

## LITTLE EFFECT OF EXTRAPAIR PATERNITY ON THE OPPORTUNITY FOR SEXUAL SELECTION IN SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

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**Abstract.**—Extrapair paternity (EPP) can dramatically increase the opportunity for sexual selection if relatively few males are able to monopolize the majority of fertilizations in a population. Although recent work with birds suggests that EPP can increase the standardized variance in male reproductive success ( $I_s$ ) as much as 13-fold, only a male's within-pair success is typically quantified with any accuracy. In most cases, nearly half of all extrapair young are of unknown parentage. A strong, negative correlation across studies between the proportion of extrapair young for which parentage is known and the apparent effect of EPP on  $I_s$  ( $r_s = -0.71$ ,  $P = 0.013$ ,  $N = 13$  studies) suggests that the incomplete sampling of extrapair sires has greatly exaggerated the influence of EPP. To achieve a more thorough accounting of EPP and its importance to variation in male fitness, we used a suite of four to six microsatellite loci to identify extrapair young and their sires in a polygynous population of Savannah sparrows (*Passerculus sandwichensis*). Pooling over the 2002 and 2003 breeding seasons, 79 of 116 females (68.1%) produced young outside of the pairbond and 194 of 411 offspring (47.2%) were extrapair. We identified sires for 96.4% of all young ( $N = 396$ ), including sires for 92.3% of the extrapair young ( $N = 179$ ), allowing us to partition  $I_s$  into within-pair and extrapair components. In both years, EPP-related fitness components generated more variation in male reproductive success than the number or quality of within-pair mates. Differences among males in the number of extrapair mates alone accounted for 56.6% of  $I_s$  in 2002 and for 23.6% of  $I_s$  in 2003. Nonetheless, in absolute terms, the occurrence of EPP on Kent Island increased the opportunity for sexual selection less than two-fold. Averaging over the two years,  $I_s$  was only 78% higher than  $I_{s,app}$ , the variance in male reproductive success that would have occurred had EPP been nonexistent and males sired all young on their territories. Likewise, across nine socially monogamous species, we found no correlation between the extent of EPP and its effect on the opportunity for sexual selection ( $I_s/I_{s,app}$ ) and only a marginally significant positive correlation between EPP and  $I_s$  itself. Taken together, our results suggest that the relationship between EPP and sexual selection in birds may be much less strong and much less straightforward than commonly thought.

**Key words.**—Extrapair paternity, individual optimization, mixed reproductive strategies, sexual selection, sperm competition.

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Sexual selection is usually attributed to variance in male reproductive success caused by competition for mates or, in socially monogamous species, to variance in male reproductive success caused by competition for a high-quality mate (Williams 1975; Arnold and Wade 1984; Endler 1986; Andersson 1994). It is increasingly clear, however, that a full accounting of sexual selection must also consider how females distribute fertilizations across multiple reproductive partners. Whenever females mate with more than one male, males with similar mating success can differ substantially in fertilization success owing to the sperm competition (and cryptic female choice) that multiple mating engenders (Eberhard 1996; Birkhead and Møller 1998; Ligon 1999; Jennions and Petrie 2000).

Multiple mating by females is now known to occur in numerous taxa (Birkhead and Møller 1998; Simmons 2001; Zeh and Zeh 2001; Stockley 2003), which has focused attention on its evolutionary causes and consequences (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Tregenza and Wedell 2000). This is particularly true in birds; only in the last decade has multiple mating by females (in the form of extrapair paternity, EPP) been recognized as an important component of male and female reproductive strategies (Birkhead and Møller 1998; Griffith et al. 2002; Westneat and Stewart 2003). Here, the evolutionary causes of multiple mating by females are particularly interesting because there

seems to be little direct benefit associated with EPP that might compensate for many potential costs (e.g., Dixon et al. 1994; Weatherhead et al. 1994; Valera et al. 2003; but see Gray 1997). Although elements of a female's social and genetic environment are emerging as the dominant explanations for the occurrence of extrapair fertilizations in birds (Griffith et al. 2002; Westneat and Stewart 2003), it is not always clear at what level these factors have the most explanatory value: among individuals within populations (Hasselquist et al. 1996; Chuang et al. 1999), among populations (Weatherhead and Yezerinac 1998; Griffith 2000) or among species (Petrie et al. 1998; Stutchbury 1998).

In comparison, the evolutionary consequences of EPP for males seem well established. By generating variation among males in fertilization success, sperm competition can increase the opportunity for sexual selection (Webster et al. 1995; Møller and Ninni 1998). For example, sexual selection will be strong if only a subset of males—those with a particular phenotype—ensure their own mate's fidelity while also achieving fertilizations outside the pairbond. EPP is potentially of greatest importance in socially monogamous systems, where variation in male success is otherwise limited to variation arising from female quality, timing of breeding, and male mating status (paired or unpaired; Yezerinac et al. 1995; Webster et al. 2001).

A growing body of work supports the link between sperm

TABLE 1. Effect of extrapair paternity on the opportunity for sexual selection in passerine birds. Species arranged in order of percent extrapair young (%EPY) assigned.

