



Original Article

Extrapair mating and the strength of sexual selection: insights from a polymorphic species

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Extrapair mating could drive sexual selection in socially monogamous species, but support for this hypothesis remains equivocal. We used lifetime fitness data and a unique model species, the dimorphic white-throated sparrow (*Zonotrichia albicollis*), to examine how extrapair mating affects the potential for sexual selection. In this species, the morphs employ distinct reproductive strategies, with white males pursuing extrapair mating at higher rates than tan counterparts. Social and extrapair mating is disassortative by morph, with paternity exchange occurring primarily between pairs composed of white males and tan females. Bateman gradients and Jones indexes indicated stronger sexual selection via mate numbers in white males than in females and tan males, and generally did not differ between females as compared with tan males. Extrapair mating contributed more to the Bateman gradient for white than tan males, and white males also had higher variance in annual reproductive success. However, variance in lifetime reproductive success did not differ between morphs or sexes. Moreover, extrapair mating did not increase variance in male reproductive success relative to apparent patterns, and within-pair success accounted for much more variance than extrapair success. Thus, extrapair mating by white males increases Bateman gradients and the potential for sexual selection via mate numbers. However, our latter results support previous research suggesting that extrapair mating may play a limited role in driving the overall potential for sexual selection.

Key words: Bateman gradients, extrapair mating, polymorphic species, sexual selection, white-throated sparrows.

INTRODUCTION

Darwin (1859, 1871) introduced the concept of sexual selection, and evoked this force to explain the existence of behavioral and morphological sexual dimorphisms. Multiple mating is often more common in males than in females, and is generally predicted to increase variance in reproductive success and the strength of sexual selection. Based on seminal experiments on sexual selection, Bateman (1948) predicted that males should display more variation in both 1) mate number and 2) reproductive success than females, leading to 3) stronger sexual selection on males, as indicated by the correlation between these 2 variables (Arnold 1994; Arnold and Duvall 1994). Thus, variance in mate numbers can set limits on the strength of sexual selection, making explaining the presence of sexually selected traits in monogamous species difficult (Andersson 1994; Shuster 2009).

In the 1990s to early 2000s, genetic data revealed that many socially monogamous bird species are not truly genetically monogamous, in that “extrapair” copulations commonly occur outside of the social pair bond (reviewed by Griffith et al. 2002). Since this discovery, it has been widely proposed that multiple mating with extrapair partners drives sexual selection in these species (Dolan et al. 2007; Webster et al. 2007; Poesel et al. 2011). However, whether extrapair mating is commonly the primary force behind sexual selection in species that display predominately monogamous social systems remains far from clear. Indeed, there are alternative avenues through which sexual (or social) selection might act. For instance, as originally proposed by Darwin (1871), mate quality in addition to mate number could act as a vehicle for sexual selection, and contribute to selection on elaborate sexually selected traits in monogamous species (Kirkpatrick et al. 1990; Jones and Ratterman 2009).

Studies that test the effects of extrapair mating on the strength of sexual selection have yielded equivocal results. Some find that extrapair mating substantially increases standardized variance in

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reproductive success (I , which sets the upper limits for selection) and the strength of sexual selection as measured by Bateman gradients (the regression between number of mates and reproductive success; Webster et al. 1995; Yezerinac and Weatherhead 1997; Dolan et al. 2007; Webster et al. 2007; Vedder et al. 2011). On the other hand, others find little evidence that extrapair mating increases variance in reproductive success, and thereby elevates the potential for sexual selection (Freeman-Gallant et al. 2005; Whittingham and Dunn 2005; Grunst and Grunst 2014). Indeed, extrapair mating even has the potential to dampen sexual selection, for instance if males that pursue extrapair mates are those unsuccessful at attracting social partners (Jones et al. 2001; Lebigre et al. 2012; Schlicht and Kempenaers 2013).

In addition, the fitness implications of multiple mating for females remain debated. In promiscuous mating systems, Bateman gradients are commonly found to be significantly steeper in males than females, as predicted by Bateman (1948), even when positive gradients are observed in females (Jones et al. 2002; Snyder and Gowaty 2007; Gerlach et al. 2012). However, some studies in promiscuous mating systems find positive Bateman gradients in females that are equal in magnitude to those observed in males (Bergeron et al. 2012). Females may gain genetic or direct benefits for offspring through multiple, extrapair mating (Foerster et al. 2003; Suter et al. 2007; Townsend et al. 2010). However, the hypothesis that females elevate fitness through multiple mating is not consistently supported, and substantial costs are also possible, for instance, injury, disease transmission, and loss of paternal support (Westneat and Rambo 2000; Westneat and Stewart 2003; Albrecht et al. 2006; Akçay and Roughgarden 2007; Chaine et al. 2015). Rather than deriving benefits, extrapair mating by females may instead occur due to male coercion (Westneat and Stewart 2003), or arise through nonadaptive genetic correlation with males (Halliday and Arnold 1987; Forstmeier et al. 2014). Thus, more research is needed to better understand how extrapair mating contributes to variance in reproductive success and sexual selection in females, and what accounts for variation between species and populations.

To gain new insights into how extrapair mating affects variance in reproductive success and the strength of sexual selection, we studied a unique model species, the dimorphic white-throated sparrow (*Zonotrichia albicollis*). In the white-throated sparrow, both males and females occur as 1 of 2 morphs, either white or tan. Morph is genetically determined by an inversion-based, >100 Mbp supergene on the second chromosome (the ZAL2^m rearrangement), with white birds heterozygous for the supergene and tan birds homozygous noncarriers (Tuttle et al. 2016). White birds display more colorful crown plumage than tan birds (Rathbun et al. 2014; Grunst et al. 2017a), and the morphs also display dramatically different behavioral and reproductive strategies (Tuttle 2003). White males and females are more aggressive and less parental than tan counterparts (Kopachena and Falls 1993a, 1993b; Horton et al. 2014). Moreover, white males display higher testosterone levels during breeding (Spinney et al. 2006; Maney 2008), and higher rates of song and extrapair mating than tan males (Formica and Tuttle 2009). In lieu of extrapair activity, tan males instead invest in mate guarding (Tuttle 2003). White-throated sparrows display a unique disassortative mating system, with white males socially pairing with tan females ($W \times T$) and tan males with white females ($T \times W$), almost exclusively (Falls and Kopachena 2010; Tuttle et al. 2016). In addition, tan females are the primary recipients of extrapair copulations (EPCs) by white males. Thus, both extrapair paternity and cuckoldry rates are much higher in white males than in tan males

(Tuttle 2003; Formica and Tuttle 2009). Although the reproductive strategies of the 2 morphs are not completely distinct, in that both morph types invest to some extent in parental care, the dramatic, genetically determined difference in extrapair mating and singing activity between males of the 2 morphs, the presence of song only in white females, and the near-obligate disassortative mating pattern, means that the morphs display clearly differentiated, non-conditional reproductive strategies (Grunst, Grunst, Rathbun, et al. 2017; Grunst, Grunst, Gonser, et al. 2017; 2017b; Grunst, Grunst, Formica, et al. 2018; Tuttle 2003; Tuttle et al. 2018).

Based on the characteristics of this intriguing system, we predicted that white morph males, which pursue multiple mating and exhibit bright, potentially sexually selected coloration and high song rates (Tuttle 2003; Grunst, Grunst, Rathbun, et al. 2017; Grunst, Grunst, Gonser, et al. 2017; Grunst, Grunst, Formica, et al. 2018), should exhibit higher variance in reproductive success and steeper Bateman gradients than tan males. However, as a caveat that adds interest, multiple, extrapair mating might not increase variance in reproductive success or affect the magnitude of the Bateman gradient if pursuing extrapair mates is primarily a best-of-a-bad-job strategy employed, for instance, by unpaired males (Schlicht and Kempenaers 2013). Over 25 years of field observations suggest that extrapair mating is male driven in our study population, often involving aggressive, unsolicited approach of tan females by white males (unpublished data). This does not preclude benefits of extrapair mating for females, because female resistance could serve to enforce extrapair mate quality (Eberhard 2002; Forstmeier 2004; Parker 2006). Nonetheless, we predicted shallower Bateman gradients in females of both morphs relative to in males. In addition, we predicted that compared to white males, tan males should exhibit a Bateman gradient relatively more similar to that observed in females. Thus, we expected that the discrepancy in the Bateman gradient should be greater between white males and females than between tan males and females, which could lead to evolutionary sexual conflict over genes controlling mate numbers in the white morph (Parker 2006).

