# Morph-Specific Patterns of Reproductive Senescence: Connections to Discrete Reproductive Strategies

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ABSTRACT: How reproductive strategies contribute to patterns of senescence in natural populations remains contentious. We studied reproductive senescence in the dimorphic white-throated sparrow, an excellent species for exploring this issue. Within both sexes the morphs use distinct reproductive strategies, and disassortative pairing by morph results in pair types with distinct parental systems. White morph birds are more colorful and aggressive than tan counterparts, and white males compete for extrapair matings, whereas tan males are more parental. Tan males and white females share parental care equally, whereas white males provide little parental support to tan females. We found morph-specific patterns of reproductive senescence in both sexes. White males exhibited greater reproductive senescence than tan males. This result likely reflects the difficulty of sustaining a highly competitive reproductive strategy as aging progresses rather than high physiological costs of competitiveness, since white males were also long-lived. Moreover, morph was not consistently related to reproductive senescence across the sexes, arguing against especially high costs of the traits associated with white morph identity. Rather, tan females exhibited earlier reproductive senescence than white females and were short-lived, perhaps reflecting the challenges of unsupported motherhood. Results underscore the importance of social dynamics in determining patterns of reproductive senescence.

*Keywords:* senescence, reproductive strategies, parental care, genetic polymorphism, life history.

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## Introduction

Senescence, or the gradual deterioration of performance with age, places critical limits on lifetime fitness and has been increasingly documented in nonhuman populations. A recent review identified 340 studies from 175 species that provide evidence for senescence in free-living populations (Nussey et al. 2013). However, quantifying senescence requires tracking marked individuals over long periods of time and determining reproductive success across the life span and thus remains challenging in the field (Nussey et al. 2008; Bouwhuis et al. 2009, 2012). Due to practical difficulties, work on mechanisms of senescence remains dominated by laboratory-based studies. These studies yield incomplete conclusions about patterns of senescence and underlying causal factors, due to the absence of natural social and environmental challenges (Monaghan et al. 2008; Briga and Verhulst 2015).

Life history–based theories predict that reproductive strategies and behavioral traits are critically connected to rates of senescence (Williams 1957; Kirkwood 1977; Nussey et al. 2013). Individuals who invest intensely in reproduction may suffer a "cost of reproduction," jeopardizing somatic maintenance and accelerating system-wide senescence, as manifest by deterioration of body condition, performance, and survivorship with age. For instance, experimentally increasing parental effort through brood size manipulations can increase rates of molecular aging as indicated by telomere dynamics (Reichert et al. 2014) and accelerate actuarial senescence, or the increase in mortality rate with age (Boonekamp et al. 2014). Costs of reproduction may also affect rates of reproductive senescence, or the decline in reproductive performance with age. For example, male houbara buzzards (*Chlamydotis undulata*) who invest more into extravagant sexual

displays exhibit faster rates of senescence in sperm quality (Preston et al. 2011), and female red deer with higher early-life fecundity show faster senescent declines in maternal performance traits (Nussey et al. 2006).

A common conception is that the competitive reproductive strategy of males is more costly than the more parental strategy of females, promoting a "live fast die young" strategy and higher rates of senescence (Bondurianksy et al. 2008). However, empirical data lend equivocal support to this hypothesis (Lemaître and Gaillard 2013), with some studies suggesting that parental care is more costly than investment into sexually selected competitive traits or displays (Owens and Bennett 1994). Thus, the relative costs and life-history implications of competition for mates versus parental care remains an outstanding question (Liker and Székely 2005; Tidiére et al. 2015).

Furthermore, system-wide senescence and reproductive senescence are commonly predicted to occur in concert in response to life-history trade-offs, such as costs of reproduction. However, the degree to which reproductive strategies involve competition versus cooperation may shape patterns of reproductive senescence, potentially independent of the system-wide costs of different strategies. This is because more competitive strategies may be harder to maintain as body condition declines. For instance, faster senescence in polygynous males compared to females could reflect high physiological costs of competitive reproductive strategies and associated sexually selected traits (Bondurianksy et al. 2008; Nussey et al. 2009; Beirne et al. 2015). However, this pattern could also arise because successful competition is not possible for aging males, lowering reproductive success in old age and potentially feeding back to weaken selection for late-life performance (Graves 2007). In contrast, cooperative interactions, such as sharing parental duties, may dampen costs of reproduction (Cram et al. 2015) while also making sustained performance more feasible in aging individuals (Sharp and Clutton-Brock 2010).

Our objective was to examine rates of reproductive senescence and life span in a system that exhibits a well-documented polymorphism in competitive and parental reproductive strategies. We studied patterns of reproductive senescence in the polymorphic white-throated sparrow (*Zonotrichia albicollis*) using a long-term data set spanning 18 years. White-throated sparrows provide an excellent system for investigating the relationship between reproductive strategies, social dynamics, and patterns of senescence due to the presence of morph-specific reproductive strategies and a unique social structure (Tuttle 2003). Birds of both sexes occur in two alternative morphs, the white morph and tan morph. Morph is genetically determined by a complex rearrangement on chromosome 2, with white birds heterozygous for the rearrangement and tan birds homozygous, lacking the rearrangement (Thorneycroft 1966; Tuttle

et al. 2016). Gene variants within the rearrangement are divergent and function as a coadapted supergene to alter multiple aspects of physiology and behavior (Tuttle et al. 2016). White males have higher testosterone and corticosterone concentrations during breeding than tan males, which may mediate differences in behavior including higher territorial aggression, singing, and extrapair copulation (Kopachena and Falls 1993*a*; Tuttle 2003; Maney et al. 2005; Swett and Breuner 2009; Horton and Holberton 2010). In contrast, tan males invest more into mate-guarding and parental behavior. In parallel to males, white females sing and engage in territorial aggression, whereas tan females do not sing and are less aggressive. White-throated sparrows pair disassortatively by morph, seemingly because the rearrangement is deleterious in homozygotes and due to behavioral incompatibilities within same-morph pairs (Tuttle et al. 2016). The two alternative pair types, W × T and T × W (male morph appears first), display distinct parental systems. In W × T pairs, parental care is female biased, with white males contributing little. In T × W pairs, males and females share parental duties more equally (Knapton and Falls 1983; Kopachena and Falls 1993*b*, 1993*c*; Tuttle 2003; Falls and Kopachena 2010).

