

Aging and Senescence across Reproductive Traits and Survival in Superb Fairy-Wrens (*Malurus cyaneus*)

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ABSTRACT: Why do senescence rates of fitness-related traits often vary dramatically? By considering the full aging trajectories of multiple traits, we can better understand how a species' life history shapes the evolution of senescence within a population. Here, we examined age-related changes in sex-specific survival, reproduction, and several components of reproduction using a long-term study of a cooperatively breeding songbird, the superb fairy-wren (*Malurus cyaneus*). We compared aging patterns between traits by estimating standardized rates of maturation, age of onset of senescence, and rates of senescence while controlling for confounding factors reflecting individual variability in life history. We found striking differences in aging and senescence patterns between survival and reproduction as well as between reproductive traits. In both sexes, survival started to decline from maturity onward. In contrast, all reproductive traits showed improvements into early adulthood, and many showed little or no evidence of senescence. In females, despite senescence in clutch size, number of offspring surviving to independence did not decline in late life, possibly due to improvements in maternal care with age. Superb fairy-wrens have exceptionally high levels of extragroup paternity, and while male within-group reproductive success did not change with age, extragroup reproductive success showed a dramatic increase in early ages, followed by a senescent decline, suggesting that male reproductive aging is driven by sexual selection. We discuss how the superb fairy-wrens' complex life history may contribute to the disparate aging patterns across different traits.

Keywords: aging, senescence, *Malurus*, life-history theory, sexual selection, extrapair paternity.

Introduction

The aging pattern of any fitness-related trait is often characterized by both a period of early-adulthood improvement (maturation) and a period of later-life deterioration

(senescence; Baudisch 2011; Jones et al. 2014). The diversity of aging patterns observed between species and between individuals within species has motivated a wealth of theoretical work describing how aging should evolve under the framework of life-history theory (for recent reviews, see Shefferson et al. 2017; Gaillard and Lemaître 2020). There is now increasing evidence that reproductive- or survival-related traits do not age synchronously even within an individual (Froy et al. 2013; Hayward et al. 2013, 2015; Zhang et al. 2015; Piper et al. 2017). Despite great progress in the evolutionary understanding of aging, in practice it is still not possible to accurately predict how specific traits will age relative to other traits in any given species (Brunet-Rossinni and Austad 2006; Jones et al. 2014; Bouwhuis and Vedder 2017; Lemaître and Gaillard 2017). For example, in likely the most taxonomically rigorous study to date, which included 45 animal, plant, and algae species, Jones et al. (2014) were unable to identify any discernible association between the shape of a species' survival curve or rate of survival senescence and the shape or rate of reproductive aging in that species. The lack of discernible patterns reflects the complexity of selection pressures and life-history characteristics that are likely acting simultaneously to produce the diversity of aging patterns observed in natural populations.

In general, traits with a greater contribution to fitness should be expected to senesce slower or later than traits with lower implications for survival or reproduction (Lemaître and Gaillard 2017; Cohen et al. 2020). However, empirical evidence suggests that relative fitness costs are not able to fully explain differences in onset and rate of senescence (Brunet-Rossinni and Austad 2006; Bouwhuis and Vedder 2017). Age-dependent trade-offs (Lemaître and Gaillard 2017), constraints (Cohen et al. 2020), indirect genetic effects (Moorad and Nussey 2016), and relative strength of sexual selection in a population (Bonduriansky et al. 2008; Hooper et al. 2018) may all explain some of these inconsistencies and differences in trait-specific aging. However, to date, there is little information

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about how these different factors work together to produce asynchronous aging of fitness-related traits in ecologically realistic conditions. Useful insights can be provided by studies of aging involving long-term monitoring of wild populations and by focusing on how a suite of fitness-related traits change with age instead of focusing on only reproduction or survival (Brunet-Rossini and Austad 2006; Lemaître and Gaillard 2017; Gaillard and Lemaître 2020). Investigating how a suite of traits rather than only reproduction or survival change with age can thus help to elucidate how life history modulates patterns of aging (Nussey et al. 2009; Hayward et al. 2013, 2015).

