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Author(s): Angelika Poesel, H. Lisle Gibbs, and Douglas A. Nelson

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EXTRAPAIR FERTILIZATIONS AND THE POTENTIAL FOR SEXUAL SELECTION IN A SOCIALLY MONOGAMOUS SONGBIRD

ANGELIKA POESEL,^{1,2,3} H. LISLE GIBBS,¹ AND DOUGLAS A. NELSON^{1,2}

¹Department of Ecology, Evolution and Organismal Biology, The Ohio State University, Columbus, Ohio 43210, USA; and

²Borror Laboratory of Bioacoustics, The Ohio State University, Columbus, Ohio 43210, USA

ABSTRACT.—Variation in mating success among individuals is the basis for sexual selection and the evolution of elaborate secondary sexual traits. In socially monogamous species, variation in mating success is generally thought to be small, but a skewed adult sex ratio, differences in female fecundity, and extrapair fertilizations that arise from matings outside the social pair bond can increase variance in reproductive success. We investigated how these factors generate the opportunity for sexual selection in the socially monogamous White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). We found a 38% increase in the standardized actual variance in reproductive success compared to the apparent standardized variance of males because of the contribution of extrapair fertilizations to total reproductive success. However, partitioning variance into within-pair and extrapair components showed that the majority of variance in male reproductive success was attributable to within-pair success and a skewed adult sex ratio. Finally, reproductive success increased significantly with the number of mates in males but not in females, which suggests a stronger potential for sexual selection in males than in females in this population. Our results confirm that social mating success may increase the variance in reproductive success more than extrapair fertilizations in some monogamous species. Thus, the evolution of sexual ornaments may be influenced equally or more by the number of available mates and their fecundity than by extrapair matings. Received 10 June 2011, accepted 24 August 2011.

Key words: Bateman gradient, extrapair paternity, opportunity for sexual selection, variance in reproductive success, White-crowned Sparrow, *Zonotrichia leucophrys*.

Fertilizaciones Extra-Pareja y Potencial de Selección Sexual en un Ave Canora Socialmente Monógama

RESUMEN.—La variación en el éxito de apareamiento entre individuos es la base de la selección sexual y de la evolución de rasgos sexuales secundarios elaborados. Generalmente se piensa que en especies socialmente monógamas la variación en el éxito de apareamiento es pequeña, pero un cociente sesgado de sexos de los adultos, diferencias en la fecundidad de las hembras y fertilizaciones extra-pareja que emergen del apareamiento por fuera del vínculo de la pareja social pueden aumentar la varianza en el éxito reproductivo. Investigamos cómo estos factores generan oportunidades de selección sexual en el ave socialmente monógama *Zonotrichia leucophrys pugetensis*. Encontramos un aumento del 38% en la varianza estandarizada verdadera en el éxito reproductivo comparada con la varianza estandarizada aparente de los machos debido a la contribución de las fertilizaciones extra-pareja al éxito reproductivo total. Sin embargo, la partición de la varianza en componentes intra- y extra-pareja demostró que la mayoría de la varianza en el éxito reproductivo de los machos fue atribuible al éxito intra-pareja y a un cociente de sexos adultos sesgado. Finalmente, el éxito reproductivo aumentó significativamente con el número de apareamientos en los machos pero no en las hembras, lo que sugiere un mayor potencial para selección sexual en los machos que en las hembras en esta población. Nuestros resultados confirman que el éxito de apareamiento social puede aumentar la varianza en el éxito reproductivo en un mayor grado que las fertilizaciones extra-pareja en algunas especies monógamas. Así, la evolución de los ornamentos sexuales puede estar igualmente o más influenciada por el número de parejas disponibles y su fecundidad que por apareamientos extra-pareja.

SEXUAL SELECTION DRIVES the evolution of elaborate traits that confer a mating advantage and, consequently, a fitness gain in many animals (Darwin 1871, Andersson 1994). To understand the potential for sexual selection to operate on individuals of a given sex, we need to know the difference between the sexes in the variance of reproductive success (Arnold and Wade 1984).