In formulating predictions regarding how reproductive strategy and social dynamics influence reproductive senescence in the white-throated sparrow, we recognized that a bidirectional relationship may exist between reproductive strategy and reproductive senescence. First, we generated two alternative predictions based on the concept that energy-intensive strategies potentially accelerate senescence system-wide and in turn cause reproductive senescence. In line with theory proposing a central role for sexual selection and competitive behaviors in accelerating senescence (Clutton-Brock and Isvaran 2007; Bondurianksy et al. 2008; Tidiére et al. 2015), white males could experience higher costs of reproduction and faster senescence (system-wide) than tan males because they compete more intensely for mates, as evidenced by higher song rates, aggression, and promiscuity. If competitive behavior drives faster senescence, one would also predict faster senescence in white females due to costs of similar, morph-linked behaviors, including aggressiveness and song production (Vercken et al. 2007). On the other hand, given high costs of parental behavior, tan males and females might senesce faster than white morph counterparts. Costs of parental care are expected to be particularly high in tan females, since they receive little parental support. Second, we also reasoned that the highly competitive reproductive strategy of white males and the unsupported parental effort of tan females might be hard to sustain as system-wide senescence proceeds. Thus, the members of the less cooperative pair type might both be more susceptible to reproductive senescence, even if system-wide senescence occurs at equivalent rates regardless of reproductive strategy.

## Methods

### Population Monitoring

Our data derive from a long-term study of white-throated sparrows breeding at the Cranberry Lake Biological Station (State University of New York, College of Environmental Science and Forestry; 44°15′N, 74°48′W) in the Adirondack region of New York. The data set on reproductive success and survivorship spans 18 years (1998–2015) and includes 145 white males, 128 tan males, 100 white females, and 118 tan females.

White-throated sparrows at our study site are banded with Fish and Wildlife bands bearing unique identification numbers and color band combinations that allow visual identification in the field (Master Banding Permit 22296). In addition, all nestlings are uniquely banded and color banded at day 6 of age to allow for monitoring of recruits throughout their lives. Blood samples are taken at the time of banding (~80 μL for nestlings and ~200 μL for adults) for later genetic work. We store hematocrit in lysis buffer at 4°C until use (Longmire et al. 1992). For this analysis, unbanded adults on the central study site were assumed to be young breeders (1 year old), since the majority (~90%) of birds on central territories are banded each year and adults are philopatric. This assumption introduces a degree of error to initial ages but should not affect the longitudinal analysis (within individuals).

White-throated sparrows at Cranberry Lake establish territories in bogs and glades and along habitat edges of forests, streams, and ponds. Territories are located in similar areas each year, facilitating population monitoring. Each year, we survey the population to determine the occupants of each territory and between-year survivorship. White-throated sparrows can fledge two clutches per year and repeatedly renest following nest depredation. We use systematic search and behavioral observations across the season to identify all nesting attempts. Most nests are found during building, laying, or incubation, allowing for determination of clutch sizes and hatching rates.

We visit nests every other day to monitor the progression of the nesting cycle and nest depredation. When nestlings are banded on day 6, we place Thermochron iButtons in nests. We do not revisit the nest until after the nest should have fledged, on day 9 or 10. We consider nests depredated if temperature profiles from iButtons indicate that the nest was empty before day 9 and parents are not seen feeding fledglings. We consider nests successful if data indicate that nestlings fledged on approximately day 9 and parents are observed with fledglings.

We determine the sex of adults at capture by the presence of a brood patch or cloacal protuberance and confirm sex through behavioral observations. We assess the morph of adults using the visual criteria set forth by Lowther (1961),

Piper and Wiley (1989), and Tuttle (1993, 2003). We also use genetic methods to confirm the sex (Griffiths et al. 1998) and morph (Michopoulos et al. 2007; Romanov et al. 2009) of adults and to sex and morph nestlings.

### Genetic Paternity Analyses

To determine cuckoldry levels, extrapair paternity, and the actual reproductive success of males, we employ genetic paternity analysis. We extract DNA from blood samples using the DNA IQ magnetic extraction system (Promega, Madison, WI) or the Qiagen DNeasy extraction kit. We conduct paternity analysis using five to eight microsatellite loci: Gf01 and Gf12 (Petren 1998), MME1 (Jeffery et al. 2001), Dpμ01 and Dpμ03 (Dawson et al. 1997), and Zole_C02, Zole_C07, and Zole_H02 (Poesel et al. 2009). Procedural details are described in Formica and Tuttle (2009). For this study, we determined the actual reproductive success of males by adjusting apparent reproductive success for the occurrence of 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 due to binning errors, and rates of intraspecific brood parasitism are low (Tuttle 2003). Out of 1,536 nestlings genotyped, 254 (16.5%) were extrapair offspring. We were able to assign only 127 (50.0%) of the extrapair offspring to a social father, likely due to the presence of unbanded males on the boundaries of our study site. Thus, our estimates of reproductive success underestimate the reproductive success of white males, who are cuckolded and pursue extrapair mating at high rates (Tuttle 2003). This should not bias our results regarding patterns of reproductive senescence.