Species	$I_{s,app}^1$	$I_s^1$	$I_s/I_{s,app}$	Mating system	%EPY	%EPY assigned to local males	Ref
<i>Passerculus sandwichensis</i>	0.27	0.48	1.8	Poly	47%	92.3%	this study (both years combined)
<i>Agelaius phoeniceus</i> (ON)	0.67	0.73	1.1	Poly	26%	78.5%	Weatherhead and Boag (1997)
<i>Parus caeruleus</i>	0.16	0.27	1.7	Mono	11%	72.3%	Kempnaers et al. (1992)
<i>Dendroica caerulescens</i>	0.49	0.71	1.4	Mono	21%	62.3%	Webster et al. (2001)
<i>Agelaius phoeniceus</i> (NY)	1.02	1.21	1.2	Poly	24%	60.0%	Westneat (1993)
<i>Junco hyemalis</i>	0.55	0.72	1.3	Mono	28%	54.7%	Ketterson et al. (1997)
<i>Wilsonia citrina</i>	0.18	0.46	2.6	Mono	27%	54.7%	Stutchbury et al. (1997)
<i>Ficedula albicollis</i>	0.03	0.14	4.7	Mono	16%	53.8%	Sheldon and Ellegren (1999)
<i>Progne subis</i>	0.05	0.33	6.6	Mono	19%	53.8%	Wagner et al. (1996) and Møller (1998)
<i>Tachycineta bicolor</i>	0.09	0.79	8.8	Poly <sup>2</sup>	52%	47.2%	Kempnaers et al. (2001)
<i>Poecile atricapillus</i>	0.04	0.10	2.5	Mono	9%	46.9%	Otter et al. (1998)
<i>Icterus galbula</i>	0.07	0.17	2.4	Mono	32%	44.6%	Richardson and Burke (2001)
<i>Dendroica petechia</i>	0.04	0.53	13.3	Mono	37%	35.4%	Yezerinac and Burke (1995)

<sup>1</sup> Standardized variance in realized fertilization success ( $I_s$ ) and apparent fertilization success ( $I_{s,app}$ );  $I_{s,app}$  assumes extrapair paternity is nonexistent and males sire all offspring on their territories.

<sup>2</sup> A total of 21.1% of males are socially polygynous.

competition and the opportunity for sexual selection in birds. The standardized variance in male reproductive success ( $I_s$ ), an upper-bound estimate of the strength of sexual selection (Arnold and Wade 1984), is increased by EPP in all species examined to date, sometimes dramatically so (Table 1; Møller 1998; Møller and Ninni 1998). These estimates must be considered preliminary, however, because in most studies the sampling of extrapair sires is largely incomplete. While it is relatively easy to assess a male's success at siring young on his own territory, it is often difficult to tally the number of young he produces outside the pairbond either because the geographic scale of reproductive interactions exceeds the boundaries of the study site or because of methodological limitations associated with the molecular techniques used to include or exclude potential sires (Webster and Westneat 1998; Ligon 1999).

This sampling bias is problematic because it can potentially inflate  $I_s$  in two ways, one statistical (Møller and Ninni 1998) and the other biological (Webster et al. 1995; Jones et al. 2001). First, when excluded young remain unallocated to extrapair sires, the mean reproductive success of males ( $\bar{T}$ ) is artificially decreased, leading to an increase in the standardized variance:

$$I_s = \frac{\text{var}(T)}{\bar{T}^2}. \quad (1)$$

Second, while variation among males in their ability to secure extrapair fertilizations can increase  $I_s$ , it can also decrease it if males trade extrapair success against within-pair success. It seems likely, then, that current estimates of the influence of EPP on  $I_s$  are upwardly biased. In fact, there exists a significant negative correlation across studies between the proportion of extrapair young for which parentage is known and the apparent effect of EPP on  $I_s$  (Table 1; Spearman rank,  $r_s = -0.71$ ,  $P = 0.013$ ). Studies that identify sires for fewer than 60% of extrapair young often find that EPP increases the opportunity for sexual selection by 100–700%, while studies with a more complete accounting of EPP estimate the increase at only 10–80%.

Unfortunately, few studies have identified sires for all extrapair young and these tend to be special cases for passerines, either because of very low rates of EPP (Hasselquist et al. 1995) or because of small local population sizes (Whittingham and Lifjeld 1995). A more thorough accounting of male fertilization success in other species is necessary before conclusions regarding the importance of multiple mating to  $I_s$  and sexual selection can be drawn. This is of interest because different components of extrapair mating systems not only interact to influence the overall strength of selection, but can themselves affect phenotypes in different ways (Yezerinac and Weatherhead 1997).

We used microsatellite loci to identify extrapair young and their sires in a population of Savannah sparrows (*Passerculus sandwichensis*) where over 40% of offspring can derive from extrapair copulations (Freeman-Gallant et al. 2003). We use Webster et al.'s (1995) approach to parse variation in male fertilization success into within-pair and extrapair components, identify which aspects of the birds' mating system are likely to generate the strongest selection on male phenotypes, and discuss the overall effect of EPP on the opportunity for sexual selection.

## MATERIALS AND METHODS

We observed a known-age population of Savannah sparrows on Kent Island, New Brunswick, Canada, during the 2002 and 2003 breeding seasons. This population has been studied intensively since 1987 (for details of basic field methodology, see Wheelwright and Mauck 1998). All adults nesting in our study site were banded with an aluminum band and a unique, randomly assigned combination of three colored leg bands. At the time of banding, we measured the unflattened wing chord, tarsus length, and weight of each adult and obtained a small (50- $\mu$ l) sample of blood from the brachial vein. Social pairings were identified by observations of mate guarding, territoriality, and parental care. We located nests by following females during the incubation stage and monitored nests every other day until hatching. We examined

TABLE 2. Microsatellite loci used to assign paternity in Savannah sparrows.