We used a long-term dataset to characterize the effect of mate numbers, as determined by extrapair paternity and social polygyny (which occurs at low rates in our population), on both within-season and lifetime reproductive success. We calculated standardized variance in reproductive success (I ; the opportunity for selection), standardized variance in mating success (I_s ; the opportunity for sexual selection via mate numbers) and Bateman gradients across both of these timeframes, and partitioned reproductive success and Bateman gradients between within-pair and extrapair components. In addition, we also calculated the Jones index (s'_{max}), which is the product of the relative Bateman gradient and the square root of I_s . The Jones index corrects the Bateman gradient for variance in mating success, sets an upper limit on premating sexual selection, and has recently been proposed to serve as a better metric of the potential for sexual selection than the Bateman gradient (Jones 2009; Henshaw et al. 2016). Our data grant new insights into the potential for extrapair mating to increase the strength of sexual selection.

METHODS

Field monitoring and determining reproductive success

This study utilized data from white-throated sparrows breeding at the Cranberry Lake Biological Station (State University of New York College of Forestry and Environmental Sciences) between

1998 and 2014. For analyses involving lifetime reproductive success, we only included birds that were accurately monitored across their entire tenure as breeding adults. White-throated sparrows at Cranberry Lake establish territories in bogs, forested glades and riparian corridors. Each year, we comprehensively surveyed the study site to locate all breeding pairs. New recruits were captured in mist nets using passive netting or conspecific playback, banded and bled to obtain blood samples (80–200 μ L) for paternity analysis. We located nests across each breeding season, from early May through early August, through a combination of behavioral observations and systematic search. Nest checks occurred every other day to monitor depredation and the progression of the nesting cycle. We obtained blood samples from ~6-day old nestlings for use in genetic paternity analysis. All ~6-day old nestlings were also uniquely banded and color banded. After banding nestlings, we placed ThermoChron iButtons® in nests, and did not check the nest again until after the projected fledging date, on nestling day 10–12. Nests were considered depredated if ThermoChron data documented that the nest was empty before day 9, and parents were not observed feeding fledglings. Nests were considered successful if data indicated that nestlings fledged on day 9 or later, and/or parents were observed with fledglings. We used the number of genetic fledglings produced as our metric of reproductive success.

Genetic paternity analysis

We stored hematocrit from blood samples in lysis buffer at 4 °C (Longmire et al. 1992) until extracting DNA using the DNA IQ® magnetic extraction system (Promega Corp; Madison, WI). We conducted paternity analysis using 8 microsatellite loci; Gf01 and Gf12 (Petren 1998), MME1 (Jeffery et al. 2001), Dp μ 01 and Dp μ 03 (Dawson et al. 1997), and ZLC02, ZLC07 and ZLH02 (Poesel et al. 2009), with a minimum of 4 microsatellites used per nestling. We used fluorescently labeled primers and ran PCR products on an ABI PRISM 310 Genetic Analyzer® (GMI Inc., Ramsey, MN) to identify alleles. To determine whether nestlings were within-pair or extrapair offspring, we first directly compared nestling and adult alleles, and assigned nestlings as extrapair offspring if their genotype mismatched paternal alleles at any one locus. We then used CERVUS 3.0 (Field Genetics, London, UK) to assign extrapair fathers and confirm within-pair fathers (Kalinowski et al. 2007), with paternity assigned at a minimum confidence level of 80%. Further procedural details can be found in Formica and Tuttle (2009). We determined the actual reproductive success of males by adjusting apparent reproductive success for extrapair offspring. Females were assigned as the genetic mother of all nestlings in their nests. We did not encounter cases in which female and offspring alleles mismatched, except in the case of binning errors, and rates of intraspecific brood parasitism are low in this species (Tuttle 2003).

In addition, we used the same microsatellite data and COLONY 2.0 (Jones and Wang 2010) to perform sibship analysis. COLONY assigns offspring to full and half-sibships, and creates artificial identities for fathers not included in the genetic database. Thus, in cases in which we could not assign a known extrapair father to multiple nestlings from the same mother, COLONY allowed us to assess whether or not multiple extrapair males sired these nestlings.

Determining number of mates

We determined number of mates by taking both social and extrapair patterns into account. All social partners were counted as

mates, even if reproductive success was zero, or if nests contained no genetic offspring from a given partner. Social partners most likely engaged in copulations even if no genetic offspring were produced. Out of 168 male breeding attempts (years) that produced genotyped offspring, 16.6% (28) produced no genetic offspring with the social mate. We retained this 16.6% within the category of one, rather than zero, mating partners, because the male invested in attracting and defending a social mate (and likely mated with this partner, as indeed observed in some cases) despite gaining no paternity from this effort. We also repeated the analysis with these males assigned as having obtained zero social mates, which slightly increased the magnitude of the Bateman gradients calculated using total and social mate numbers, but did not qualitatively change most results. Where discrepancies between the 2 analyses arose, they are noted in the results section, and results from the latter analysis can be found in the **Supplementary Material** (Supplementary Tables S1–S4).

Males were assigned extrapair mates when they fathered genotyped extrapair young with a given female. For females that had more than one extrapair offspring in their nests, we determined the number of mates by counting the number of known-identity extrapair fathers, and additionally using COLONY to estimate the number of unknown fathers (Jones and Wang 2010). Note that in our analysis an individual can have reproductive success of zero despite having more than one mate because we obtained genetic paternity data for some nestlings that subsequently perished.

Statistical analyses

Reproductive success and mate numbers

We performed statistical analyses using R version 3.1.2 (R Core Team 2014). We first examined the relationship between number of mates and both annual and lifetime reproductive success (LRS) using generalized linear mixed effects models (GLMMs; R package lme4; Bates et al. 2012) with a Poisson distribution, to account for the non-normal distribution of count data. In the model for annual reproductive success, we used the number of mates per year as the fixed effect predictor variable. We had multiple observations per individual across years, so entered band number and year as random effects. In the model for LRS, our fixed effects were the average number of mates per year obtained across a lifespan (total mates/breeding years) and longevity (breeding tenure). We entered first breeding year as a random effect, to account for cohort effects. In both models, we also added an observation level random effect to control for overdispersion (Harrison 2014).

We first performed Poisson GLMMs in males and females separately, in which we entered an interaction between morph and number of mates. We then performed models within each morph separately, in which we entered an interaction between sex and number of mates. In addition, we performed models across all birds combined, and entered an interaction between morph-sex class (e.g., white males versus tan females) and number of mates. Finally, we also performed models within each morph-sex class separately to more clearly elucidate the strength of the relationship between reproductive success and mate numbers within each morph-sex class. Finally, for males only, we examined the relative effect of social versus extrapair mating success on reproductive success by constructed models in which we predicted annual or lifetime reproductive success from number of social and extrapair mates. When interactions were included in the model, we centered mate number and specified Helmert contrasts so that main effects were estimated across different classes of birds.

Linear Bateman gradients and the Jones index

We also estimated the linear slope of Bateman gradients using linear-mixed effects models. We used the same fixed and random effects as described above, with the exception of the observation level random effect. We calculated gradients using both relative (scaled to the mean) and absolute differences in reproductive success and mate numbers. We then calculated the Jones index ($s'max$) by multiplying the relative linear Bateman gradient (β_{ss}) by the square root of I_s (standardized variance in mating success; see below): $s'max = \beta_{ss} \times \sqrt{I_s}$ (Jones 2009; Henshaw et al. 2016). We used function `bootMer` (package `lme4`) to generate 95% confidence intervals (CI) for linear Bateman gradients and the Jones index. To establish whether statistically significant differences between estimates existed, we examined whether the 95% CI for the difference between estimates overlapped zero, when comparing 2 groups (e.g., males versus females). When comparing the 4 morph-sex classes, we examined whether the 98% CI for the differences between estimates overlapped zero, to account for multiple comparisons.