### Statistics

We performed statistical analyses in R, version 2.15.2 (R Development Core Team 2012). To analyze the relationship between annual reproductive success and individual age, we employed generalized linear mixed-effects models (GLMMs) with a Poisson distribution using R package lme4 (Bates et al. 2012). Significance levels were determined using Wald $Z$-tests, as recommended for generalized linear models with Poisson error structure in the absence of overdispersion (Bolker et al. 2009). We performed analyses in males and females separately, because breeding males and females are paired in nonconstant combinations across years and thus cannot be treated as independent data points. Moreover, we were interested in testing for morph differences in senescence, and conducting separate models within the sexes was the simplest way to achieve this objective. We included year and individual identity as random effects to account for variation in breed-

ing conditions between seasons and for multiple measurements on the same individual in different years. We additionally retained an observation-level random effect to control for overdispersion (Harrison 2014). The observation-level random effect effectively eliminated overdispersion in this model and elsewhere where applied, as assessed by the overdispersion function authored by Ben Bolker and available online (https://bbolker.github.io/mixedmodels-misc/glmmFAQ .html). We tested linear and quadratic effects of age and also included morph, longevity, and a binary term to indicate final breeding attempt (1, 0; 1 = final breeding attempt, 0 = otherwise) in the model as fixed effects. We included two-way interactions between morph and other parameters (age, age² [quadratic term], longevity, final breeding attempt) in the initial model. The quadratic term models the potential for nonlinear changes in reproductive success with age. Including longevity in the model controls for selective disappearance of low-quality individuals, which could otherwise obscure longitudinal (within-individual) changes in reproductive performance with age. The final breeding attempt term tests for terminal effects on reproductive performance. Negative terminal effects might arise if individuals in their last breeding season manifest pathologies that subsequently result in mortality, whereas positive terminal effects could occur if individuals with low residual reproductive value invest more into reproduction (Bouwhius et al. 2009; Zhang et al. 2015). We centered continuous variables to alleviate problems with multicollinearity (particularly between age and age²) and facilitate interpretation of main effects when also including interaction terms (Schielzeth 2010).

Within males, we assessed whether levels of cuckoldry change with age using GLMMs with a binomial distribution (R package lme4; Bates et al. 2012). We used the number of extrapair nestlings as the dependent variable and total number of nestlings as the binomial denominator. We investigated how male success at obtaining extrapair paternity varied with age using a GLMM with a Poisson distribution. We conducted this model within white males only because tan males rarely obtain extrapair paternity (Tuttle 2003). Within females and males, we tested how clutch size and hatching success change with age. For the clutch size model, we used a GLMM with a Poisson distribution. For the hatching success model, we used a binomial GLMM with number of unhatched eggs as the dependent variable and total number of eggs as the binomial denominator. The hatching success and clutch size models included clutch number as a fixed effect and clutch ID as an additional random effect. Otherwise, we used the same random and fixed effects as above.

We also compared annual and lifetime reproductive success and longevity between the sex-morph classes. To assess differences in annual reproductive success we used a GLMM with a Poisson distribution with sex-morph type as the fixed effect and individual, year, and observation as random effects. We compared lifetime reproductive success of the sex-morph classes using GLMMs with a Poisson distribution and first breeding year as a random effect. To assess differences in longevity we used pairwise Wilcoxon tests with a Holm correction for multiple comparisons.

We reduced all models by sequentially removing predictor variables with the highest $P$ value, until all predictor variables were significant (or near significant) at the $\alpha = 0.05$ level. Model reduction may increase the probability of type I error. Thus, some advocate for presentation of full models (Forstmeier and Schielzeth 2011). However, parameter estimates can be unstable in full models, and our conclusions would not be qualitatively altered if presenting full models. For these reasons and for conciseness, we present simplified models that do not contain nonsignificant terms.

## Results

### Age and Reproductive Performance

In both males and females, reproductive success varied with age in a morph-specific fashion. In males, there was a significant negative interaction between age² and morph (table 1, pt. A). This interaction reflected a negative quadratic effect of male age on reproductive success within white males (table 1, pt. B; fig. 1*a*) but not tan males. In white males, reproductive success first increased slightly with age and then declined (fig. 1*a*). In tan males, the effect of age on reproductive success was linear and positive (table 1, pt. C; fig. 1*a*). The model predicting reproductive success in males also contained a positive interaction between age and whether it was an individual's last breeding season (table 1, pt. A). This interaction reflected greater negative terminal effects in older birds and was significant only within white males (table 1, pt. B). Tan morph males had higher annual reproductive success than white morph males (table 1, pt. A; fig. 1*a*). There was no relationship between male longevity and annual reproductive success ($\beta = 0.093 \pm 0.105$, $Z = 0.883$, $P = .377$).