This variance is mainly caused by the number of mating partners and the number of sired offspring. In most songbirds these factors depend not only on social pairing success but also on extrapair copulations (i.e., matings outside the social pair bond; Petrie and Kempenaers 1998). However, it is not clear how much social and extrapair mating success contribute to the opportunity for sexual

³E-mail: poesel.1@osu.edu

selection (reviewed in Freeman-Gallant et al. 2005, Whittingham and Dunn 2005). Differences in the contributions of mating components may ultimately explain differences in trait evolution between the sexes, among populations, and among species (Kempnaers and Schlicht 2010).

In strictly monogamous species, there is no variance in mate number and variation in offspring numbers is equal for males and females. However, a skewed adult sex ratio and differences in female fecundity can still lead to variance in mating success and generate an opportunity for sexual selection (Fisher 1958, Darwin 1871, Kirkpatrick et al. 1990), as can extrapair matings. Such promiscuous matings are common in birds (Griffith et al. 2002) and can lead to an increase in variance in mating success if some individuals excel at both gaining and protecting paternity (Webster et al. 1995).

We investigated the contributions of within- and extrapair matings to the opportunity for sexual selection in the White-crowned Sparrow (*Zonotrichia leucophrys*), a socially monogamous species with high levels of extrapair paternity (*Z. l. oriantha*; MacDougall-Shackleton et al. 2002). The two sexes are similar in appearance, with only slight dimorphism in size and plumage (Banks 1964). Here, we test the hypothesis that extrapair fertilizations increase the variance in male mating success and make the following predictions. Variance in actual reproductive success (number of young sired) will be larger than variance in apparent success (number of social young). A large proportion of the total variance in reproductive success will be explained by differences among males in extrapair fertilization success. Further, if some males excel in both within- and extrapair matings, the covariance between these components of fitness will be positive and the number of offspring produced will increase with the number of mates.

METHODS

Study site and population.—We studied a migratory population of Puget Sound White-crowned Sparrows (*Z. l. pugetensis*) at Bullard's Beach State Park in Bandon, Oregon, between late March and June in 2005 through 2007. We began complete population counts and banding in 2004 and continued through 2007. We walked or drove through the study area daily, noted any newly singing males (i.e., males new on territory), and did focal observations on the majority of males once a week. Older males arrived in late March to early April, whereas females and yearling males arrived about 2 weeks later (Nelson and Poesel 2009). We noted the arrival date and observed pair formation. The number of occupied territories in the study area ranged from 65 to 77 territories each year. We caught individuals in mist nets or Potter traps. To confirm the sex of the bird we used behavioral and morphological measures: only males produce full song in this species, breeding males show a cloacal protuberance, and males' wings are, on average, 4.5% longer than females' (Banks 1964, Fugle and Rothstein 1985). Males also have a cleaner white median crown stripe than females (D. A. Nelson pers. obs.). More than 83% of the territorial males were color banded each year; the banding rate for females was lower (55.4%). We are confident that we observed all females in the area, because males stop singing as soon as they are paired and we searched territories to confirm pairing status of males (Nelson and Poesel 2011). Although polygyny occurs at a

low level in a related subspecies (*Z. l. oriantha*; Morton 2002), we did not observe any polygynous males in this population. Puget Sound White-crowned Sparrows nest on the ground or low in bushes and raise 1 to 2 broods year⁻¹ (Lewis 1975). Here, we focus on broods during the main laying period in this population (latest laying date on 2 June). Some broods were initiated later in the season, but these were often replacement broods that had smaller clutches. Predation on eggs and females is high, mainly by American Crows (*Corvus brachyrhynchos*) and small mammals such as weasels (*Mustela* spp.), respectively. Only the female incubates, but both male and female feed nestlings and fledglings. Over the 3-year period, we sampled 10 males twice in different years with identical social partners. To avoid pseudoreplication, we included these pairs only once using data from their first year in across-year analyses. Sixteen other males changed their social partner between years, and we treated these pairs as independent samples (Suter et al. 2007).