Locus	Repeat motif	T <sub>a</sub> <sup>1</sup>	MgCl <sub>2</sub> (mM)	Year	No. alleles	H <sub>e</sub>	H <sub>o</sub>	p <sup>2</sup>
<i>Psa29</i> <sup>3</sup>	(CA) <sub>7</sub> CG(CA) <sub>8</sub>	60	7.7	2002	24	0.93	0.90	0.12
				2003	23	0.93	0.95	0.13
<i>Psa12</i>	(TG) <sub>7</sub> TA(TG) <sub>3</sub>	60	8.3	2002	11	0.84	0.86	0.21
				2003	11	0.82	0.83	0.22
<i>Psap61</i>	(GT) <sub>17</sub>	52	3.3	2002	20	0.92	0.93	0.14
				2003	21	0.92	0.91	0.14
<i>Escu6</i>	(CA) <sub>15</sub> CG(CA) <sub>10</sub>	59	5.7	2002	18	0.89	0.82	0.18
				2003	16	0.89	0.84	0.17
<i>Mme8</i>	(TG) <sub>3</sub> TC(TG) <sub>13</sub>	65	4.0	2002	22	0.93	0.86	0.12
				2003	21	0.93	0.90	0.12
<i>Mme1</i>	(TG) <sub>3</sub> TC(TG) <sub>13</sub>	57	5.0	2002	24	0.93	0.75	0.12
				2003	21	0.93	0.77	0.12

<sup>1</sup> Annealing temperature (°C).

<sup>2</sup> Probability of false inclusion (Jamieson 1994).

<sup>3</sup> Z-linked; observed (H<sub>o</sub>) and expected heterozygosities (H<sub>e</sub>) calculated for males only.

nestlings for survival on day 7 (hatching occurs on day 1), and on day 8, we measured each offspring's weight and wing chord and obtained a sample of blood from the brachial vein. Young found dead in the nest on day 7 or 8 were also sampled. Blood was stored in a lysis buffer (Seutin et al. 1991) at 5°C until DNA could be isolated following standard protocols (Freeman-Gallant et al. 2002).

In cases where eggs or young were preyed upon before day 7 (whole brood or clutch loss), we have no information on parentage. Females almost always produced replacement nests, however, and young from these nests were used in subsequent analyses.

#### Microsatellites

We used six microsatellite loci to identify extrapair offspring and their sires (Table 2). Two of the loci (*Psa29* and *Psa12*) were identified by screening a pUC18-Savannah sparrow library with a pool of dinucleotide repeats and sequencing positive clones. Primer sequences were designed from regions flanking each microsatellite: *Psa29*-F (5'-TGGTAGT AGGAGTTCCATTCAC-3'), *Psa29*-R (5'-AGCCGGTA CGTATCACCCATC-3'), *Psa12*-F (5'-GATCAGAAGAAA TTTATAATGTATGTA-3'), and *Psa12*-R (5'-CCATGAGT CATCCAATAACTGA-3'). We also tested primers from other passerines for cross-species amplification in Savannah sparrows. We selected four loci that showed both strong amplification and variability: *Psap61* (*P. s. princeps*; Temple 2000), *Escu6* (*Emberiza schoeniclus*; Hanotte et al. 1994), and *Mme1* and *Mme8* (*Melospiza melodia*; Jeffery et al. 2001).

Locus-specific annealing temperatures and MgCl<sub>2</sub> concentrations are given in Table 2. Our standard 15-μl reaction contained 20 mM Tris-HCl, 50 mM KCl, 0.3 mM dNTPs, 16 pmol of each primer, and 0.5 U hot-start Taq. Polymerase chain reaction (PCR) was typically run over 30 cycles on a Hybaid Omn-E PCR machine following an initial denaturation step at 94°C for 3 min. Products were sized using a single-capillary automated DNA sequencer (310 Genetic Analyzer, Applied Biosystems, Foster City, CA) and GeneScan analytical software (Applied Biosystems).

#### Paternity Assignment

We screened for the presence of extrapair young by comparing the *Escu6*, *Psa12*, *Mme1*, and *Mme8* genotypes of each

offspring to the genotypes of its putative parents. All but one of the 411 offspring matched their putative mother at the four loci, allowing us to identify unambiguously the set of alleles inherited from each offspring's sire. The single problematic offspring matched its mother at three of the four loci; at the single mismatched locus (*Psa12*), the offspring appeared homozygous for the paternal allele. A total of 217 offspring matched their putative father at all four loci; these young were assumed to derive from within-pair fertilizations. The 194 offspring possessing one or more novel alleles were assumed to derive from extra-pair fertilizations.

By chance, some males that were not actually the sires of offspring on their territories might possess paternal alleles at all four loci, causing some extrapair young to be incorrectly assigned to social mates (false inclusion). Based on the distribution of allele frequencies among adults, the probability that a randomly chosen (nonsire) male would nonetheless match an offspring at any one of the four loci ranged between 0.12 and 0.21 in 2002 and between 0.12 and 0.22 in 2003 (Table 2). However, it is unlikely that true extrapair young matched social mates at all four loci simultaneously (combined probability of false inclusion less than  $5.5 \times 10^{-4}$ ). Because we observed a total of 194 extrapair young, our expectation is that less than one offspring (0.11) has been misclassified over the two years of the study.