In females, there was a significant positive interaction between age and morph and a negative interaction between age² and morph (table 2, pt. A). These interactions reflected different linear and quadratic effects of age on reproductive success in white and tan females. As in white males, age had a negative quadratic effect on the reproductive success of white females, with success first increasing with age and then declining (table 2, pt. B; fig. 1*b*). Conversely, there was a positive quadratic effect of age on the reproductive success of tan females, suggesting large early declines in reproductive success followed by lower rates of decline (table 2, pt. C;

Table 1: Poisson generalized linear mixed-effects models predicting reproductive success from age and morph in dimorphic white-throated sparrow males (A), more polygamous and aggressive white males (B), and more paternal tan males (C)

| A. Males | Estimate ($\beta \pm$ SE) | $Z$ | $P > |Z|$ |
|---|---|---|---|
| Intercept | .730 $\pm$ .080 | 9.148 | <.001 |
| Age | .231 $\pm$ .075 | 3.094 | .002 |
| Age$^2$ | −.182 $\pm$ .041 | −4.485 | <.001 |
| Morph[a] | −.100 $\pm$ .058 | −1.731 | .083 |
| Last year | −.122 $\pm$ .093 | −1.305 | .192 |
| Age × morph[a] | .018 $\pm$ .064 | .284 | .776 |
| Age$^2$ × morph[a] | −.099 $\pm$ .039 | −2.491 | .013 |
| Age × last year | .208 $\pm$ .096 | 2.171 | .0299 |
| Random effects | Variance | SD | $N$ |
| Observation | .563 | .750 | 607 |
| Individual | .025 | .159 | 277 |
| Year | .021 | .146 | 18 |
| B. White males | Estimate ($\beta \pm$ SE) | $Z$ | $P > |Z|$ |
| Intercept | .609 $\pm$ .104 | 5.860 | <.001 |
| Age | .242 $\pm$ .111 | 2.178 | .029 |
| Age$^2$ | −.298 $\pm$ .061 | −4.854 | <.001 |
| Last year | −.244 $\pm$ .147 | −1.657 | .098 |
| Age × last year | .306 $\pm$ .145 | 2.107 | .035 |
| Random effects | Variance | SD | $N$ |
| Observation | .842 | .918 | 341 |
| Individual | <.001 | <.001 | 147 |
| Year | <.001 | .023 | 18 |
| C. Tan males | Estimate ($\beta \pm$ SE) | $Z$ | $P > |Z|$ |
| Intercept | .782 $\pm$ .082 | 9.508 | <.001 |
| Age | .215 $\pm$ .063 | 3.381 | <.001 |
| Random effects | Variance | SD | $N$ |
| Observation | .380 | .617 | 267 |
| Individual | .035 | .188 | 130 |
| Year | .029 | .172 | 18 |

[a] White relative to tan morph.

fig. 1*b*). There was also evidence of a negative terminal effect on reproductive success in females (table 2, pt. A). Within morphs, this effect was significant only in tan females (table 2, pt. C). White females had higher annual reproductive success than tan females (table 2, pt. A). As in males, female longevity was unrelated to annual reproductive success ($\beta = -0.034 \pm 0.087$, $Z = -0.389$, $P = .698$).

### Paternity Retention and Extrapair Paternity

Retention of paternity varied with age in a morph-specific fashion, as reflected by a negative interaction between male age and morph (table 3, pt. A). White males had lower paternity retention than tan males (table 3, pt. A). Within the white morph, there was a linear decline in paternity retention with age (table 3, pt. B; fig. 2*a*), indicating that older males were cuckolded more frequently than younger individuals. In contrast, paternity retention was relatively stable or even slightly increased across age classes within the tan morph (table 3, pt. C; fig. 2*b*). Paternity retention was not related to male longevity ($\beta = 0.239 \pm 0.500$, $Z = 0.479$, $P = .632$) or whether it was an individual's last breeding season ($\beta = 0.171 \pm 0.675$, $Z = 0.255$, $P = .799$), and associated interaction terms were also nonsignificant ($P > .10$ in all cases).

Within white males, success at obtaining extrapair paternity first increased with age and then declined (fig. 3), as indicated by a negative quadratic relationship between extrapair paternity and age ($\beta = -0.664 \pm 0.191$, $Z = -3.465$, $P < .001$). The main effect of age on extrapair paternity was positive ($\beta = 1.125 \pm 0.286$, $Z = 3.92$, $P < .001$).

### Clutch Size and Hatching Success

Hatching success tended to relate to female age in a morph-specific fashion (table 4, pt. A), as reflected by a marginally nonsignificant positive interaction between morph and age. There was a weak, negative quadratic effect of age on hatching success in white females (table 4, pt. B; fig. 4*b*). Indeed, the overall negative quadratic relationship between hatching success and age (table 4, pt. A) seemed to be driven by white females. As tan females aged, there was a strong linear decline in hatching success (table 4, pt. C; fig. 4*b*), with no quadratic component apparent. Female longevity and terminal effects had no influence on hatching success ($P > .50$). Male age, longevity, and terminal effects were all unrelated to hatching success. Clutch size was unrelated to any age-related parameter ($P > .10$ for simple and quadratic effects of age, longevity, and terminal effects, as well as interaction terms).

### Variation in Reproductive Success and Longevity

Annual reproductive success ranged from 0 to 9 and was lower in white males than in all other sex-morph classes (GLMM: $P < .001$ in all cases, $n = 1,016$ observations, 491 individuals, 18 years). White females had higher annual reproductive success than white males ($\beta = 0.253 \pm 0.089$, $Z = 2.844$, $P = .004$), whereas other pairwise comparisons were nonsignificant ($P > .10$). Annual reproductive success had a mean $\pm$ SE of 2.865 $\pm$ 0.148 in tan females, 2.586 $\pm$ 0.141 in tan males, 3.186 $\pm$ 0.163 in white females, and 1.754 $\pm$ 0.111 in white males.