Genetic sampling procedure and microsatellite genotyping.—We obtained DNA from blood (10–40 μ L) drawn from adults by puncturing the brachial vein. A smaller amount of blood (5–25 μ L) was drawn from nestlings (1–8 days posthatch) by puncturing either the brachial or the femoral vein. The blood was immediately suspended and stored in Queen's lysis buffer (Seutin et al. 1991). We extracted DNA using phenol–chloroform, and quantified DNA suspended in TE buffer with a Smart Spec 3000 spectrophotometer (BIO-RAD). All samples were aliquoted to 20 ng DNA for paternity analysis.

On the basis of amplicon size we chose five microsatellite loci from a set of previously developed microsatellite primers for the Puget Sound White-crowned Sparrow that allowed genotyping of all loci in a single multiplex reaction (Poesel et al. 2009). The forward primer of each pair was labeled using the fluorescent dyes FAM, HEX, or NED; two primer pairs with the same fluorescent dye differed unambiguously in amplicon size (FAM: Zole_A02, Zole_C12; HEX: Zole_C11, Zole_B01; NED: Zole_H02). All five primer pairs were combined into one multiplex PCR (Multiplex kit; Qiagen, Valencia, California) reaction that was performed on an MJ PTC 100 thermal cycler. Each 10- μ L mix contained 20 ng DNA, 5 μ L Multiplex PCR master mix (Qiagen), 1 μ L primer mix (containing 1 μ M of Zole_B01, Zole_C11, Zole_C12 and 1.5 μ M of Zole_A02, Zole_C02, Zole_H02), and 3 μ L RNase-free water. We used the following cycler conditions optimized for the Multiplex kit: an activation step at 95°C for 15 min followed by denaturation at 94°C for 30 s, annealing at 59°C for 90 s, and extension at 72°C for 60 s. The last three cycles were repeated 29 times. The program ended with a final extension step at 60°C for 30 min. After completed amplification, 1 μ L of the multiplex mixture was mixed with a loading buffer containing 9.7 μ L formamide and 0.3 μ L of size standard (GS509ROX; DeWoody et al. 2004). Samples were run on an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, California) and scored using GENEMAPPER, version 3.0 (Applied Biosystems). To verify repeatability of genotype scores, we re-extracted and again blindly genotyped 10 randomly chosen samples from 2005 and 2006. We compared 200 alleles (i.e., a total of 10 samples typed twice for 10 alleles). We identified five genotyping errors, which gave an error rate of 1.6% that was incorporated into the analyses in CERVUS, version 3.0.3 (Marshall et al. 1998, Kalinowski et al. 2007).

Parentage analyses.—The five loci had a combined exclusion probability (Jamieson and Taylor 1997, Marshall et al. 1998) of 0.983 for the first parent and 0.998 for the second parent (i.e., when one parent [the mother] was known). Four of the five markers had observed heterozygosity values close to the expected value and, thus, did not show signs of null alleles. The fifth marker (Zole_B01) showed some indications of a nonamplifying allele, and we estimated a null allele frequency of 0.035 using CERVUS. In three nests, seven offspring showed a single mismatch at locus Zole_B01 with the social female. All offspring and females were homozygous for that locus. Similarly, two social fathers mismatched with 11 offspring only at Zole_B01, where both males and offspring were homozygous. We accepted these mismatches and assumed that the offspring was sired by the respective parent.