To identify extrapair sires, we compared the set of four paternal alleles to the genotypes of all males captured on Kent Island in 2002 or 2003. Because the probability that a randomly chosen male would match an extrapair young at all four loci was extremely low (see above), we assigned extrapair young to matching males. We used the full complement of six microsatellite loci only for the subset of young ( $n = 29$ ) that showed some ambiguity, that is, young who appeared to match no male at the four loci and young who matched multiple males.

#### Variance in Male Reproductive Success

To obtain a complete picture of I<sub>s</sub>, we partitioned variance in male reproductive success into within-pair and extrapair components following Webster et al. (1995). The total number of young a male sires (T) in any particular reproductive

attempt is the sum of his within-pair (W) and extrapair (E) fertilization success,

$$\text{var}(T) = \text{var}(W) + \text{var}(E) + 2 \text{cov}(W, E). \quad (2)$$

Both W and E can be partitioned further into components describing the number of mates a male attracts (M), the number of young produced per mate (N), and the percentage of these young he sires (P). The variance and covariance terms, then, can be parsed into components that address the individual contributions of M, N, and P as well as their respective interactions.

To avoid conflating variance estimates across fitness components, individuals that had zero success in one component were not included in the analysis of subsequent components (after Webster et al. 1995). For example, if a male remained unpaired ( $M_w = 0$ ), he was included only in the variance estimates for  $M_w$  and not  $N_w$  or  $P_w$ .

All variance estimates are expressed as standardized variances (variance divided by mean reproductive success squared; Arnold and Wade 1984). To assess the influence of EPP on the opportunity for sexual selection, we compared the realized variance in male success ( $I_s$ ) to the variance in apparent success ( $I_{s,app}$ ).  $I_{s,app}$  describes the variance among males that would have occurred had males sired all young on their territories. Because of nestling mortality, variance in reproductive success is likely to increase as the season progresses. All variance estimates described here are based on the number (and parentage) of day 7 offspring.

### Second Broods

Female Savannah sparrows may lay a second clutch if the first brood successfully fledges. In 2002, 15 of 64 females (23.4%) produced 42 young in these late-season nests. In 2003, 15 of 52 females (28.8%) produced 47 second-brood young. Because second broods represent a separate reproductive bout, a male's total fertilization success in each year should be considered the sum of his first and second brood success, each partitioned into within-pair and extrapair fitness components. This approach would allow for an explicit consideration of how elements of first-brood success covary with elements of second-brood success and affect the opportunity for selection. However, because this approach greatly inflates the number of variance and covariance terms (a total of 78 terms would appear in the full model, making it intractable), another possibility is to combine the number and parentage of first- and second-brood young when estimating M, N, and P (sensu Ketterson et al. 1997). We have elected to avoid this latter approach so that patterns of variation apparent during one reproductive bout are not conflated with (or masked by) patterns of variation apparent during the other.

In 2003, the 47 second-brood offspring accounted for 22.0% of the overall variance in male reproductive success, but the relative contribution of within-pair and extrapair fitness components was similar in analyses whether we included or excluded these young. In the full dataset, the occurrence of EPP increased the standardized variance in male reproductive success by 28% ( $I_s/I_{s,app} = 1.28$ ), and extrapair components of male fitness collectively contributed 31.8% of  $I_s$ . When we included second-brood young, covariance terms

between the number of within-pair and extrapair young a male produced collectively summed to -6.4% of  $I_s$ . These figures are similar to those derived from an analysis of first-brood young alone (see Results below, Table 3). Because we were unable to sample all second-brood offspring in 2002 and because the results in 2003 were similar regardless of how the data were analyzed, we restrict further discussion to a full accounting of first-brood reproductive success.

## RESULTS

In 2002, the 127 adult sparrows in our sample produced a total of 278 first-clutch eggs, 264 (95.0%) of which hatched. Only 223 of these young (84.5%) survived to day 7. We took blood samples from 216 offspring on day 8, including 10 offspring that had died in the nest between days 7 and 8. Seven of the day 7 offspring were not available for sampling, either because of mortality or premature fledging. In 2003, the 85 adult sparrows in our sample produced 218 eggs and 208 nestlings (95.4% hatching success). A total of 194 of these young (93.3%) survived to day 7. We sampled all of these young on day 8, plus one additional offspring found dead in the nest.

### Parentage

Five of the six microsatellite loci had 18 or more alleles (Table 2) and one locus (*Psa29*) was found to be sex linked. Observed and expected heterozygosities were similar for three loci; for the other three (*Mme8*, *Mme1*, and *Escu6*), fewer heterozygotes were observed than expected ( $\chi^2$  tests,  $P < 0.05$ ). Segregation analysis of maternal and paternal genes revealed the presence of one or more null alleles at *Mme1* and *Mme8*; therefore, it was necessary to take null alleles into account during paternity analysis. A homozygous male was considered to match an offspring if the offspring appeared to be homozygous for the maternal allele. Null alleles were not considered during paternity analyses involving *Escu6*, however. Pooling over 2002 and 2003, a total of 24 females and 16 males were apparently homozygous at *Escu6*, but in no case was it necessary to posit the existence of a null allele to account for the distribution of *Escu6* genotypes among young.