Lifetime reproductive success ranged from 0 to 33 ($n = 375$; 101 tan females, 89 tan males, 81 white females, 104 white males, 17 years), and tan females had lower life-
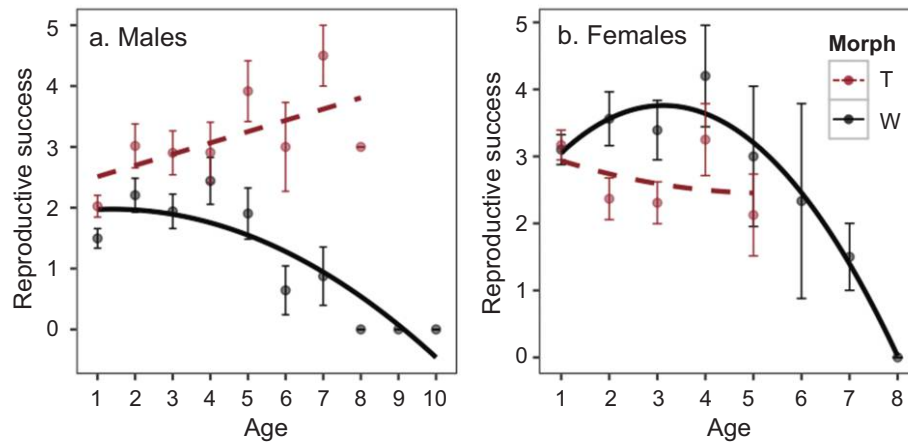
**Figure 1:** Relationship between reproductive success and age in dimorphic white-throated sparrow males (*a*) and females (*b*). In this species, white morph males are more polygamous and aggressive than tan counterparts, which invest more in paternal care. White morph females are more aggressive and receive more paternal support than tan females. Plotted relationships use raw data and quadratic functions in all groups except for tan morph males, in which a linear model best fit the data. Bars denote standard error within age classes.

time reproductive success than tan males (GLMM: $\beta = 0.311 \pm 0.063$, $Z = 4.942$, $P < .001$), white females ($\beta = 0.272 \pm 0.064$, $Z = 4.236$, $P < .001$), and white males ($\beta = 0.126 \pm 0.063$, $Z = 2.011$, $P = .044$). The lifetime reproductive success of tan males was higher than that of white males ($\beta = 0.182 \pm 0.061$, $Z = 2.985$, $P = .003$) but similar to that of white females ($\beta = -0.031 \pm 0.063$, $Z = -0.496$, $P = .620$). White females had higher lifetime reproductive success than white males ($\beta = 0.135 \pm 0.063$, $Z = 2.149$, $P = .032$). Lifetime reproductive success had a mean $\pm$ SE of $4.842 \pm 0.424$ in tan females, $6.517 \pm 0.698$ in tan males, $6.346 \pm 0.590$ in white females, and $5.635 \pm 0.526$ in white males. As stated above, the reproductive success of white males is underestimated due to failure to assign genetic paternity to all extrapair nestlings.

Longevity ranged from 0 to 10 and was higher in white males than in tan females (pairwise Wilcoxon test, $P = .02$). Longevity did not differ between other sex-morph classes ($P \geq .30$ in all cases). Longevity had a mean of $2.702 \pm 0.102$ in tan females, $3.222 \pm 0.107$ in tan males, $3.105 \pm 0.147$ in white females, and $3.935 \pm 0.116$ in white males.

## Discussion

We demonstrate morph-specific patterns of reproductive senescence in a species with genetically determined alternative reproductive strategies. Morph-specific relationships between age and reproductive performance were present in white-throated sparrows of both sexes and are likely related to morph differences in aggressive behavior and reproductive strategy. Morph-specific reproductive and behavioral strategies could entail different physiological costs, explaining dif-

ferences in reproductive senescence. Alternatively, certain reproductive strategies could be more difficult to sustain given age-related declines in body condition and physiological systems. Below we discuss these two contingencies and what our results suggest regarding the relative costs and life-history outcomes of intrasexual competition versus parental care.

Given high physiological costs of intrasexual competition, we predicted faster reproductive senescence in white than in tan birds. In agreement with this prediction, the reproductive success of white males was stable or increased slightly at young ages and declined thereafter (fig. 1*a*), whereas the success of tan males linearly increased with age, perhaps due to reproductive experience (Forslund and Pärt 1995; Martin 1995; Préault et al. 2005; fig. 1*b*). Older white males exhibited declines in paternity retention and extrapair paternity that contributed to reproductive senescence. High physiological costs of reproduction in white males could promote senescence in reproductive performance traits, including sexual display, sperm quality, and competitive ability (Møller et al. 2009; Velando et al. 2011; Noguera et al. 2012; Rivera-Gutierrez et al. 2012; Lemaître et al. 2014; Preston et al. 2015). Indeed, compared to tan males, white males exhibit higher levels of aggression (Kopachena and Falls 1993*a*; Tuttle 2003; Maney et al. 2005), testosterone (Maney et al. 2005; Swett and Breuner 2009), and sexual display, which all may increase physiological costs, for instance, by causing oxidative stress and reducing immunocompetence (Torres and Velando 2007; Peron et al. 2010; Preston et al. 2011; Noguera et al. 2012). Testosterone has been specifically proposed to mediate a trade-off between aggression, sexual attractiveness, and immune function (immunocompetence handicap hypothesis; Folstad and Karter 1992). High testosterone con-

