maximum temperatures during the fertile period at the 2-day level ($\Delta AICc=2.0$, $\chi^2_{1,\ 56}=0.2$, $P=0.68$), or mean precipitation accumulation during the fertile period at the 2-day ($\Delta AICc=2.3$, $\chi^2_{1,\ 56}<0.01$, $P=0.96$) or 5-day level ($\Delta AICc=2.2$, $\chi^2_{1,\ 56}=0.03$, $P=0.85$). Also, no additional blocking effects were significant or increased model rank (including year within site: $\Delta AICc=8.7$, $\chi^2_{5,\ 52}=0.5$, $P=0.65$; and Julian date: $\Delta AICc=2.2$, $\chi^2_{1,\ 56}=0.1$, $P=0.77$), and hence all were dropped.

Discussion

Our results show a clear relationship between putative measures of male quality and the presence of extrapair young. Relative to their neighbors, males with smaller rusty cap patches (Fig. 3) and larger black forehead patches (Fig. 4) were more likely to suffer losses in paternity, although males with both a large forehead and a large cap patch were not (Figs. 1 and 2). Thus, a larger forehead patch size was only a liability when the cap size was small.
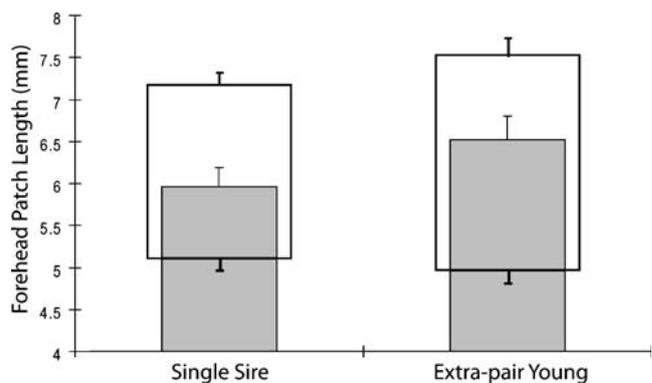

Fig. 4 A comparison of the black forehead patch size of focal male swamp sparrows versus neighboring males within a distance of two mean territory diameters. The *gray bars* indicate the mean forehead patch length (+SE) for the nests of focal males that did ($N=27$) or did not ($N=36$) include extrapair young. The *solid, open rectangles* indicate the forehead patch lengths of neighboring males in each of these two scenarios. The *top* and *bottom of the solid-lined rectangles* indicate the mean length (±SE) of the largest and smallest neighboring black forehead patches, respectively

Males with the smallest forehead patches in their neighborhoods suffered losses in paternity relatively infrequently compared to males with the smallest cap patch in their neighborhood. It thus seems clear that there is a larger cost in terms of paternity for males with a small cap patch than for males with a small forehead patch. Males that suffered losses in paternity also had smaller territory sizes in neighborhoods with larger maximum forehead sizes.

These results match our predictions for an extrapair mating system controlled by female preference. Males with large rusty signals of parental care in areas with less rusty neighbors were unlikely to suffer losses in paternity, while darker crowned, more aggressive males in areas with less aggressive, rustier males were likely to suffer such losses unless they also possessed a relatively large cap. If males controlled EPCs and the resulting EPFs (the two are not necessarily tightly linked: Fossoy et al. 2006), we would expect that small, not large, forehead patches would predict extrapair mating by the female.

The tradeoff between the aggressive forehead signal (that is likely necessary for territorial establishment) and the rusty cap signal (that is necessary for female fidelity) deserves study. It should be advantageous in terms of habitat quality for females to mate with aggressive males, so long as such behavior does not impede the male's parental provisioning ability. That males with both a large forehead patch and a large cap patch were unlikely to suffer losses in paternity (Figs. 1 and 2) supports this claim and shows at the very least that having an aggressive forehead signal is not as dangerous from a paternity standpoint as lacking a rusty parental signal. It should be pointed out that males in this study all successfully defended a territory capable of producing young that survived to at least 5 days post-hatch. It is possible that males without some minimum forehead size (i.e., degree of territorial aggression) would not be able to do this and thus were not measured.