EPP was common on Kent Island in 2002: 121 of 216 offspring (56.0%) were extrapair, and 47 of 64 females (73.4%) produced young outside of the pairbond. Rates of EPP tended to be lower in 2003: 73 of 195 offspring (37.4%) were extrapair and 32 of 52 females (61.5%) produced young outside the pairbond. Pooling over the two years, 165 of the 194 extrapair young (85.1%) matched only a single male at *Mme8*, *Escu6*, *Psa12*, and *Mme1*; these young were assigned unambiguously to those males. Seven of the 194 extrapair young (3.6%) matched two or more males at the four loci. For these offspring, we used two additional loci (*Psa29* and *Psap61*) to identify the extrapair sire. However, in three cases, two males continued to match at all loci. In each case, one of the candidate males was an immediate neighbor while the other defended a territory at least four territory diameters away. We assigned these three offspring to the neighbor.

Twenty-two of the 194 extrapair young (11.3%) matched no male at the four loci. For these offspring, we screened



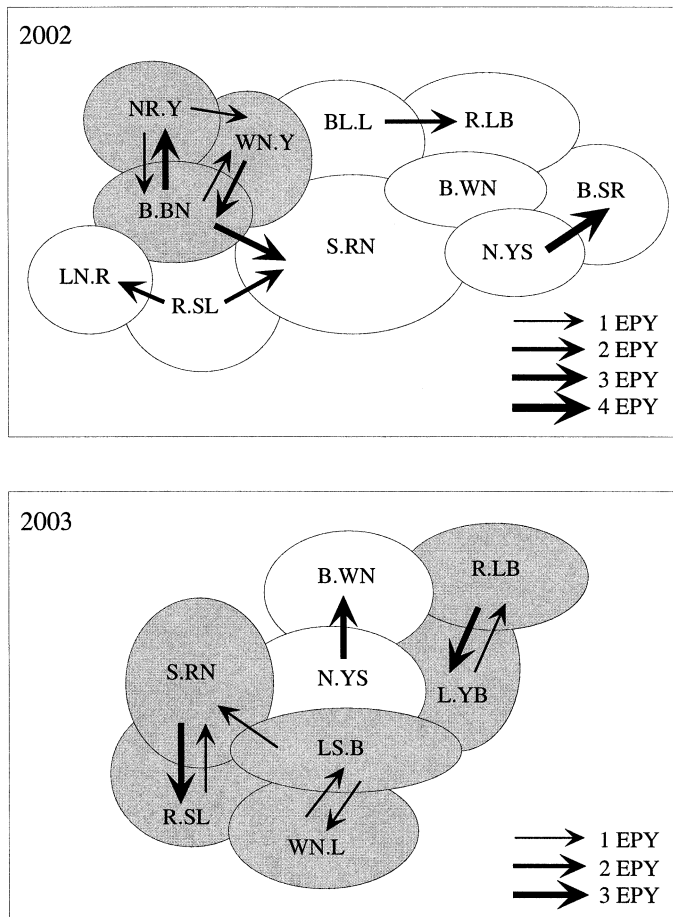


FIG. 1. Geography of extrapair paternity in Savannah sparrows for a  $130 \times 130$ -m area in 2002 and 2003. Size of arrows indicates number of extrapair young (EPY); opposing arrows and shaded territories show cases of reciprocal cuckoldry.

*Psa29* and *Psap61* and then compared the full complement of six paternal alleles to the genotypes of all males captured on Kent Island. In seven cases, a close neighbor matched at five of the six loci, and these offspring were assigned to those males. We were unable to assign paternity to only 15 of the 194 extrapair young, all distributed in nests at the periphery of our study site. Overall, we were able to assign parentage to 396 of 411 offspring (96.4%).

#### Geography of Extrapair Paternity

Our assignments can be used to describe the spatial scale at which reproductive interactions occurred. Pooling over 2002 and 2003, 95% of the extrapair young with known parentage were sired by males whose own social mates nested no more than 87.1 m away. Because the average territory diameter in Savannah sparrows is approximately 38 m (Wheelwright and Mauck 1998), this result suggests that local interactions are important in determining patterns of EPP. Indeed, 154 of the 169 extrapair young with unambiguous assignments were sired by males occupying an adjacent territory (for an example, see Fig. 1).

Reciprocal cuckoldry was common in both 2002 and 2003 (Fig. 1) and always occurred between neighbors. In 2002, 12

of 34 males (35.3%) who sired at least one extrapair young were involved in reciprocal cuckoldry; in 2003, 11 of 21 extrapair sires (52.4%) traded extrapair young with neighboring males. The exchange of extrapair young also occurred across years. In at least one case, a female nesting in 2003 left her social mate from 2002 and paired with the extrapair sire of her 2002 young only to cuckold him in favor of her original social mate. Both males were thus the source and recipient of each other's extrapair young over the two years of the study.

#### Variance in Male Reproductive Success

The standardized variance in reproductive success ( $I_s$ ) among males was 0.58 in 2002. This is 3.6 times the variance in reproductive success observed among females at the same stage of the reproductive cycle, and 2.1 times the variance in apparent reproductive success among males ( $I_{s,app}$ ). In 2003, the standardized variance in reproductive success among males was 0.37, 8.2 times the variance in reproductive success observed among females but only 1.5 times the variance in apparent reproductive success observed among males.