**Table 2:** Poisson generalized linear mixed-effects models predicting reproductive success from age and morph in dimorphic white-throated sparrow females (A), more aggressive white females (B), and more parental tan females (C)

| A. Females | Estimate ($\beta \pm$ SE) | Z | P > \|Z\| |
|---|---|---|---|
| Intercept | $1.070 \pm .073$ | 14.602 | <.001 |
| Age | $-.025 \pm .058$ | $-.430$ | .667 |
| Age$^2$ | $.011 \pm .038$ | .279 | .780 |
| Morph[a] | $.157 \pm .051$ | 3.073 | .002 |
| Last year | $-.195 \pm .074$ | $-2.632$ | .009 |
| Age × morph[a] | $.142 \pm .057$ | 2.467 | .014 |
| Age$^2$ × morph[a] | $-.110 \pm .038$ | $-2.875$ | .004 |
| Random effects | Variance | SD | N |
| Observation | .179 | .423 | 418 |
| Individual | .015 | .124 | 224 |
| Year | .028 | .169 | 18 |
| **B. White females** | Estimate ($\beta \pm$ SE) | Z | P > \|Z\| |
| Intercept | $1.173 \pm .067$ | 17.589 | <.001 |
| Age | $.141 \pm .079$ | 1.771 | .077 |
| Age$^2$ | $-.103 \pm .036$ | $-2.836$ | .004 |
| Random effects | Variance | SD | N |
| Observation | .218 | .467 | 201 |
| Individual | <.001 | <.001 | 102 |
| Year | .007 | .083 | 18 |
| **C. Tan females** | Estimate ($\beta \pm$ SE) | Z | P > \|Z\| |
| Intercept | $.976 \pm .106$ | 9.162 | <.001 |
| Age | $-.181 \pm .084$ | $-2.134$ | .033 |
| Age$^2$ | $.133 \pm .069$ | 1.939 | .052 |
| Last year | $-.326 \pm .107$ | $-3.057$ | .002 |
| Random effects | Variance | SD | N |
| Observation | .132 | .363 | 218 |
| Individual | .059 | .242 | 122 |
| Year | .033 | .181 | 17 |

[a] White relative to tan morph.

centrations could suppress immunity, resulting in cumulative damage and mediating senescence (Mougeot et al. 2004; Alonso-Alvarez et al. 2007; Mills et al. 2009).

In addition, morph differences in responsiveness to endocrine signals could affect patterns of reproductive senescence. The ZAL2$^m$ supergene encompasses multiple hormone receptors, including estrogen receptor 1 (ESR1), serotonin receptor 1B and 1E (HTR1B and 1E), and the follicle-stimulating hormone receptor (FSHR; Tuttle et al. 2016). Polymorphism in the ESR1 gene alters receptor expression in the brain, affecting morph-specific behaviors (Horton et al. 2014; Maney et al. 2015). Receptor function could also have pleiotropic effects on senescence, for example, by affecting maintenance of immune and reproductive function.

However, rates of reproductive senescence were not consistently associated with morph across the sexes. Rather, in contrast to males, tan females showed higher rates of reproductive senescence than white females. Terminal effects were also more pronounced in white males but tan females. Costs of aggressive behaviors may be mitigated in white females if they engage in these behaviors only during a brief period before nesting commences (Arcese et al. 1988; Pavlova et al. 2007). Nonetheless, the inconsistent pattern across the sexes argues against a strong connection between costs of reproduction and traits associated with the ZAL2$^m$ supergene. Indeed, neither white males nor white females showed shorter life spans than tan counterparts, with white males instead showing the highest life expectancies. However, senescence in different systems may or may not proceed in parallel (Nussey et al. 2013). Thus, white males but not white females could experience high physiological costs that affect their reproductive system (e.g., spermatogenesis) but not survivorship (e.g., immunity).

**Table 3:** Binomial generalized linear mixed-effects models predicting paternity retention from age and morph in dimorphic white-throated sparrow males (A), more polygamous and aggressive white males (B), and more paternal tan males (C)

| A. Males | Estimate ($\beta \pm$ SE) | Z | P > \|Z\| |
|---|---|---|---|
| Intercept | $3.596 \pm .255$ | 14.122 | <.001 |
| Age | $.012 \pm .293$ | .042 | .966 |
| Morph[a] | $-1.392 \pm .255$ | $-5.466$ | <.001 |
| Age × morph[a] | $-.741 \pm .293$ | $-2.524$ | .011 |
| Random effects | Variance | SD | N |
| Observation | 6.950 | 2.636 | 403 |
| Individual | .290 | .538 | 208 |
| Year | <.001 | <.001 | 18 |
| **B. White males** | Estimate ($\beta \pm$ SE) | Z | P > \|Z\| |
| Intercept | $1.723 \pm .184$ | 9.378 | <.001 |
| Age | $-.615 \pm .182$ | $-3.389$ | <.001 |
| Random effects | Variance | SD | N |
| Observation | 3.324 | 1.823 | 214 |
| Individual | .268 | .517 | 106 |
| Year | <.001 | <.001 | 17 |
| **C. Tan males** | Estimate ($\beta \pm$ SE) | Z | P > \|Z\| |
| Intercept | $6.237 \pm .696$ | 8.964 | <.001 |
| Age | $.710 \pm .746$ | .952 | .341 |
| Random effects | Variance | SD | N |
| Observation | 15.317 | 3.913 | 189 |
| Individual | 2.773 | 1.665 | 102 |
| Year | <.001 | .006 | 18 |