To determine paternity of 190 offspring in 62 broods we used a combination of exclusion and likelihood analysis to identify the genetic fathers in CERVUS. Where possible we included a known parent (mother) for 66.3% of offspring in our analyses. In a first step we assessed whether the genotype of the mother matched the genotype of the respective offspring. One of 190 (0.5%) offspring mismatched the genotype of the putative mother at three loci and we assume that this indicated a case of intraspecific brood parasitism. This chick also mismatched the male attending the nest at three loci and could be assigned to a different male in the neighborhood. In a second step we tried to match the genotype of the offspring with the genotype of the observed social male attending the nest. We accepted the social male as the genetic father when his genotype matched the offspring's multilocus genotype. When the putative father had one allelic mismatch with the offspring but was more likely ($\geq 80\%$ confidence level) than any other male in the population to have fathered the chick, we accepted him as the actual father. One mismatch may have been due to genotyping error or germ-line mutation. When the putative father had one allelic mismatch with the offspring but another male was more likely to have fathered the chick or when we found two or more mismatches, we rejected the putative male as the genetic father and identified the offspring as extrapair (i.e., sired by another male in the population).

Paternity was then assigned to these extrapair offspring. We compared the genotype of each extrapair offspring with all genotypes of males that we sampled in the study area. Our study area was bordered by the Pacific Ocean on one side, the Coquille River on two sides, and habitat unsuitable for breeding by White-crowned Sparrows on the fourth. On the basis of our censuses within this area, we estimate that we sampled 97.3% of all territorial males in 2005,

97.1% in 2006, and 95.3% in 2007. We accepted males other than the social male as the sire of offspring in a brood when the extrapair sire and offspring did not have any mismatches and the extrapair male was more likely ($\geq 80\%$ confidence level) to have fathered the chick than any other male in the population. In addition, we also accepted a male when it had low likelihood ($< 80\%$) and did not have a mismatch but had sired another chick in the same brood at a higher confidence level. We identified the extrapair father for all but 1 of 55 extrapair offspring (98.2%). This single offspring was most likely sired by an unsampled male.

Male reproductive success and the potential for sexual selection.—We based calculations of reproductive success on the number of young genotyped between the ages of 1 and 8 days. Following Arnold and Wade (1984) we calculated standardized variances in reproductive success by dividing the total variance by the mean squared. We compared the standardized variance of apparent reproductive success (i.e., the number of young in a male's brood) with that of actual reproductive success (i.e., the number of young sired with social and extrapair mates). Following Webster et al. (1995) we partitioned male actual reproductive success into variance due to within-pair and extrapair components and their covariance. We partitioned each component into number of social and extrapair mates, number of within-pair and extrapair young produced by each mate, and the proportion of within-pair and extrapair young sired. Finally we calculated sexual selection or Bateman gradients for both males and females. We regressed the number of genetic young produced on the number of mates for both males and females (Bateman 1948, Arnold 1994, Arnold and Duvall 1994). For this analysis we excluded males that remained unpaired and pairs whose nests were depredated. All statistical analyses were performed in SPSS, version 17.0. We present means \pm SD. Sample sizes vary among analyses because not all information was available for all males. In particular we included information on pairing success for 161 males, apparent and actual reproductive success for a subset of 133 (74 paired) males, and detailed paternity for 52 broods.

RESULTS

Variation in social pairing success, adult sex ratio, and female fecundity.—Across years, 36% of all territorial males remained unpaired (Table 1). This was because the population's adult sex ratio deviated from a 50:50 distribution in two of the three study years (Table 1). Among social pairs nest predation was moderate

TABLE 1. Adult sex ratio, social pairing success, and frequency of extrapair fertilizations in Puget Sound White-crowned Sparrows from Bullard's Beach State Park in Bandon, Oregon (2005–2007). Sample sizes (n) of number of breeding males and males with analyzed paternity are given in parentheses. Note that the sample sizes across years are not the sum of the sample sizes of the individual years, because some males were present in more than one year and were only selected once unless (1) the pairing status (paired–unpaired) or (2) the identity of the mate changed between years. The binomial test investigated whether the adult sex ratio deviated significantly from a 50:50 distribution.