Standardized variance in reproductive success (I) and mating success (I_s), and partitioning of variance

We calculated the standardized variance in annual and lifetime reproductive success (I , the opportunity for selection) using the formula: $I = \text{Var}(\text{reproductive success})/(\text{mean success})^2$, and the standardized variance in annual and lifetime mating success (I_s , the opportunity for sexual selection via mate numbers) using the formula: $I_s = \text{Var}(\text{mating success})/(\text{mean success})^2$ (Wade and Arnold 1980; Kempenaers et al. 1992). For males, we partitioned the total variance in reproductive success ($\text{Var}(T)$, or I) into within-pair ($\text{Var}(W)$) and extrapair ($\text{Var}(E)$) components, where $\text{Var}(T) = \text{Var}(W) + \text{Var}(E) + 2 \text{Cov}(W, E)$ (Webster et al. 1995). To obtain standardized values for all components, we divided all components by the mean squared of total success. We additionally calculated the standardized variance in longevity to determine the potential for differences in longevity to contribute to variance in LRS.

To assess whether values differed significantly between classes of birds, we used nonparametric bootstrapping (R package `boot`; Davison and Hinkley 1997; Canty and Ripley 2016) to generate median \pm SE values and bias-corrected, accelerated (BCa) 95% CI. Statistical differences between groups were explored using 95% CIs, as described in the section above.

RESULTS

Extrapair paternity rates

Of 1532 genotyped nestlings, 241 (15.7%) were extrapair offspring. Out of 412 pairs (breeding attempts) that produced genotyped offspring, 30.6% (126) produced at least one extrapair offspring. We were able to assign 127 (52.7%) of the extrapair nestlings to an extrapair father. Our relatively low success in assigning extrapair fathers probably largely reflects the presence of unbanded males along the border of our study site, and unbanded males who did not establish permanent territories (floaters). Males from our population might also have sired offspring beyond the boundaries of the study area. Thus, our estimates of reproductive success and mate numbers represent a minimum for white males, which are cuckolded and pursue extrapair paternity at the highest rates.

Annual reproductive success and mate numbers

In both sexes and both morphs, annual reproductive success increased with mate numbers (Poisson GLMMs; Table 1, a–d). The

magnitude of this relationship not differ significantly between the morphs within either sex, as reflected by nonsignificant morph by mate number interaction terms (Table 1, a, b). However, the coefficient estimate was larger for white males than tan males (Table 1, e, f; Figure 1a,b), and for tan females than white females (Table 1, g, h; Figure 1c,d). Within the white morph, males had a significantly steeper gradient than females, as indicated by a significant sex \times mate number interaction term (Table 1, c). In contrast, within the tan morph, there was not a statistically significant difference between males versus females (nonsignificant interaction term; Table 1, d).

When all morph-sex classes were combined, the relationship between annual reproductive success and mate number was significantly larger in the white morph than the tan morph (interaction term: $\beta = 0.059 \pm 0.025$, $\chi^2 = 2.336$, $P = 0.019$), and in males than females (interaction term: $\beta = 0.090 \pm 0.027$, $\chi^2 = 3.324$, $P < 0.001$). White males drove these differences, displaying a stronger positive relationship than both white ($\beta = 0.293 \pm 0.092$, $\chi^2 = 3.197$, $P = 0.001$) and tan ($\beta = 0.195 \pm 0.060$, $\chi^2 = 3.264$, $P = 0.001$) females. In contrast, the relationship in tan males did not differ significantly from that found in either white ($\beta = 0.215 \pm 0.143$, $\chi^2 = 1.511$, $P = 0.131$) or tan ($\beta = 0.103 \pm 0.125$, $\chi^2 = 0.829$, $P = 0.407$) females.

In males, annual reproductive success was positively related to both the number of social mates (Poisson GLMM; $\beta = 0.863 \pm 0.231$, $\chi^2 = 3.740$, $P < 0.001$) and the number of extrapair mates ($\beta = 0.730 \pm 0.102$, $\chi^2 = 7.165$, $P < 0.001$). The interactions between morph, number of social mates ($\beta = -0.010 \pm 0.051$, $\chi^2 = -0.190$, $P = 0.849$) and number of extrapair mates ($\beta = 0.089 \pm 0.081$, $\chi^2 = 1.096$, $P = 0.273$) were nonsignificant, indicating no detectable morph differences. However, within the morphs, there were significant positive relationships between reproductive success and both social ($\beta = 0.836 \pm 0.329$, $\chi^2 = 2.543$, $P = 0.011$) and extrapair mate ($\beta = 0.797 \pm 0.119$, $\chi^2 = 6.713$, $P < 0.001$) numbers in white males, whereas only the relationship between social mates and reproductive success was significant in tan males ($\beta = 0.891 \pm 0.333$, $\chi^2 = 2.676$, $P = 0.007$). The relationship between extrapair mates and annual reproductive success was nonsignificant within tan males ($\beta = 0.243 \pm 0.409$, $\chi^2 = 0.594$, $P = 0.553$).

LRS and mate numbers

In both sexes and both morphs, LRS increased with mate numbers (Poisson GLMMs; Table 2, a–d), although this relationship was marginally nonsignificant within the tan morph. The relationship between LRS and mate number tended to be stronger in white males than tan males (Poisson GLMM; Table 2, a), and in tan females than white females (Table 2, b). These patterns were indicated by marginally nonsignificant interactions between average number of mates per year and morph (Table 2, a). Furthermore, the relationship between average number of mates and LRS was highly significant and positive in white males (Table 2, e), but nonsignificant in tan males (Table 2, f). However, when males that obtained no paternity with their social mate were coded as having zero rather than one social mates, the overall relationship became significant in tan males, due to an increase in the size of the gradient as determined by social mating success (Supplementary Material; Supplementary Table S3). The relationship between average number of mates per year and LRS was nonsignificant in white females (Table 2, g), but positive and significant in tan females (Table 2, h). Longevity was strongly related to LRS in all morph-sex classes (Table 2).

Table 1

GLMMs (Poisson distribution) describing the relationship between mate number and annual reproductive success in males and females (a, b), white morph birds and tan morph birds (c, d), white morph males versus tan morph males (e, f), and white morph females versus tan morph females (g, h)

Fixed effects	a) All males			b) All females		
	$\beta \pm SE$	Z	P	$\beta \pm SE$	Z	P
Intercept	0.503 ± 0.075	6.744	<0.001	0.971 ± 0.043	22.435	<0.001
Mates	0.304 ± 0.063	4.802	<0.001	0.135 ± 0.043	3.155	0.002
Morph	-0.262 ± 0.049	-5.396	<0.001	0.100 ± 0.039	2.535	0.011
Mates × morph	0.028 ± 0.063	0.063	0.653	-0.061 ± 0.043	-1.438	0.151
Random effects	Variance	SD	N	Variance	SD	N
Current year	0.037	0.191	18	0.019	0.138	18
Individual	0.087	0.296	277	<0.001	<0.001	222
Observation	0.505	0.711	601	0.213	0.462	415
	c) All whites	Z	P	d) All tans	Z	P
	$\beta \pm SE$			$\beta \pm SE$		
Intercept	0.635 ± 0.058	10.956	<0.001	0.855 ± 0.069	12.330	<0.001
Mates	0.224 ± 0.044	4.999	<0.001	0.247 ± 0.063	3.945	<0.001
Sex	-0.335 ± 0.045	-7.364	<0.001	0.063 ± 0.045	1.391	0.164
Mates × sex	0.139 ± 0.044	3.185	0.001	0.074 ± 0.063	1.178	0.239
Random effects	Variance	SD	N	Variance	SD	N
Current year	0.010	0.103	18	0.038	0.196	18
Individual	0.031	0.177	248	0.039	0.199	251
Observation	0.415	0.644	539	0.231	0.480	477
	e) White males	Z	P	f) Tan males	Z	P
	$\beta \pm SE$			$\beta \pm SE$		
Intercept	-0.711 ± 0.174	-4.084	<0.001	0.110 ± 0.286	0.386	0.700
Mates	0.809 ± 0.111	7.274	<0.001	0.630 ± 0.257	2.449	0.014
Random effects	Variance	SD	N	Variance	SD	N
Current year	0.002	0.042	17	0.050	0.223	18
Individual	0.059	0.243	147	0.072	0.268	130
Observation	0.652	0.807	340	0.339	0.583	261
	g) White females	Z	P	h) Tan females	Z	P
	$\beta \pm SE$			$\beta \pm SE$		
Intercept	0.880 ± 0.166	5.298	<0.001	0.459 ± 0.125	3.683	<0.001
Mates	0.142 ± 0.134	1.053	0.292	0.325 ± 0.065	5.012	<0.001
Random effects	Variance	SD	N	Variance	SD	N
Current year	0.008	0.092	18	0.021	0.144	17
Individual	<0.001	<0.001	101	0.016	0.126	121
Observation	0.233	0.484	199	0.140	0.374	216