Compared to 2003, relatively few males were polygynously mated in 2002. Only 13 of 57 males (22.8%) attracted multiple mates, and variation among males in number of social mates ( $M_w$ ) was relatively unimportant, accounting for only 10.4% of the overall variance in male reproductive success (Table 3). Among the 52 males whose social mates fledged at least one offspring, 41 (78.8%) lost paternity in their own nests. Differences among males in their ability to protect their within-pair paternity ( $P_w$ ) accounted for 29.6% of  $I_s$  (Table 3), and the total number of fertilizations ( $T$ ) increased with increasing within-pair paternity (Spearman rank,  $r_s = 0.66$ ,  $P < 0.0001$ ). Elements of a male's extrapair success were even more influential. Many males (59.6%) sired young outside the pairbond, and differences in the number of extrapair mates ( $M_e$ ) alone accounted for 56.6% of  $I_s$ . Overall fertilization success ( $T$ ) increased significantly with increasing number of extrapair mates (Spearman rank,  $r_s = 0.75$ ,  $P < 0.0001$ ).

In 2003, 15 of 33 males (45.5%) attracted more than one social mate, and differences in the number of social mates accounted for 22.4% of the total variance in male reproductive success (Table 3). Unlike in 2002, variance among males in their ability to sire young on their own territories ( $P_w$ ) was more important than their ability to acquire extrapair mates ( $M_e$ ). Nevertheless, many males (70.0%) sired young outside the pairbond, and the number of extrapair mates was positively correlated with a male's total reproductive success ( $T$ ; Spearman rank,  $r_s = 0.40$ ,  $P = 0.04$ ). Overall, extrapair components of male reproductive success contributed 65.3% of  $I_s$  in 2002 and 36.9% of  $I_s$  in 2003 (Table 3).

There was little positive covariance between the within-pair and extrapair components of male reproductive success in either year (Table 3). In 2002, males that sired young outside the pairbond were just as likely to be cuckolded as males that failed to produce extrapair young (Fisher's exact,  $P = 0.17$ ), and no element of a male's within-pair success predicted any element of his extrapair success in a series of

TABLE 3. Partitioning of variation in male reproductive success ( $I_s$ ) into within-pair (WP) and extrapair (EP) components. On Kent Island, the standardized variance in reproductive success among males was 0.58 in 2002 and 0.37 in 2003.

Source	2002		2003	
	Value	% Total	Value	% Total
Total WP variance due to	0.199	34.6%	0.277	75.1%
var no. social mates ( $M_w$ )	0.060	10.4%	0.083	22.4%
var female fecundity ( $N_w$ )	0.025	4.4%	0.010	2.8%
var % young sired ( $P_w$ )	0.172	29.6%	0.126	34.0%
covar ( $M_w, N_w$ )	-0.014	-2.5%	0.010	2.8%
covar ( $M_w, P_w$ )	0.008	1.3%	0.035	9.5%
covar ( $N_w, P_w$ )	-0.021	-3.6%	0.007	1.9%
Total extrapair variance due to	0.375	65.3%	0.136	36.9%
var no. EP mates ( $M_e$ )	0.325	56.6%	0.087	23.6%
var EP female fecundity ( $N_e$ )	0.008	1.4%	0.001	0.3%
var % young sired ( $P_e$ )	0.057	10%	0.023	6.2%
covar ( $M_e, N_e$ )	-0.033	-5.8%	0.002	0.5%
covar ( $M_e, P_e$ )	0.034	5.9%	0.001	0.3%
covar ( $N_e, P_e$ )	0	0%	-0.002	-0.5%
Total within-pair and extrapair covariance due to	-0.004	-0.6%	-0.044	-11.9%
cov between no. social mates and				
no. EP mates	0.012	2.1%	0.033	9.0%
fecundity of EP females	-0.012	-2.1%	0	0%
% young sired with EP females	-0.025	-4.4%	-0.028	-7.6%
cov between WP female fecundity and				
no. EP mates	-0.013	-2.3%	-0.011	-3.0%
fecundity of EP females	-0.004	-0.8%	0.002	0.5%
% young sired with EP females	0.012	2.1%	-0.008	-2.1%
cov between % WP young and				
no. EP mates	0.073	12.6%	-0.047	-12.4%
fecundity of EP females	0	0%	0.009	2.4%
% young sired with EP females	0.052	9.1%	0.049	13.2%

bivariate analyses (Spearman rank,  $P > 0.26$ ). In 2003, males appeared more likely to maintain full paternity in their own nests if they did not sire young outside the pairbond (Fisher's exact,  $P = 0.07$ ), but if they did produce extrapair young, the percentage of within-pair and extrapair offspring sired by a given male tended to be positively correlated (Table 3; Spearman rank,  $P = 0.06$ ). Nonetheless, trade-offs appeared to occur between a male's ability to protect his within-pair paternity ( $P_w$ ) and acquire extrapair mates ( $M_e$ ) and, conversely, between his extrapair paternity ( $P_e$ ) and ability to attract multiple social mates ( $M_w$ ). Negative correlations between pairs of fitness components were never significant, however ( $P > 0.09$ ).