Year	Adult sex ratio (males:females)	Binomial test (exact P)	Percentage of males paired	Percentage of broods with extrapair young	Percentage of extrapair young
2005	1.35 (77)	0.23	75.3 (77)	37.5 (24)	40.3 (62)
2006	1.52 (67)	0.05	65.7 (67)	29.4 (17)	28.0 (50)
2007	1.66 (65)	0.03	60.0 (65)	28.6 (21)	26.9 (78)
Across years	1.56 (161)	<0.001	64.0 (161)	38.5 (52)	35.4 (164)

(19–22.2% each year), and over the years of the study at least 8 females were presumably taken by predators while incubating. In the latter cases activity around the nest ceased and the male resumed singing (an indication that a male is unpaired). Among paired males the number of eggs per clutch varied from 2 to 4 (mean = 2.20 ± 1.66 eggs; $n = 74$).

Extrapair reproductive success.—Around one-third of all sampled broods contained extrapair offspring, and similar numbers of all sampled offspring were sired by an extrapair male (Table 1). Ten of the 20 males that lost paternity (50%) did not father any young in their own brood despite some apparent reproductive success, whereas the other 10 males lost paternity of 25–75% of their offspring to extrapair sires. Most of the 20 males (80%) lost paternity to 1 extrapair male each, whereas 4 males lost paternity to 2 males.

Opportunity for sexual selection.—The standardized variance in actual male reproductive success was 38% larger than the variance in apparent male reproductive success (Table 2). Among males most of the variance in actual reproductive success was attributable to variance in pairing success ($W = 69.9\%$; Table 2). Still, nearly one-third (29.9%) of the variance was due to variance in extrapair matings, in particular the number of extrapair mates (M_e) and the proportion of young sired in the social brood (P_w ; Table 2). Thirteen males that sired young with an extrapair mate increased their reproductive success by, on average, 2.5 ± 1.26 offspring (range: 1–5); for 8 males this was the only reproductive success they gained because either these males were unpaired ($n = 3$) or the brood of their social mate was depredated

($n = 5$). Actual reproductive success was significantly lower in males that lost paternity than in those that did not lose paternity (Fig. 1A) and higher in males that gained paternity than in those that did not gain paternity (Fig. 1B). Apparent reproductive success did not differ in either comparison (both $P > 0.24$). The covariance between within-pair and extrapair success was positive but explained only a small proportion (4.7%) of the total variance (Table 2).

Finally, the actual reproductive success of males was closely tied to the number of mates (social and extrapair) as shown by a strongly positive Bateman gradient (Fig. 2A). By contrast, in females the number of sired young did not increase significantly with the number of mates (Fig. 2B). The slopes of males and females were significantly different from each other (Student's $t = 3.24, P = 0.002$).

DISCUSSION

We showed that three factors contributed to the opportunity for sexual selection in a socially monogamous songbird: adult sex ratio, female fecundity, and extrapair mating success. Our results further demonstrate that both social and extrapair mating success can increase variance in male reproductive success. Most importantly, our results confirm Darwin's prediction for sexual selection that variation in mating success is larger among males than among females and that this may be caused by a male-biased adult sex ratio.

TABLE 2. Variation in apparent and actual reproductive success in 133 male Puget Sound White-crowned Sparrows from Bullard's Beach State Park in Bandon, Oregon (2005–2007). The standardized variance in actual male reproductive success has been partitioned into the amount of variance contributed by within-pair (W) and extrapair (E) paternity success, along with their covariance. W and E were each further partitioned into contributors to overall variance in success: number of within-pair (M_w) and extrapair (M_e) mates; number of within-pair (N_w) and extrapair (N_e) young per mate; and proportion of within-pair (P_w) and extrapair (P_e) young sired by the male.