[a] White relative to tan morph.
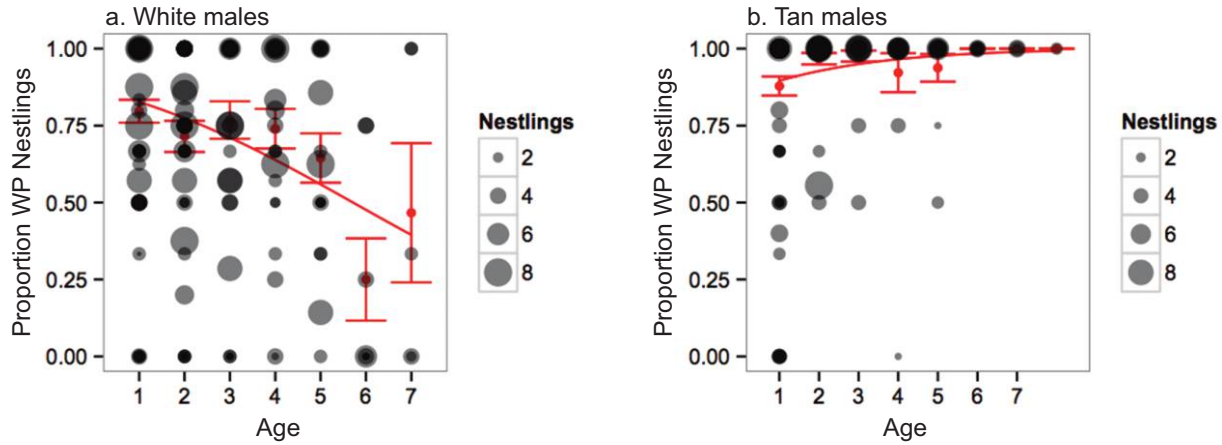
**Figure 2:** Relationship between paternity retention (proportion of within-pair [WP] nestlings) and age in white male (*a*) and tan male (*b*) white-throated sparrows. White males exhibit high rates of extrapair paternity relative to more paternal tan males. Red dots are mean proportions ± SE within age groups. Black dots are proportions within nests and are scaled to the number of nestlings in broods. Plots use raw data, and red lines are binomial functions.

Alternatively, rather than reflecting differences in costs of reproduction and rates of systemic decline, faster reproductive senescence in white relative to tan males could result because the competitive reproductive strategy of white males is difficult to sustain given age-related declines in performance. Aging birds will likely be outcompeted for the best territories, social mates, and paternity (via sperm competition; e.g., Bowers et al. 2015) in white but not necessarily in tan males. Moreover, senescent declines in testosterone levels occur in many species (Ottinger 1992, 2007; Wilcoxen et al. 2013) and could have a larger detrimental effect on reproductive performance in competitive white males than in paternal tan males. This could in turn

drive evolution of faster systemic senescence in white males, due to reduced selection for late-life performance. However, results do not support this outcome since white males exhibit long life spans. Rather, intrasexual competition could impose selection on body condition, favoring genes with positive pleiotropic effects on viability (Graves 2007; Bondurianksy et al. 2008).

Given high costs of parental care, we expected higher reproductive senescence in the tan morph, particularly in females. We did not observe faster reproductive senescence in tan relative to white males, perhaps because white females and tan males share parental duties. On the other hand, tan females perform parental care with little paternal support,
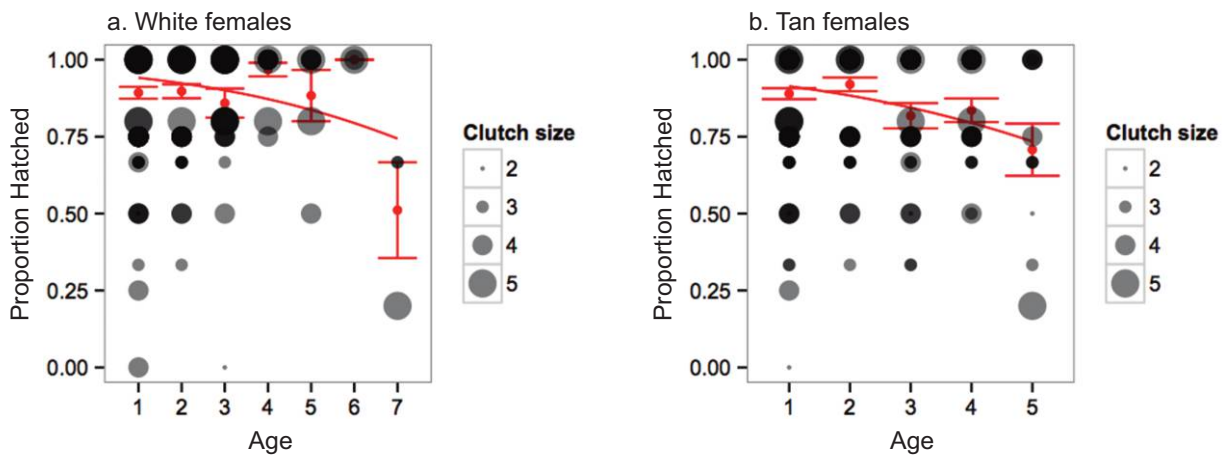


**Figure 3:** Relationship between hatching success and age for white female (*a*) and tan female (*b*) white-throated sparrows. White females are more aggressive and receive more paternal support than tan females. Red dots are mean proportions ± SE within age groups. Black dots are proportions within nests and are scaled to clutch size. Red lines are binomial functions.

**Table 4:** Binomial generalized linear mixed-effects models predicting hatching success from age and morph in dimorphic white-throated sparrow females (A), more aggressive white females (B), and more parental tan females (C)

| A. Females | Estimate ($\beta \pm$ SE) | $Z$ | $P > |Z|$ |
|---|---|---|---|
| Intercept | $2.961 \pm .321$ | 9.237 | <.001 |
| Age | $-.189 \pm .155$ | $-1.216$ | .224 |
| Age$^2$ | $-.154 \pm .074$ | $-2.081$ | .037 |
| Morph[a] | $.204 \pm .199$ | 1.025 | .306 |
| Clutch | $-.314 \pm .143$ | $-2.193$ | .028 |
| Age × morph[a] | $.373 \pm .196$ | 1.900 | .057 |
| Random effects | Variance | SD | $N$ |
| Nests | .746 | .864 | 434 |
| Individuals | .064 | .254 | 188 |
| Year | .050 | .224 | 16 |