Theoretical models predict that physiological fertility and other reproductive traits, such as maternal care, are expected to age in varied asynchronous ways depending on life-history characteristics (Pavard et al. 2007; Gillespie et al. 2013; Moorad and Nussey 2016; Barks and Laird 2020). For instance, if the ability to provide maternal care improves with experience, resulting in improved offspring survival with maternal age, the rate of fertility senescence should be reduced through natural selection, as there is greater benefit to having offspring later in life when more experience has been accrued (Gillespie et al. 2013; Barks and Laird 2020). By quantifying aging in both female prenatal traits that are indicative of fertility (e.g., clutch size) and postnatal traits that are indicative of offspring quality (e.g., offspring survival to independence), the relative roles of physiological aging versus the aging of maternal care in driving overall reproductive maturation and senescence rates can be empirically tested (Karniski et al. 2018).

Measuring multiple components of reproductive aging can also clarify the role of sexual selection in shaping overall aging patterns. In males, aging in reproductive success could be a result of changes in investment in secondary sexual traits, with implications for female mate choice (Cleasby and Nakagawa 2012), or changes in paternal effects via parental care (Lemaître and Gaillard 2017; Barks and Laird 2020). Age-related improvements and/or subsequent senescence in male reproductive success may be driven by female choice if females prefer particular male age classes (Kokko 1997; Promislow 2003; Bonduriansky et al. 2008). For example, female preference for older males may be adaptive if age is an honest signal of male quality or if intersexually selected traits are age dependent (Akçay and Roughgarden 2007; Hsu et al. 2015). Alternatively, male reproductive aging could be driven by paternal effects, such as age-related associations with territory quality (Lemaître and Gaillard 2017). In socially monogamous but promiscuous species, in which males sometimes provide only sperm but other times also share a common territory with young, the relative roles of female choice and paternal effects can be disentangled. We are not

aware of any study to date that has explicitly separated age-related changes in extrapair and within-pair reproductive success in measuring male reproductive aging.

Measuring sex-specific survival rates can also be insightful in determining the impact of life history on aging, especially when the sexes experience considerably different sexual selection pressures (Bonduriansky et al. 2008). Increased promiscuity and more pronounced secondary sexual traits have both been linked with earlier onset or faster senescence in males relative to females across species (Clutton-Brock and Isvaran 2007; Tidière et al. 2015). Although, note that Lemaître and Gaillard (2013) did not find any evidence that variation in male allocation to copulatory traits explained variation in male senescence rates in herbivore species. To date, most of the research on the role of sexual selection in sex-biased aging has focused on mammals (for a review, see Tidière et al. 2015), and only one cross-species review has included birds (Clutton-Brock and Isvaran 2007). Furthermore, the bird studies included in this review are of species that are predominantly monogamous and without male-biased investment in dramatic secondary sexual traits. As a result, little inference can be made about the general effect of sexual selection on male senescence in birds. The paucity of empirical data on aging via sexual selection in birds (relative to mammals) is especially important because, in mammals, much of the sexual selection is mediated via intrasexual competition, favoring evolution of secondary sexual traits used in duels between males (Cassini 2020). Thus, it is not clear whether the negative effects of sexual selection on male senescence observed in mammals are broadly applicable to instances of intersexual competition, where selection on male secondary sexual traits is driven by female choice rather than by male-male competition.

Since aging trajectories in a species will depend on the ecological context, an understanding of the ultimate and proximate mechanisms of aging requires analyses of wild populations. There are several practical constraints that make this sort of analysis challenging. It requires that individuals are accurately aged and (ideally) tracked until their death. To adequately investigate patterns occurring in the oldest age classes, where sample sizes will be heavily restricted by mortality, the overall sample size must be substantial and may take decades to collect (Nussey et al. 2008). Additionally, factors that are not a direct consequence of aging, including heterogeneity between individuals, in the environment, and in individual life history, should be controlled for in order to accurately assess the specific effect of age on trait expression (van de Pol and Verhulst 2006).