	Range	Mean	Variance	$S_{var}(\%)^a$
Apparent male reproductive success	0–4	1.20	2.67	1.87
Actual male reproductive success	0–8	1.01	2.64	2.58
W	0–4	0.80	1.84	1.80 (69.9)
E	0–5	0.28	0.79	0.77 (29.9)
Cov(W, E)			0.06	0.12 (4.7)
Within-pair sources of variance				
M_w	0–1	0.58	0.25	0.54 (21.1)
N_w	0–4	2.12	2.71	0.44 (17.1)
P_w	0–1	0.71	0.17	0.25 (9.5)
Extrapair sources of variance				
M_e	0–2	0.15	0.16	0.41 (15.8)
N_e	1–4	2.34	1.33	0.01 (0.6)
P_e	0.33–1	0.69	0.07	0.01 (0.3)

^a S_{var} is the standardized variance weighted by appropriate multipliers from the model (see Webster et al. 1995) and the percentage of the total variance in actual reproductive success explained. Not all covariance and remainder terms that contributed to the total variance are shown; thus, W , E , and Cov(W, E) do not sum to 100%. Similarly, the within-pair and extrapair sources of variance do not sum to 69.9% and 29.9%, respectively.

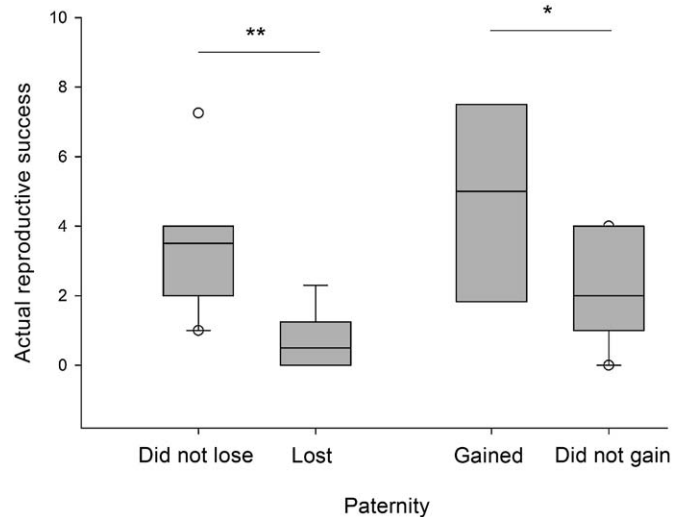


FIG. 1. The actual reproductive success (number of sired young) of Puget Sound White-crowned Sparrows breeding at Bullard's Beach State Park in Bandon, Oregon (2005–2007), differed (A) between 34 males that did not lose paternity and 18 males that lost paternity (Mann-Whitney $U, Z = -4.59, P < 0.001$) and (B) between 5 males that gained paternity and 47 males that did not gain paternity ($Z = -2.20, P = 0.03$). One male both lost and gained paternity. The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, and small open circles the 5th and 95th percentiles.

Social mating success contributed the most, by far, to variance in total male reproductive success. It varied among males because of differences in pairing success and number of young produced. Variance in the latter was caused by both female fecundity and nest predation. Some females produced larger clutches than others, and males mated to highly fecund females enjoyed high reproductive success (Fisher 1958, Kirkpatrick et al. 1990). As is common in open-cup ground nesters (Martin 1993), nest predation occurred regularly and males whose nests were depredated did not have any within-pair success. Still, excluding males whose broods were depredated from the analysis and focusing on successful males, males that produced at least one young with the social mate did not qualitatively change the variance components (data not shown). Thus, predation did not seem to contribute to variance in reproductive success as much as has been shown in other species with high predation rates (Webster et al. 2007).

A male-biased adult sex ratio caused most of the variance in social mating success because it left many males without a social mate. As the operational sex ratio becomes more biased toward

males, competition among males and mate choice in females increase, with the consequence that sexual selection should be stronger in the more abundant sex (Kvarnemo and Ahnesjö 1996, Dunn et al. 2001). Indeed, as demonstrated for other taxa by Clutton-Brock (1988), female White-crowned Sparrows showed little variation in mating success and generally weak sexual selection, and a weaker sexual selection (Bateman) gradient than males (Fig. 2).