Within the white morph, the Bateman gradient for LRS was stronger in males than in females, as indicated by a significant interaction term (Table 1, c). In contrast, the Bateman gradient for LRS did not differ significantly between tan males and females (Table 1, d).

With all morph-sex classes combined, the relationship between LRS and mate numbers did not differ between the morphs (interaction term: $\beta = 0.05 \pm 0.05$, $Z = 0.975$, $P = 0.329$), but was larger in males than females ($\beta = 0.11 \pm 0.05$, $Z = 2.18$, $P = 0.029$). This pattern was driven by differences between white males as compared to both tan ($\beta = 0.64 \pm 0.24$, $Z = 2.67$, $P = 0.007$) and white females ($\beta = 1.05 \pm 0.26$, $Z = 3.97$, $P = <0.001$). In contrast, the relationship in tan males did not differ significantly from that found in either tan ($\beta = -0.060 \pm 0.38$, $Z = -0.16$, $P = 0.875$) or white females ($\beta = 0.25 \pm 0.39$, $Z = 0.651$, $P = 0.515$), as assessed by interaction terms.

Social (average per year) ($\beta = 1.12 \pm 0.37$, $Z = 3.02$, $P = 0.002$) and extrapair ($\beta = 0.78 \pm 0.24$, $Z = 3.26$, $P = 0.001$) mate numbers were positively related to LRS across all males. The interactions between both social ($\beta = 0.10 \pm 0.07$, $Z = 1.35$, $P = 0.174$) and extrapair ($\beta = 0.13 \pm 0.07$, $Z = 1.64$, $P = 0.100$) mates and morph were nonsignificant, indicating no statistically significant morph differences. However, in white males, we found significant, positive

relationships for both social ($\beta = 1.63 \pm 0.58$, $Z = 2.79$, $P = 0.005$) and extrapair ($\beta = 0.96 \pm 0.26$, $Z = 3.68$, $P = <0.001$) mate numbers. In contrast, in tan males, neither social ($\beta = 0.65 \pm 0.47$, $Z = 1.37$, $P = 0.172$) nor extrapair ($\beta = -0.26 \pm 0.64$, $Z = -0.40$, $P = 0.688$) mate numbers were significantly related to LRS. However, when tan males that achieved no reproductive success with their social mates were coded as having obtained zero mates, the relationship for social mate numbers became significant within tan males (Supplementary Material; Supplementary Table S4).

Linear Bateman gradients, standardized variance in mate numbers (I_s), and the Jones index

The absolute and relative linear (β_s) Bateman gradients, and the Jones index for annual reproductive success were larger in males than in females, but did not differ between the morphs (Table 3, a). When comparing the morph-sex classes, the absolute and relative linear Bateman gradients for annual reproductive success were larger in white males than in both morphs of females, but did not differ significantly between white and tan males (this was also true for gradients calculated using extrapair and social mate numbers), or between tan males as compared to females of either morph (Table 3, a; Figure 1a–d). Standardized variance in annual mate numbers (I_s) was higher in white males and tan females than

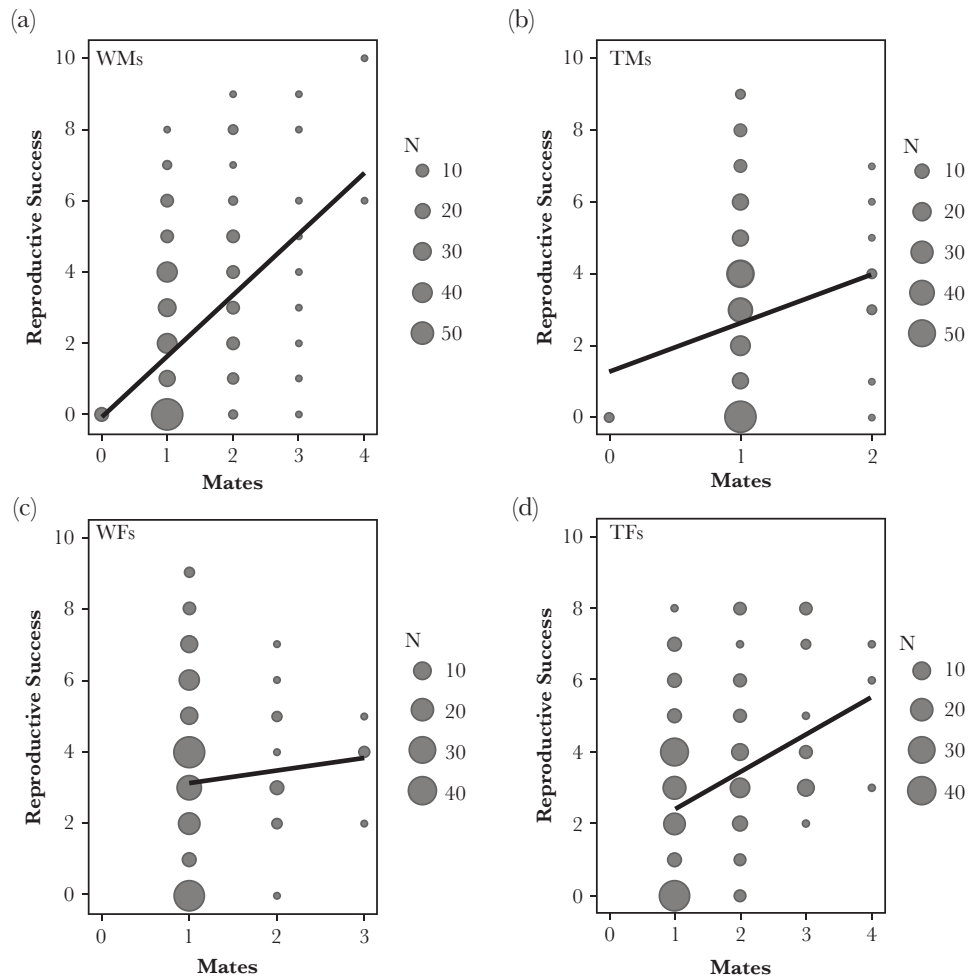


Figure 1 Linear Bateman gradients for annual reproductive success across the sexes and morphs of the white-throated sparrow. WM = white males (a), TM = tan males (b), WF = white females (c), TF = tan females (d).

in tan males and white females, reflecting the greater prevalence of extrapair mating among white male by tan female pairs. I_s was also higher in white females than in tan males, but did not differ between the 2 sexes or the 2 morphs. Thus, the Jones index, which corrects the relative Bateman gradient for variance in mate numbers, was greater in white males than in tan males and white females, but did not differ between the other morph-sex classes (Table 3, a).