| B. White females | Estimate ($\beta \pm$ SE) | $Z$ | $P > |Z|$ |
|---|---|---|---|
| Intercept | $2.813 \pm .258$ | 10.904 | <.001 |
| Age | $.185 \pm .240$ | .775 | .439 |
| Age$^2$ | $-.198 \pm .107$ | $-1.848$ | .064 |
| Random effects | Variance | SD | $N$ |
| Nests | 1.256 | 1.121 | 203 |
| Individuals | <.001 | <.001 | 89 |
| Year | <.001 | <.001 | 16 |

| C. Tan females | Estimate ($\beta \pm$ SE) | $Z$ | $P > |Z|$ |
|---|---|---|---|
| Intercept | $2.796 \pm .388$ | 7.199 | <.001 |
| Age | $-.319 \pm .114$ | $-2.809$ | .005 |
| Clutch | $-.328 \pm .190$ | $-1.720$ | .085 |
| Random effects | Variance | SD | $N$ |
| Nests | .530 | .728 | 231 |
| Individuals | <.001 | <.001 | 101 |
| Year | .195 | .441 | 16 |

[a] White relative to tan morph.

senescence advances. The hypothesis that cooperative behavior facilitates maintenance of reproductive performance in aging individuals has rarely been considered, but a study addressing this idea in meerkats (*Suricata suricatta*) yielded null results (Sharp and Clutton-Brock 2010). In females, results regarding hatching success might seem unlikely to have arisen through this second pathway, because little paternal investment occurs prior to hatching. However, early in the season, tan males could buffer white females from reproductive stress through mate guarding, which can protect females from sexual harassment (Lovell-Mansbridge and Birkhead 1998) and increase foraging efficiency (Fedy and Martin 2009).

Tan males and white females also achieved higher lifetime reproductive success than white males and tan females, with tan females having the lowest lifetime success. The fitness of white males is underestimated due to incomplete paternity assignment. Nonetheless, these results again suggest that the more cooperative parental system yields higher fitness, at least for females, with disassortative mating maintaining the polymorphism. However, fitness differences between pair types might also vary geographically.

Differences in detectability or dispersion between sex-morph classes could bias our analysis of life span. However, meticulous population monitoring makes it unlikely that breeding individuals go undetected. Moreover, long-term field observations suggest that males of both morphs display high site fidelity and return repeatedly to the same territory in subsequent years. Females switch territories more often than males (which may in part explain slightly lower recapture estimates in females) but with no evidence of a morph bias. Also consistent with the current interpretation, a recent analysis of actuarial senescence using long-term mark-recapture data shows an age-dependent increase in mortality that is
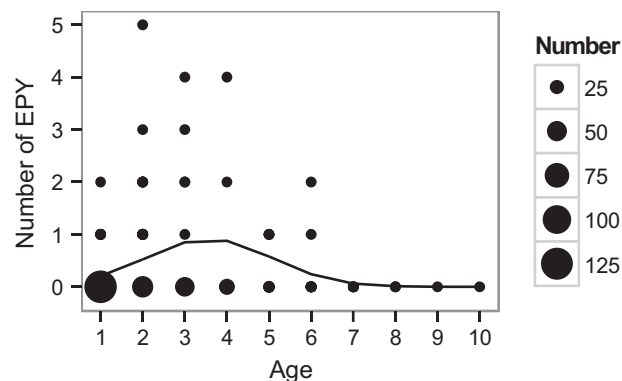
displayed faster reproductive senescence than white females, and had the shortest life span of any sex-morph class. These results suggest that tan females display rapid senescence in condition and survivorship, as well as reproductive success. Indeed, sex-biased parental care predicts sex-biased mortality in Palearctic birds (Owens and Bennett 1994), and single motherhood is associated with stress, disease, and mortality risk in humans (Berkman et al. 2015), demonstrating substantial costs of unsupported parental effort. Conversely, parental support may lower costs of reproduction and rates of reproductive senescence. For instance, cooperative breeding lowers oxidative costs of reproduction in sparrow weavers (*Plocepasser mahali*; Cram et al. 2015).

In addition to lowering reproductive costs, the cooperative parental system of T × W pairs could allow tan males and white females to better sustain reproduction as system-wide



**Figure 4:** Relationship between number of extrapair young (EPY) and age in white morph males of the dimorphic white-throated sparrow. The black line represents predicted values from the zero-inflated Poisson model. Dots represent the number of EPY per male and are scaled to the number of observations.

most pronounced in tan females and least pronounced in white males, but with no baseline difference in resighting probability between sex-morph classes (M. L. Grunst et al., unpublished manuscript). Importantly, even if sex, morph, or age-dependent dispersal does occur in the white-throated sparrow, this would likely not bias our analysis of age-dependent reproductive success (trajectories shown in fig. 1*a*), which suggest morph differences in reproductive senescence.

Overall, our study suggests that more competitive and less cooperative or supported reproductive strategies are associated with faster reproductive senescence. Results regarding longevity differences between the morphs do not support high self-maintenance costs of intrasexual competition but rather suggest high costs of unsupported parental care. Gaining further insight into why the sex-morph classes display distinct patterns of reproductive senescence will require quantifying age-related changes in physiology, body condition, and behavior. For instance, it will be informative to assess age-related changes in endocrine signaling. These data will allow us to better disentangle whether certain sex-morph classes display faster reproductive senescence due to physiological trade-offs that drive declines in key functions or due to the difficulty of succeeding in highly competitive (white males) or unsupported (tan females) reproductive behaviors as aging advances. Of course, these two processes are also likely to interact, on both ecological and evolutionary time frames.

Data availability: data are deposited to the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.vj5pn (Grunst et al. 2017).

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Female white-striped sparrow (*Zonotrichia albicollis*) perched showing brood patch. Photo credit: Indiana State University Photo Services.