The adult sex ratio may have been less biased than assumed, given that unpaired females are difficult to detect and in some songbird populations a floater population of nonbreeding females exists because of, for example, shortage of suitable breeding habitat (Cooper et al. 2009). However, this seems unlikely in this population because unpaired males defended territories suitable for breeding and because many territories of unpaired males hosted breeding pairs in other years without obvious changes to the habitat between years (A. Poesel and D. A. Nelson pers. obs.). We would therefore expect floater females to pair with these unpaired males. Similarly, females depredated during incubation ($n = 8$) were not replaced by floater females in the area (A. Poesel and D. A. Nelson pers. obs.). Hence, nest predation eliminated females from the breeding pool and contributed to the observed male-biased adult sex ratio.

A male-biased sex ratio may be caused by demographic phenomena such as a skewed sex ratio at hatching or differential male and female mortality. In this population the sex ratio among chicks did not deviate from unity (A. Poesel unpubl. data). Differences in overwinter survival probably played a lesser role because it has been shown in the closely related and also migratory subspecies *Z. l. oriantha* that males and females are equally likely to survive to the next breeding season (Morton 2002). Overall, this agrees with results across bird species that higher female mortality, rather than skewed offspring sex ratio, is the main driver of male-skewed adult sex ratios (Donald 2007). The observed bias (1.35–1.6 males female⁻¹) did not differ from the slightly male-biased sex ratio (1.2–1.8 males female⁻¹) typically observed in monogamous bird species (Breitwisch 1989). Thus, our finding that a slight bias can increase variance in reproductive success and affect sexual selection may be important to consider in studies on sexual selection in other monogamous bird species. However, this conclusion may not generalize to species with other mating systems (e.g., Webster et al. 2007).

The best indication that extrapair matings contributed to the variance in reproductive success is a positive Bateman gradient indicating an increase in number of offspring sired with the number of mates. In this socially monogamous species, differences in the number of mates occurred because of additional mates gained through extrapair copulations. Thus, any male trait closely associated with extrapair mating success should be favored by selection. Indeed, male White-crowned Sparrows in our population that share songs with territorial neighbors are more likely to gain extrapair paternity than males that do not share songs (A. Poesel et al. unpubl. data).

When we partitioned variance into within-pair and extrapair components, both the proportion of young sired in the social brood and the number of extrapair mates contributed to the variance in total male reproductive success. This was also supported by a small but positive covariance between extrapair and within-pair success. Our results suggest that males should guard their mates to minimize loss of paternity as well as attract extrapair females.