#### DISCUSSION

Recent studies have demonstrated that females of many taxa mate with multiple males, including socially monogamous species in which females copulate with males outside of the pairbond (e.g., most birds; Birkhead and Møller 1998). Although variation among males in their ability to obtain extrapair fertilizations has been shown to select for male size and exaggerated secondary sexual characteristics in some species (Kempnaers et al. 1992; Weatherhead and Boag 1995; Hasselquist et al. 1996; Yezerinac and Weatherhead 1997; Thusius et al. 2001), the overall effect of EPP on the opportunity for sexual selection remains unclear. Extrapair components of fitness may increase or decrease the standardized variance in male reproductive success ( $I_s$ ), depending on how within-pair and extrapair fertilization success

covary (Webster et al. 1995; Jones et al. 2001). If the covariance is minimal or negative, EPP may have little effect on the opportunity for sexual selection.

We found that the occurrence of EPP in an island population of Savannah sparrows increased the opportunity for sexual selection less than two-fold, despite the fact that about half of all offspring were extrapair and nearly 70% of females produced young outside the pairbond. This increase is smaller than the five-fold effect derived from a meta-analysis of nine passerines showing more typical (lower) levels of EPP (Møller and Ninni 1998) and substantially less than the 13-fold effect reported for yellow warblers (*Dendroica petechia*; Yezerinac et al. 1995). However, the effect of EPP on the opportunity for sexual selection was similarly weak in red-winged blackbirds (*Agelaius phoeniceus*, Westneat 1993; Weatherhead and Boag 1997) and great reed warblers (*Acrocephalus arundinaceus*; Hasselquist et al. 1995), suggesting that the influence of EPP might be muted in socially polygynous species. This could occur if any trade-off between within-pair and extrapair success is more severe when males attract and guard multiple females (see Hasselquist and Sherman 2001) or if differences among males in the number of social mates swamp other sources of variation. There exists little support for either explanation in Savannah sparrows where variation in the number of social mates ( $M_w$ ) contributed relatively little to  $I_s$  and where the covariance between  $M_w$  and any component of extrapair success was minimal.

The local scale of interaction between males and females might explain why EPP did not more strongly increase the

variance in male reproductive success. Like many passerines (Stutchbury et al. 1997; Webster et al. 2001; but see Foerster et al. 2003), most extrapair sires were within two territories of the focal nest and reciprocal cuckoldry was common (Fig. 1), making it impossible for a small subset of males to account for a disproportionate number of fertilizations. The factors that constrained females to acquire extrapair mates so close to their nesting site are unknown. The fact that only local males sired extrapair young suggests that females may prefer to mate with males with whom they are familiar (see Slagsvold and Lifjeld 1997; Slagsvold et al. 2001).

Despite the local scale of interaction, variation in extrapair success was relatively substantial, and we emphasize that the components of male fitness that best reflect the occurrence of EPP ( $P_w$ ,  $M_e$ ) together accounted for much of  $I_s$  (Table 3). Indeed, it was the lack of a strongly positive covariance between within-pair and extrapair success—and not the absence of variation in any one component—that limited the influence of EPP on the opportunity for sexual selection. For example, the male with the greatest extrapair fertilization success in 2002 (siring 10 extrapair young with four different females) was cuckolded completely by two neighboring males, while the two males with the most within-pair success (fledging six young each) had little extrapair success, siring between them only a single extrapair young. Variation in realized reproductive success could have been increased greatly beyond variation in apparent reproductive success, had the most successful extrapair sires also produced the most within-pair young.

The lack of strongly directional female mating preferences might explain the absence of any positive covariance between a male's within-pair and extrapair success. We have recently shown that the genetic similarity between adults is a better predictor of female mating fidelity than the size, age, or condition of males, regardless of whether the similarity is measured at the major histocompatibility complex (Freeman-Gallant et al. 2003) or, more broadly, across the entire genome (with microsatellites, C. R. Freeman-Gallant, N. T. Wheelwright, K. E. Meiklejohn, and S. V. Sollecito, unpubl. ms.; see also Blomqvist et al. 2002; Foerster et al. 2003). Such disassortative mating would reduce the influence of EPP on the opportunity for sexual selection, because only genetically similar females should agree on male quality.

Might other studies have detected little effect of EPP on the opportunity for sexual selection had they also achieved a more complete sampling of extrapair sires? We think such a scenario is likely, as indicated by the strong negative correlation across studies between the proportion of extrapair young for which parentage is known and the apparent effect of EPP on  $I_s$  (Table 1). When the majority of extrapair young cannot be assigned to local males, the true reproductive success of these males will be underestimated if the influx of foreign males into the study site belies an equally strong efflux of local males from the study site. Importantly, there is little reason to assume that offsite fertilizations originate from the set of individuals already identified as extrapair sires, as some have argued (Møller and Ninni 1998). To the contrary, just as unassigned extrapair young tend to occur at the periphery of study sites (Webster et al. 2001) so too should males breeding at the periphery be more likely to sire

young further afield where they are never tallied. Thus, many males that appear to have zero extrapair success might in fact have sired some extrapair young outside the study area, making extrapair success more uniform across males—and  $I_s$  much smaller—than actually observed (see Westneat 1993). Alternatively, if many extrapair young are sired by floaters not included in the sample (Kempnaers et al. 2001), the study will fail to reveal a negative covariance between within-pair and extrapair success among true breeders since, by definition, floaters sire no within-pair offspring.  $I_s$  will thus be overestimated while variation in apparent success ( $I_{s,app}$ ) will be underestimated, making EPP seem much more influential than it truly is in generating variance in reproductive success among males (Jones et al. 2001).