The absolute and relative linear Bateman gradients for LRS were greater in white males than in white females, but did not significantly differ between the sexes, the morphs, or the other morph-sex classes (Table 3, b; Figure 2a–d). However, the relative Bateman gradient for LRS and extrapair mate numbers was greater in white males than in tan males. I_s for LRS was higher in females than in males, but did not differ between the morphs. I_s was lower in tan males than in all other morph-sex classes, and higher in tan females than all other morph-sex classes, but did not differ between white males and white females. The Jones index for LRS was greater in white males than in tan males and white females, and also greater in tan females than in white females, but did not differ between the sexes, the morphs, or tan males as compared to females of either morph (Table 3, b).

Standardized variance in reproductive success (I) and partitioning of variance in reproductive success

The overall opportunity for selection (I ; standardized variance in reproductive success) was significantly higher in white males than in tan males and both morphs of females (Table 4, a). In contrast, the values for tan males, white females, and tan females did not differ significantly. Furthermore, a greater proportion of variance in annual reproductive success was attributable to extrapair performance in white males than tan males (Table 4, a). However, for males of both morphs, the amount of variance in annual reproductive success that was related to within-pair performance was much higher than the amount related to extrapair mating. Moreover, although the actual amount of variance in reproductive success (taking extrapair mating into account) was slightly greater than the apparent variance (based on number of social fledglings) in white males, this effect was very marginal, with 95% CIs overlapping (Table 4, a). Covariation between annual within- and extrapair mating success was low in males of both morphs (Table 4, a).

As for annual reproductive success, a greater proportion of variance in LRS was related to extrapair mating in white males than in tan males. However, standardized variance in LRS (I) did not differ significantly between white and tan males, actually being slightly

Table 2

GLMMs (Poisson distribution) describing the relationship between the average number of mates per breeding season and lifetime reproductive success in males and females (a, b), white morph birds and tan morph birds (c, d), white morph males versus tan morph males (e, f), and white morph females versus tan morph females (g, h)

Fixed effects	a) All males			b) All females		
	$\beta \pm SE$	Z	P	$\beta \pm SE$	Z	P
Intercept	0.41 ± 0.11	3.73	<0.001	0.69 ± 0.09	7.36	<0.001
Average mates/year	0.20 ± 0.07	2.94	0.003	0.12 ± 0.05	2.39	0.016
Morph	-0.23 ± 0.06	-4.10	<0.001	0.09 ± 0.05	1.82	0.063
Breeding years	0.36 ± 0.02	12.64	<0.001	0.40 ± 0.03	11.86	<0.001
Mates × morph	0.11 ± 0.07	1.66	0.096	-0.10 ± 0.05	-1.87	0.061
Random effects	Variance	SD	N	Variance	SD	N
First Year	<0.001	<0.001	17	<0.001	<0.001	17
Observation	0.325	0.570	189	0.184	0.429	180
	c) All whites			d) All tans		
Fixed effects	$\beta \pm SE$	Z	P	$\beta \pm SE$	Z	P
Intercept	0.647 ± 0.102	6.319	<0.001	0.493 ± 0.107	4.596	<0.001
Average mates/year	0.203 ± 0.051	3.949	<0.001	0.189 ± 0.100	1.886	0.059
Sex	-0.278 ± 0.055	-5.066	<0.001	0.028 ± 0.063	0.442	0.658
Breeding years	0.333 ± 0.028	11.868	<0.001	0.444 ± 0.033	13.206	<0.001
Mates × sex	0.203 ± 0.052	3.946	<0.001	-0.016 ± 0.099	-0.162	0.871
Random effects	Variance	SD	N	Variance	SD	N
First Year	0	0	17	0	0	17
Observation	0.258	0.508	185	0.226	0.475	184
	e) White males			f) Tan males		
Fixed effects	$\beta \pm SE$	Z	P	$\beta \pm SE$	Z	P
Intercept	-0.88 ± 0.31	-2.77	0.005	0.17 ± 0.44	0.396	0.692
Average mates/year	1.10 ± 0.23	4.77	<0.001	0.32 ± 0.38	0.831	0.406
Breeding years	0.33 ± 0.03	8.65	<0.001	0.42 ± 0.04	9.71	<0.001
Random effects	Variance	SD	N	Variance	SD	N
First Year	<0.001	<0.001	16	<0.001	<0.001	17
Observation	0.344	0.586	103	0.269	0.519	86
	g) White females			h) Tan females		
Fixed effects	$\beta \pm SE$	Z	P	$\beta \pm SE$	Z	P
Intercept	0.91 ± 0.23	3.85	<0.001	-0.07 ± 0.21	-0.34	0.743
Average mates/year	0.004 ± 0.15	0.03	0.975	0.38 ± 0.09	4.06	<0.001
Breeding years	0.35 ± 0.04	8.25	<0.001	0.49 ± 0.05	9.20	<0.001
Random effects	Variance	SD	N	Variance	SD	N
First Year	<0.001	<0.001	16	<0.001	<0.001	98
Observation	0.171	0.413	82	0.163	0.403	16

higher in tan males (Table 4, b). There was also no significant difference in variance in LRS between males and females. Apparent variance in LRS was not significantly different than actual variance in LRS for males of either morph, and white males actually displayed slightly lower actual than apparent variance in LRS. For males of both morphs, within-pair variance in LRS accounted for a much greater proportion of total variance than did extrapair variance in LRS (Table 4, b).

Standardized variance in longevity did not differ significantly between any of the morph-sex classes (Table 4, b).

DISCUSSION

How extrapair mating affects the magnitude of sexual selection in species with predominately monogamous social systems remains a contentious question (Freeman-Gallant et al. 2005; Schlicht and Kempenaers 2013). Our study yielded a combination of expected and unexpected results, which in combination shed light on this issue. First, although morph by mate number interaction terms fell short of significance in statistical models, comparisons of Bateman gradients and Jones indexes suggested a greater potential for sexual selection via mate numbers in white than tan males, as expected given the higher level of promiscuity, brighter coloration, higher

song rates (Tuttle 2003; Rathbun et al. 2014), and higher testosterone levels of white males (Spinney et al. 2006; Maney 2008; Swett and Breuner 2009). In white males, both extrapair and social mating success significantly contributed to a positive Bateman gradient, and results were similar when considering either LRS or annual performance. In contrast, in tan males, the Bateman gradient was nonsignificant for LRS, and for annual performance only the number of social mates contributed to a positive Bateman gradient. Moreover, the Jones index (s'_{max}), which refines the Bateman gradient by taking variance in mating success (I_s) into account, was significantly larger for white males than for tan males, on both the annual and lifetime scales. These results corroborate past studies that suggest that extrapair mating can strengthen the potential for sexual selection via mate numbers in socially monogamous species (Webster et al. 2007; Poesel et al. 2011), but also suggest that social mating success strongly contributes to sexual selection in this system.

As expected, females had shallower Bateman gradients and lower variance in reproductive success than males, suggesting greater potential for sexual selection via mate numbers in males than females. However, variance in mating success (I_s) was actually higher in females than in males. As a result, the Jones index did not differ between males and females when considering LRS, and did

Table 3

Variance in mate numbers (I_s), the linear slope of the Bateman Gradient (absolute: β_a ; relative: β_{ss}), and the Jones Index (s'_{\max}), calculated on the annual (a ; ARS) and lifetime (b ; LRS) scales