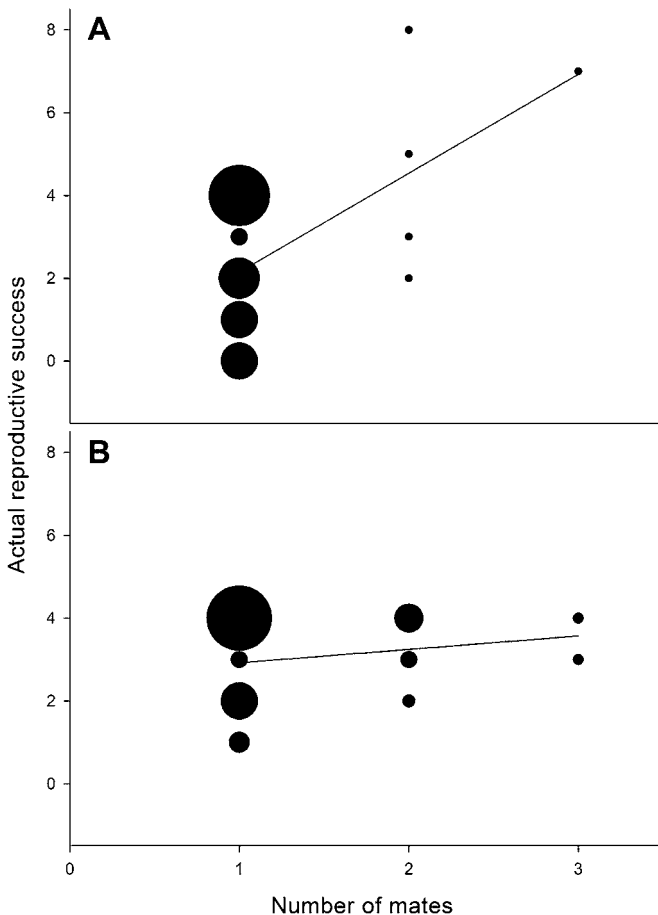


FIG. 2. Bateman gradients show the relationship between number of mates and total number of genetic offspring for 52 Puget Sound White-crowned Sparrows from Bullard's Beach State Park in Bandon, Oregon (2005–2007), for (A) males ($r^2 = 0.24$; $F = 16.18$, $df = 1$ and 50 , $P < 0.001$; $\beta = 2.39$) and (B) females ($r^2 = 0.04$; $F = 2.00$, $df = 1$ and 50 , $P = 0.16$; $\beta = 0.33$). The size of each circle is proportional to the number of entries with equal value (range: 1–16).

Furthermore, the variance in actual reproductive success was larger than the variance in apparent success. The variance increased both because only a fraction of males gained extrapair paternity and because some males lost most or even all paternity with their social mate without gaining paternity elsewhere. An increase of 38% is in line with some studies of socially monogamous, monomorphic songbird species (Freeman-Gallant et al. 2005, Whittingham and Dunn 2005, Webster et al. 2007). Differences in sample size may influence these values and, consequently, the comparison (Krakauer et al. 2011). Overall, the ratio of apparent to actual reproductive success should be interpreted with care (Webster et al. 2007) but, in combination with the other analyses, adds to our result that extrapair fertilizations contributed a small amount of variation in reproductive success.

The actual strength of selection acting on specific traits may be weaker than implied here because the opportunity for sexual selection reflects the maximum, but not necessarily the realized, strength of sexual selection (Arnold and Wade 1984, Jones and Ratterman 2009). The accuracy of variance-based measures such as the standardized variance in reproductive success as a measure of sexual selection has been debated (Klug et al. 2010, Krakauer et al. 2011), and alternative indices are available (Kokko et al. 1999). However, the advantage of variance-based estimates is their close connection to selection theory, which allows a direct interpretation with regard to underlying evolutionary processes (Jones et al. 2002, 2004).

To conclude, extrapair fertilizations occur regularly in the Puget Sound White-crowned Sparrow as well as in other species of emberizid sparrows (e.g., *Junco hyemalis*, Ketterson et al. 1997; *Z. l. oriantha*, MacDougall-Shackleton et al. 2002; *Z. albicollis*, Tuttle 2003; *Melospiza melodia*, O'Connor et al. 2006). Male White-crowned Sparrows have several main pathways to increase their reproductive success: acquire a highly fecund social mate, protect within-pair paternity, and acquire extrapair mates. The present and some previous studies have shown that the variance in social pairing success may have an equal or even larger influence on the evolution of sexually selected traits than extrapair success in socially monogamous songbirds (Whittingham and Dunn 2005). This may hold particularly for species with average levels of extrapair paternity such as Puget Sound White-crowned Sparrows. In species with high levels of extrapair paternity, we may see a greater influence of extrapair behavior on the variance of total reproductive success (e.g., Eastern Kingbird [*Tyrannus tyrannus*]; Dolan et al. 2007). Still, the recent focus on extrapair matings in studies on sexual selection in birds with average levels of extrapair paternity may neglect important fitness components due to social mating success and female fecundity. Our results highlight the importance of investigating adult sex ratios in bird populations because a skewed sex ratio can contribute to the variance in reproductive success. As a result, the evolution of sexual ornaments may be influenced equally or more by the number of available mates and their fecundity than by extrapair matings.

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