These results support the growing body of evidence suggesting a strong role for female preference in the explanation of extrapair young (Møller and Birkhead 1994; Yezerinac and Weatherhead 1997; Owens and Hartley 1998; Garamszegi and Møller 2004; Coppack et al. 2006) and for female control of EPFs (Birkhead and Møller 1993; Stutchbury et al. 1994; Gray 1996; Double and Cockburn 2000; Forstmeier 2004). Furthermore, our results support the conclusion that females follow a "trade-up" strategy (Fishman and Stone 2006), assessing the relative quality of their social mates to that of their neighbors (Langefors et al. 1998; Sheldon and Ellegren 1999; Václav et al. 2003; Olendorf et al. 2004), possibly for the benefits of superior genes (Møller 1988; Hamilton 1990; Birkhead and Møller 1992). Females may assert control of this system either through extra-territorial forays or through the acceptance of trespassing extra-territorial

males (Westneat and Stewart 2003). Anecdotally, we have witnessed females soliciting neighboring males across territory boundaries and accepting the resulting copulation from the then-trespassing neighbor.

We only found a positive correlation between the presence of EPFs and plumage signals of male territorial aggression (that represent the potential ability of males to attempt or prevent EPCs) at high cap sizes. Furthermore, males with the smallest signal of territorial aggression in their neighborhood were cuckolded less frequently than were males with the smallest signal of parental care in their neighborhoods. Thus, it appears that relative male parental quality is a more important determinant of EPFs than is territorial aggression in swamp sparrows. This conclusion is supported across a wide variety of environmental variables, two vastly different habitats, and two mating systems with different selection pressures on male territorial aggression (Olsen 2007). This lends credence to the proposition that relative male quality, determined by female choice, is the best proximate explanation for extrapair fertilizations. Alternatively, EPCs and EPFs may be disconnected (Fossoy et al. 2006) such that males control EPCs, but females exhibit cryptic mate choice with ultimate physiological control over EPFs (Ball and Parker 2003; Fossoy et al. 2008).

We found a negative effect of territory size on the presence of EPFs (controlling for relative crown patch sizes), while the density of neighboring males had no additional effect. Other studies comparing individuals within populations have shown a positive effect of territorial density on EPFs, although territory size of focal individuals was not taken into account (Griffith et al. 2002). Certainly within a given area, territory size and density are related but are not equivalent, and they may represent different effects on EPFs. In our study, the lack of a positive effect of breeding density on EPFs, while controlling for focal territory size, suggests that increased opportunities for male–male comparisons by the female or increased opportunities for male trespassing did not affect the relative level of EPFs. Rather, territory size may operate as an indicator of relative male quality, where on a small scale among neighboring males with similar crown characteristics, those males with larger territories are of higher quality. Furthermore, because our sample (like all studies of EPF) only included males that had successfully paired with females and produced offspring, we are only screening males of a minimum quality (or similarly, on a territory of a minimum quality). The strength of density as a positive indicator of EPFs in other studies (Griffith et al. 2002) may likewise be due to larger-scale correlations between territory density and neighbor, individual, or territory quality (Fretwell and Lucas 1970; Fretwell 1972). If this is the case, controlling directly for male quality in these systems may either reverse

or eliminate the reported relationships between density and EPFs. Furthermore, the necessity of controlling for individual quality *relative* to neighboring males (who may or may not have mated) may explain the lack of a density effect in other studies (Griffith et al. 2002; Westneat and Stewart 2003). Additionally, although year was not a significant effect in our model, inter-annual differences in neighborhood membership may explain the significant inter-annual variance in EPFs seen in other species (Lubjuhn et al. 1999; Dietrich et al. 2004).

Although most of the variation in extrapair fertilizations among species can be explained by phylogeny, these differences must have arisen by the relative tradeoffs of more proximate mechanisms meted out in interactions among individuals. The results of this study indicate that female preference in the swamp sparrow plays a role in extrapair fertilizations at the population scale. Environmental factors are likely to shift the relative costs and advantages associated with the strength of these preferences, ultimately opening the way for social mating system divergence, selection for specific mate phenotypes, and the larger-scale differences seen among Orders and Families.

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