(a) ARS	Males	WMs	TMs	Females	WFs	TFs	Whites	Tans
β_a	1.609 ± 0.195 ¹ (1.227, 1.989)	1.736 ± 0.193 ^a (1.365, 2.114)	1.458 ± 0.630 ^{ab} (0.237, 2.682)	0.765 ± 0.180 ² (0.414, 1.117)	0.447 ± 0.414 ^b (-0.409, 1.238)	1.037 ± 0.191 ^b (0.657, 1.420)	1.458 ± 0.190 ¹ (1.081, 1.832)	0.957 ± 0.177 ¹ (0.607, 1.315)
β_{ss}	0.744 ± 0.088 ¹ (0.567, 0.920)	0.805 ± 0.087 ^a (0.631, 0.977)	0.678 ± 0.287 ^{ab} (0.109, 1.240)	0.354 ± 0.081 ² (0.191, 0.516)	0.198 ± 0.190 ^b (-0.189, 0.572)	0.480 ± 0.089 ^b (0.304, 0.656)	0.675 ± 0.089 ¹ (0.500, 0.847)	0.445 ± 0.080 ¹ (0.281, 0.608)
I_s	0.159 ± 0.019 ¹ (0.129, 0.208)	0.218 ± 0.026 ^a (0.176, 0.284)	0.045 ± 0.011 ^b (0.026, 0.074)	0.221 ± 0.018 ¹ (0.189, 0.263)	0.123 ± 0.027 ^c (0.078, 0.185)	0.243 ± 0.020 ^a (0.211, 0.292)	0.180 ± 0.018 ¹ (0.149, 0.226)	0.196 ± 0.019 ¹ (0.162, 0.241)
s'_{\max}	0.299 ± 0.036 ¹ (0.204, 0.420)	0.378 ± 0.041 ^a (0.265, 0.521)	0.145 ± 0.065 ^b (0.018, 0.337)	0.167 ± 0.039 ² (0.083, 0.265)	0.070 ± 0.066 ^b (-0.052, 0.246)	0.238 ± 0.045 ^{ab} (0.139, 0.354)	0.284 ± 0.036 ¹ (0.193, 0.402)	0.196 ± 0.036 ¹ (0.113, 0.298)
β_a (WP)	1.555 ± 0.449 (0.669, 2.401)	1.099 ± 0.493 ^a (0.092, 2.085)	2.092 ± 0.814 ^a (0.572, 3.669)					
β_{ss} (WP)	0.606 ± 0.175 (0.274, 0.942)	0.429 ± 0.203 ^a (0.036, 0.818)	0.820 ± 0.319 ^a (0.224, 1.441)					
β_a (EP)	1.687 ± 0.231 (1.242, 2.139)	1.972 ± 0.220 ^a (1.548, 2.401)	0.351 ± 1.036 ^a (-1.614, 2.413)					
β_{ss} (EP)	0.110 ± 0.015 (0.081, 0.139)	0.128 ± 0.015 ^a (0.101, 0.156)	0.027 ± 0.067 ^a (-0.105, 0.157)					
(b) LRS	Males	WMs	TMs	Females	WFs	TFs	Whites	Tans
β_a	2.213 ± 0.921 ¹ (0.376, 3.987)	3.603 ± 0.910 ^a (1.911, 5.401)	0.764 ± 1.999 ^{ab} (-2.796, 4.512)	0.928 ± 0.356 ¹ (0.255, 1.613)	-0.044 ± 0.076 ^b (-1.415, 1.352)	1.520 ± 0.374 ^{ab} (0.797, 2.275)	1.429 ± 0.605 ¹ (0.218, 2.616)	1.401 ± 0.423 ¹ (0.586, 2.233)
β_{ss}	0.461 ± 0.220 ¹ (0.078, 0.830)	0.759 ± 0.190 ^a (0.398, 1.120)	0.178 ± 0.402 ^{ab} (-0.582, 0.939)	0.193 ± 0.071 ¹ (0.053, 0.333)	-0.006 ± 0.145 ^b (-0.293, 0.279)	0.319 ± 0.079 ^{ab} (0.165, 0.473)	0.290 ± 0.126 ¹ (0.0455, 0.544)	0.293 ± 0.088 ¹ (0.122, 0.465)
I_s	0.086 ± 0.016 ¹ (0.061, 0.128)	0.116 ± 0.025 ^a (0.078, 0.184)	0.045 ± 0.017 ^b (0.020, 0.099)	0.205 ± 0.022 ² (0.169, 0.261)	0.163 ± 0.039 ^a (0.100, 0.252)	0.208 ± 0.026 ^c (0.173, 0.286)	0.133 ± 0.024 ¹ (0.095, 0.192)	0.186 ± 0.026 ¹ (0.142, 0.249)
s'_{\max}	0.039 ± 0.016 ¹ (0.019, 0.297)	0.088 ± 0.021 ^a (0.111, 0.480)	0.008 ± 0.018 ^{bc} (-0.082, 0.295)	0.040 ± 0.014 ¹ (0.022, 0.170)	-0.001 ± 0.020 ^c (-0.093, 0.140)	0.067 ± 0.017 ^{ab} (0.069, 0.253)	0.131 ± 0.009 ¹ (0.014, 0.238)	0.128 ± 0.056 ¹ (0.046, 0.232)
β_a (WP)	3.107 ± 1.467 (0.291, 5.806)	2.698 ± 1.615 ^a (-0.382, 5.995)	2.247 ± 2.295 ^a (-2.157, 6.682)					
β_{ss} (WP)	0.534 ± 0.249 (0.049, 0.994)	0.477 ± 0.282 ^a (-0.065, 1.026)	0.383 ± 0.399 ^a (-0.369, 1.145)					
β_a (EP)	1.505 ± 1.231 (-0.849, 4.005)	4.729 ± 1.180 ^a (2.456, 7.105)	-2.004 ± 3.168 ^a (-8.220, 4.272)					
β_{ss} (EP)	0.058 ± 0.046 (-0.031, 0.148)	0.176 ± 0.043 ^a (0.090, 0.262)	-0.009 ± 0.017 ^b (-0.304, 0.158)					

For each variable, we provide the mean ± SE (top line) and 95% CIs.

Superscript numbers indicate whether males and females or the white and tan morph significantly differ.

Superscript letters indicate whether each morph-sex class significantly differ.

WM = white males; TM = tan males; WF = white females; TF = tan females.

not differ between white males and tan females on either annual or lifetime scales. We found a tendency towards a stronger Bateman gradient in tan females than white females, and tan females had a larger Jones index for LRS than did white females, likely because tan females are the primary recipients of extrapair matings.

The Bateman gradient and Jones index in tan females were positive for both annual performance and LRS, which is consistent with a benefit of multiple mating to tan females, as also suggested by empirical results from some other species (Foerster et al. 2003; Suter et al. 2007). However, this positive relationship could also arise because white males seeking EPCs preferentially target higher quality tan females (Collet et al. 2014). Furthermore, for females, the probability of detecting extrapair mates increases with the number of offspring genotyped, which may lead to a positive relationship between reproductive success and number of mates through statistical artifact (Gerlach et al. 2012; Collet et al. 2014). Thus, determining the biological significance of the positive Bateman gradient in tan females will require additional scrutiny.

Analyses revealed no differences in the Bateman gradient or Jones index for LRS between the morphs, suggesting no overall difference in selection for mate numbers between the morphs. However, whereas tan males and females did not differ in Bateman

gradients or the Jones index, white males displayed a significantly more positive gradient and larger Jones index than white females. The difference in extrapair mating behavior between white and tan males is presumably controlled by the morph-determining supergene, which is shared by white males and females (Tuttle et al. 2016). Thus, because high numbers of mates appear to be favored only in white males, evolutionary sexual conflict over genes controlling mate numbers could result within the white morph (Parker 2006). Indeed, past studies have suggested that extrapair mating behavior in females reflect nonadaptive genetic correlation with males (Halliday and Arnold 1987; Forstmeier et al. 2014). However, elevated extrapair mating rates are observed in white males but not white females, with extrapair offspring actually much more common in tan than white females. This suggests that the potential evolutionary conflict over mate numbers within the white morph has been at least partially resolved, perhaps through a combination of sex-specific expression of underlying genes and the behavioral dynamics of the system. In fact, white females copulate at higher rates than tan females, but these copulations are restricted to within the social pair bond (Tuttle 2003). Thus, shared genes controlling mating rate, which may be located within the supergene, may be expressed in different ways in the 2 sexes, ameliorating sexual conflict.