There is little doubt that EPP does increase the opportunity for sexual selection in most birds, but accurately assessing the magnitude of this increase is important. The extent of EPP is used routinely as an index of the strength of sexual selection in comparative studies (e.g., Møller and Cuervo 2003; Garamszegi and Møller 2004), a practice that implicitly assumes the proportion of extrapair young in a species predicts  $I_s$  and that  $I_s$  (the opportunity for selection) reflects the amount of selection actually experienced during the species' evolutionary history (Sheldon and Ellegren 1999). The fact that EPP appears to increase  $I_s$  many fold ( $I_s/I_{s,app} \gg 1$ ) has provided the major support for the first assumption, but we have shown here that much of this effect may be the consequence of an incomplete sampling of extrapair sires. Moreover, there is little direct evidence that greater levels of EPP reflect a greater opportunity of sexual selection even if published estimates of  $I_s$  are used. Among nine socially monogamous species, there exists no correlation between percent extrapair young and the relative impact of EPP on the opportunity for sexual selection ( $I_s/I_{s,app}$ ; Spearman rank,  $P = 0.81$ ) and only a marginally significant correlation between percent extrapair young and  $I_s$  itself (Spearman rank,  $P = 0.09$ ). It is unclear whether any correlation would exist between EPP and  $I_s$  if estimates of  $I_s$  were corrected for the incomplete sampling of extrapair sires.

Although the extent of EPP appears to be a poor predictor of  $I_s$  in an absolute sense, it might still be positively correlated across species with the relative importance of  $M_e$  and  $P_w$  to variation in male reproductive success. We cannot evaluate this hypothesis rigorously because few studies parse  $I_s$  into within-pair and extrapair fitness components. Although  $M_e$  and  $P_w$  do account for much of  $I_s$  in Savannah sparrows, gains and losses of paternity explain very little variation in male reproductive success in dusky warblers (*Pylloscopus fuscatus*; Forstmeier 2002), a socially polygynous species with equally high rates of EPP and where females appear to allocate fertilizations to high-quality males (Forstmeier et al. 2002). In comparison, fitness components related to EPP accounted for up to 90% of the sexual selection actually measured in collared flycatchers (*Ficedula albicollis*) even though only 15% of nestlings were extrapair (Sheldon and Ellegren 1999).

A positive relationship across species between testis size and the proportion of young that are extrapair indirectly supports the hypothesis that quantitative increases in EPP reflect real increases in the intensity of sexual selection (Møller and Briskie 1995). However, there exists little or no relationship



between EPP and testis size among birds showing fewer than 30% extrapair young (Møller and Briskie 1995); more than 80% of all passerines fall in this category (Griffith et al. 2002). Likewise, early reports that sexual dimorphism is more a consequence of sexual selection arising from sperm competition (and EPP) than number of social mates (Møller and Birkhead 1994; Owens and Hartley 1998) were challenged by Dunn et al. (2001), who found that social mating system was a better and more consistent predictor of dimorphism than testis mass in a study of more than 1000 species of birds. Interestingly, while  $I_s$  shows little covariance with the extent of EPP in our small sample,  $I_s$  averages higher for socially polygynous species than for socially monogamous species (Mann-Whitney,  $P < 0.021$ ) despite a relatively complete accounting of EPP in three of four studies focusing on polygynous systems (Table 1; including Hasselquist et al. [1995] and only one of the two blackbird studies). The percentage of males attracting more than one social mate might be a more informative index of sexual selection than the extent of EPP in comparative studies (Dunn et al. 2001).

We cannot assume that the relative importance of  $M_w$  and other within-pair fitness components covaries with the incidence of polygyny, however. Even in socially polygynous species, fitness components related to EPP might still generate the bulk of  $I_s$ . In Savannah sparrows, for example, variation in number of extrapair mates is of overwhelming importance, suggesting that the strongest sexual selection is on traits that affect extrapair fertilization success, at least in some years (Kempnaers et al. 2001). By contrast, in the socially monogamous black-throated blue warbler (*Dendroica caerulescens*), variation in within-pair success accounts for more than 75% of  $I_s$ , which emphasizes the importance of male phenotypes that influence the number, quality, and fidelity of social mates (Webster et al. 2001).

In conclusion, we emphasize two important caveats in the study of EPP, sperm competition and sexual selection in birds. First, if the effect of EPP on  $I_s$  is much less than commonly appreciated, other sources of variance in male fitness cannot be ignored. This is especially important in the study of socially monogamous species where EPP has routinely been invoked to explain the evolution of sexual dimorphism and more traditional explanations involving the number and quality of social mates (Darwin 1871) are currently out of favor. Second, even if EPP only minimally increases  $I_s$  and is a poor predictor of the opportunity for sexual selection in interspecific comparisons, fitness components related to EPP could still generate more sexual selection than fitness components related to within-pair paternity in any one species. This caveat is especially relevant to the study of socially polygynous species where variation in within-pair fertilization success—and in particular, variation in  $M_w$ —might seem most important. Clearly, it will take increased sampling effort in additional species before the influence of EPP can be characterized with confidence.

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