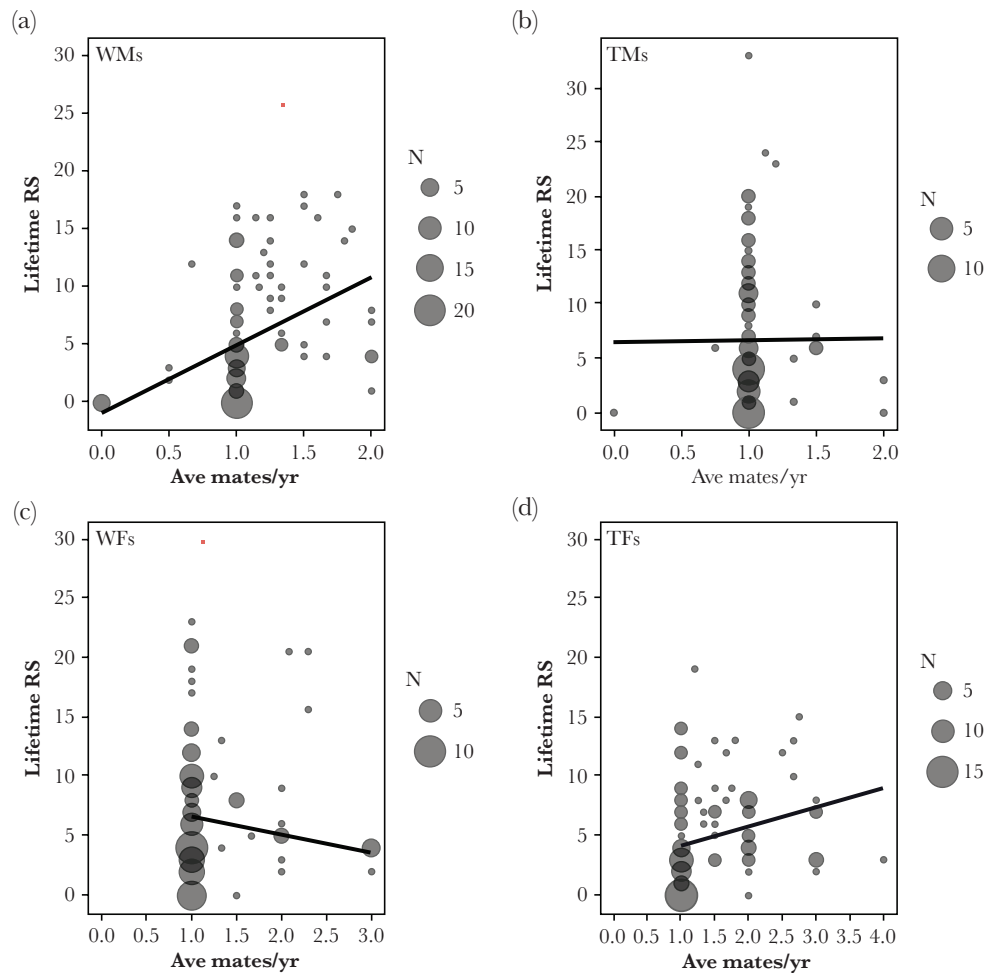


Figure 2

Linear Bateman gradients for lifetime reproductive success (RS) across the sexes and morphs of the white-throated sparrow. WM = white males (a), TM = tan males (b), WF = white females (c), TF = tan females (d).

Our examination of standardized variance in reproductive success (I) revealed some less expected results. Specifically, in male white-throated sparrows, we found that one of [Bateman's \(1948\)](#) central predictions does not hold on the scale of a lifetime; elevated extrapair mating rates do not increase variance in LRS. When considering LRS, standardized variance (I) did not differ significantly between males of the 2 morphs, or between males and females. On the other hand, for annual reproductive success, standardized variance was higher in white males than in tan males or females of either morph, as expected. These results suggest that, across a lifespan, the same white males are not consistently successful in achieving high levels of annual reproductive success, lowering variance in LRS relative to within-year patterns. Lack of consistency in the reproductive success of individual white males could arise through a variety of mechanisms, for instance inconsistent female preferences in the context of either social or extrapair mating ([Reid and Weatherhead 1990](#); [Whittingham et al. 2006](#); [Chaine and Lyon 2008](#)), between-year reproductive tradeoffs ([Low et al. 2015](#)), or context-dependency in individual performance ([Dingemanse et al. 2004](#)). Relatively few studies utilize lifetime fitness data when examining how extrapair mating affects variance in reproductive success. Our results suggest that considering within-year patterns alone may lead to overestimation of the effect of extrapair mating

on variance in lifetime reproductive success, although underestimation could also feasibly occur in cases where reproductive performance does remain consistent across years. Moreover, comparing actual to apparent reproductive success also suggested a limited role for extrapair mating in increasing variance in reproductive success. Extrapair paternity did not significantly increase standardized variance in reproductive success (I), and most of the variance in annual and lifetime reproductive success was attributable to within-pair rather than extrapair performance.

In contrast to our results, in a population of the closely related white-crowned sparrow (*Zonotrichia leucophrys*), extrapair mating increased standardized variance in reproductive success 9 times above variance in apparent success ([Poesel et al. 2011](#)). Relative to white-crowned sparrows, the “four sexes” social system of white-throated sparrows could substantially lower the effect of extrapair mating on variance in reproductive success by reducing the number of potential mating partners available to white males. Indeed, in white-throated sparrows, roughly half of the females in the population, namely white females, are largely inaccessible for extrapair matings. Why low rates of extrapair mating occur in white females is not completely clear, but is probably due to the intense mate-guarding behavior of tan males combined with the behavioral characteristics of white females ([Tuttle 2003](#)).

Table 4
Opportunity for selection (*I*) and partitioning of variance in reproductive success, for (a) annual reproductive success (ARS), and (b) lifetime reproductive success (LRS) and longevity in different morph-sex classes

a) ARS	Males	WMs	TMs	Fems	WFs	TFs	Whites	Tans
Var(T_a)	0.874 ± 0.06 (0.771, 1.01)	1.029 ± 0.09 (0.858, 1.238) ^a	0.711 ± 0.07 (0.586, 0.876) ^b					
Var(T) — <i>I</i>	1.005 ± 0.07 ¹ (0.876, 1.15)	1.249 ± 0.11 ^a (1.049, 1.518)	0.754 ± 0.08 ^b (0.619, 0.934)	0.543 ± 0.04 ² (0.462, 0.639)	0.522 ± 0.06 ^b (0.415, 0.672)	0.557 ± 0.06 ^b (0.453, 0.700)	0.919 ± 0.067 ¹ (0.798, 1.065)	0.661 ± 0.050 ² (0.571, 0.772)
Var(W)	0.916 ± 0.06 (0.797, 1.05)	0.984 ± 0.09 ^a (0.821, 1.19)	0.753 ± 0.08 ^a (0.622, 0.928)					
Var(E)	0.090 ± 0.01 (0.063, 0.131)	0.191 ± 0.03 ^a (0.137, 0.283)	0.009 ± 0.005 ^b (0.002, 0.029)					
Cov(W , E)	0.002 ± 0.01 (-0.016, 0.026)	0.045 ± 0.02 ^a (0.001, 0.102)	-0.004 ± 0.005 ^a (-0.019, 0.002)					
b) LRS	Males	WMs	TMs	Fems	WFs	TFs	Whites	Tans
Var(T_a)	0.954 ± 0.10 (0.788, 1.21)	0.947 ± 0.14 ^a (0.739, 1.30)	0.957 ± 0.16 ^a (0.732, 1.38)					
Var(T) — <i>I</i>	0.959 ± 0.12 ¹ (0.791, 1.25)	0.897 ± 0.13 ^a (0.693, 1.21)	0.993 ± 0.16 ^a (0.772, 1.46)	0.752 ± 0.08 ¹ (0.610, 0.955)	0.686 ± 0.11 ^a (0.527, 0.986)	0.761 ± 0.11 ^a (0.587, 1.05)	0.807 ± 0.085 ¹ (0.659, 0.999)	0.962 ± 0.119 ¹ (0.770, 1.256)
Var(W)	0.842 ± 0.11 (0.682, 1.13)	0.639 ± 0.10 ^a (0.477, 0.894)	0.975 ± 0.16 ^a (0.753, 1.46)					
Var(E)	0.043 ± 0.001 (0.026, 0.066)	0.079 ± 0.01 ^a (0.053, 0.121)	0.004 ± 0.002 ^b (0.001, 0.012)					
Cov(W , E)	0.036 ± 0.014 (0.012, 0.070)	0.087 ± 0.02 ^a (0.044, 0.143)	0.005 ± 0.01 ^a (-0.007, 0.053)					
Var(longevity)	0.529 ± 0.048 ¹ (0.453, 0.650)	0.533 ± 0.06 ^a (0.437, 0.697)	0.488 ± 0.06 ^a (0.398, 0.652)	0.470 ± 0.06 ¹ (0.375, 0.668)	0.513 ± 0.11 ^a (0.346, 0.800)	0.400 ± 0.04 ^a (0.331, 0.506)	0.366 ± 0.019 ¹ (0.331, 0.409)	0.361 ± 0.021 ¹ (0.322, 0.406)

For each variable, we provide the mean ± SE (top) and 95% confidence intervals (bottom).
 Superscript numbers indicate whether males and females or the white and tan morph significantly differ.
 Superscript letters indicate whether each morph-sex class are significantly different.
 white-throated.
 WM = white males; TM = tan males; WF = white females; TF = tan females.

White females are more aggressive than tan females (Kopachena and Falls 1993a), and might thus better resist extrapair matings. Past studies showing complete control of passerine females over copulation success cast some doubt on this hypothesis (Forstmeier 2004, 2007). However, less aggressive tan females, but not white females, could accept extrapair partners to avoid harassment and injury (Gowaty and Buschhaus 1998; Westneat and Stewart 2003). White females could also be less receptive to EPCs than tan females, because they risk sacrificing the superior paternal support of tan males through promiscuity (Dixon et al. 1994; Hoi-Leitner et al. 1999).

Standardized variance in longevity did not differ significantly between any of the classes of birds, and thus did not contribute to equalizing variance in LRS between the different morph-sex classes. Thus, our findings are not consistent with the hypothesis that the morph-sex classes are subject to opposing patterns of viability versus fecundity selection (Schluter et al. 1991; Tarwater and Beissinger 2013; Bleu et al. 2016), with promiscuous white males selected for a rapid reproductive rate, but tan males subject to viability selection. Nonetheless, variance in LRS may be generated through different mechanisms in the different morph-sex classes. As discussed above, LRS is related to mate numbers in white males, but not in tan males. Instead, mate quality, as determined by fecundity, parental ability, or resource holding capacity could contribute to variance in LRS in tan males, but more research is needed to explore this possibility. Importantly, because mate quality as well as mate numbers can generate sexual selection (Kirkpatrick et al. 1990), this variance has the potential to contribute to sexual selection.

Indeed, individuals that pursue alternative reproductive strategies are likely to be subject to different forms of sexual selection. For instance, “sneaker” males are often selected for sperm quality and effective fertilization capacity via postcopulatory mechanisms, rather than for the capacity to obtain multiple mates via precopulatory mechanisms (Parker 1990; Simmons and Fitzpatrick 2012; Young et al. 2013). Males that provide high levels of paternal care may also be selected to obtain high quality mates and retain paternity, rather than to mate with many females (Burley 1977; Edward and Chapman 2011). Bateman gradients and Jones indexes can only describe variation in reproductive success due to mate numbers, and thus cannot quantify the magnitude of these different potential forms of sexual selection.

As is the case for other species that exhibit alternative reproductive morphs (Gross 1996; Sinervo and Lively 1996; Küpper et al. 2016), the evolution and coexistence of the 2 morphs in the white-throated sparrow is probably promoted by the existence of dramatically different reproductive strategies, which are associated with divergent patterns of selection on mating and reproductive phenotypes (Tuttle 2003; Tuttle et al. 2016). Furthermore, mating is almost exclusively disassortative in this species, seemingly due to deleterious effects of white morph × white morph matings, and behavioral incompatibilities within same morph pairs (Tuttle et al. 2016). Thus, as required for the stable coexistence of fixed reproductive strategies within populations (Taborsky et al. 2008), the coexistence of the morph-sex types is likely promoted by negative-frequency dependent selection, with rarer types enjoying a fitness advantage due to the greater availability of compatible mating partners and the rarity of same-type competitors.

As a caveat, our relatively low levels of paternity assignment could introduce some inaccuracy into our analyses. Unfortunately, how low levels of paternity assignment affect calculated Bateman gradients, Jones indexes, and standardized variance in reproductive success (I) depends on which type of (i.e., breeders vs. floaters), and how many, unknown males are obtaining unassigned paternity, and is thus impossible to precisely predict (Schlicht and Kempenaers 2013). However, our analysis probably overestimates the effect of extrapair paternity on I (Freeman-Gallant et al. 2005), because low levels of paternity assignment are usually associated with an underestimation of mean reproductive success, which inflates the standardized variance estimate. It is also possible that low rates of paternity assignment could lead to underestimation of I (and the Bateman gradient associated with extrapair mating success), for instance if we failed to include a small number of highly successful, extrapair males in our dataset. However, across studies, Freeman-Gallant et al. (2005) reported a negative correlation between levels of paternity assignment and calculated values of I , suggesting that an overestimation is the more likely scenario. Thus, the effect of extrapair mating on variance in reproductive success and Bateman gradients may be even lower than indicated by our calculations, suggesting a strong role for within-pair performance in driving patterns of selection, even in the promiscuous white morph.

Another issue that could have affected calculated Bateman gradients is the method that we employed to assign social mates to males. We assigned social mating success to an individual male even if he obtained no paternity with his social mate. This procedural decision was based on the idea that males likely mate with their social partner even if these matings are not reflected by genetic analyses. However, an alternative approach is to assign zero social mating success in cases in which no social paternity is detected. We reanalyzed our data to assess how adopting this second approach would affect results. As is logical, assigning a social mating success of zero to males that obtained no social paternity had the effect of increasing the coefficient estimate associated with the number of mates, and magnifying the Bateman gradient. This magnification caused the relationships between lifetime reproductive success and the average number of total mates and social mates per season to become statistically significant in tan morph males, whereas these relationships were previously nonsignificant. Our other results were not qualitatively altered. It is not entirely clear which approach for assigning mate numbers results in a more valid estimate of the potential strength of sexual selection. On the one hand, our first approach might underestimate the slope of the Bateman gradient if males that failed to gain social paternity did not mate with their social partner. On the other hand, the second approach might overestimate the strength of the gradient if the males actually did mate with their social partner. We find this latter contingency most likely, based on observations of social pairs, which suggest that copulations are an important part of social dynamics, especially during the nest-building period.

We also acknowledge that the metrics used in this study, namely the Bateman gradient, Jones index and standardized variance measures, have a limited capacity to predict the actual strength of sexual selection (Klug et al. 2010; Henshaw et al. 2016). Indeed, using these metrics does not allow conclusions about the actual strength of sexual selection on specific phenotypic traits or underlying genotypes, which requires selection gradient analysis (e.g., Jones et al. 2004; Westneat 2006; Kelly et al. 2008). However, the methods applied here do give valuable information about the overall potential for whole-phenotype

sexual selection. Moreover, as recommended by experts in the field (Jones 2009; Klug et al. 2010), we have calculated multiple metrics of the potential strength of selection, to enhance our ability to draw inferences about the strength and dynamics of sexual selection in our system.

In summary, our study supports the hypothesis that morph-specific reproductive strategies, characterized especially by differences in extrapair mating rates, lead to different patterns of sexual selection. In the white-throated sparrow, promiscuous white males experience greater potential for sexual selection via mate numbers, especially via extrapair mating, than more highly parental tan males. However, variance in lifetime reproductive success is not higher in white males than in tan males or females. Thus, we cannot preclude sexual selection via mate quality in females and tan males that could be similarly strong to that via mate numbers in white males. Moreover, extrapair paternity increased variance in reproductive success relatively little, indicating that most variance in reproductive success is attributable to performance within the social pair, even for white males. Future work should aim to better quantify the strength of sexual selection acting through avenues other than mate number, which will clarify the importance of extrapair paternity in generating patterns of sexual selection, and require analytical approaches other than the Bateman gradient and Jones Index.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Grunst, Grunst, Korody, et al. (2018b).

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