In addition to the practical constraints, quantifying aging also raises several statistical and philosophical challenges. Aging trajectories may not follow simple parametric functions and ideally need to be modeled without

constricting the effect of age to a particular functional shape. Furthermore, to make quantitative comparisons of aging between traits, it is necessary to define which features of the aging function to quantify. In this study, we therefore took a two-stage approach: (a) modeling the aging trajectory across the life span of each trait nonparametrically using generalized additive mixed models (GAMMs; Wood 2017) and (b) running a break point analysis using standardized estimates from these nonparametric models to generate measures of (i) rates of early-adulthood improvement (maturation), (ii) age of onset of declines in late life, and (iii) rates of these declines (senescence) for each trait. This two-step approach to investigating aging has the potential to be applied across other traits and species. Standardized methods for investigating trait-specific aging across species are key to improving our understanding of how aging patterns evolve. For this reason, we provide an annotated code detailing our methodology with the hope of encouraging a standardized approach to aging research across other wild populations (see the code tutorial in the zip file, available online).¹

In this study, we investigate trait-specific aging in a wild population of superb fairy-wrens (*Malurus cyaneus*; hereafter, “fairy-wren”), a small passerine species endemic to southeastern Australia. The fairy-wren offers an excellent system to investigate how sexual selection and life history may impact survival and reproductive aging. A 30-year longitudinal study of a wild population of fairy-wrens provides a large sample of individuals with extremely detailed data on their reproductive histories and timing of death (Cockburn et al. 2016). With this data set, we were able to quantify survival, a suite of interrelated components of reproduction, and overall reproductive success separately for each sex.

By measuring age-related changes in survival in males and females separately, we sought to quantify how differences in the sexual selection pressures each sex experiences impact their aging. Fairy-wrens are highly sexually dimorphic: males molt into bright blue breeding plumage in advance of each breeding season, while females remain brown throughout the year. Plumage brightness heightens predation risk across a range of bird species (Huhta et al. 2003). In the fairy-wrens specifically, males increase their vigilance behavior when in blue plumage, which suggests that they may be under greater predation risk (McQueen et al. 2017). Additionally, the increased testosterone associated with molting is immunosuppressive in fairy-wrens, possibly further impacting their survival (Peters 2000). The blue molt is driven by intersexual selection, with females

strongly preferring males that molt earlier in the year (Dunn and Cockburn 1999). If the pattern observed across mammals—that intrasexual selection results in more rapid survival senescence in males—is broadly applicable to intersexual selection as well, then we predict more rapid or earlier onset of survival senescence in male fairy-wrens relative to females.

To investigate whether female reproductive aging in fairy-wrens is driven by shifts in the quantity of offspring produced (i.e., prenatal traits) or changes in the “quality” (i.e., postnatal traits), we measured aging in clutch size and breeding start date (prenatal traits) in addition to measuring the number of offspring that survive to independence (encompassing the effects of both prenatal traits and postnatal maternal care-related traits). The fairy-wren breeding season can last up to 6 months, but the breeding start date can vary widely between females in a given season (Cockburn et al. 2016; Lv et al. 2019). Females can successfully raise up to three clutches in a breeding season, and the number of clutches they raise will be impacted by how early they begin their season: earlier start dates are associated with higher numbers of young produced in a season (Lv et al. 2019). Thus, both clutch size and breeding start date are prenatal traits that will impact the quantity of reproductive output for females. If female reproductive aging is driven by changes in the quantity of offspring, we expect to see the rates of age-related changes in breeding start date and clutch size match the rates of overall reproductive aging (measured through offspring surviving to independence) in females. Conversely, if overall reproductive aging is asynchronous with these traits, this would suggest that age-related changes in maternal effects related to quality (notably, maternal care) rather than quantity of offspring are driving reproductive aging (Moorad and Nussey 2016; Barks and Laird 2020).

In males, we measured overall reproductive aging using the total number of nestlings produced annually. In addition, we analyzed aging of extragroup and within-group reproductive success separately and age-related changes in the dates on which males molted into their blue breeding plumage each year. There are two different pathways to reproductive success for males in this socially monogamous, group-living social structure—through either within-group or extragroup mating (Hajduk et al. 2018). While within-group reproductive success is impacted by paternal effects (e.g., shared environment), extragroup reproductive success is driven by female choice (Double and Cockburn 2000). If female mate choice is strongly determined by a male’s age, we expect to see the age-related changes in overall male reproductive success match those of extragroup success. Conversely, if other paternal effects change with age more strongly, we expect to see the age-related changes in overall reproductive success match those

1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

of within-group success. Last, measuring aging of the sexually selected trait of molt date will demonstrate whether and how sexual selection is age dependent in this population. The level of similarity between aging patterns in extragroup success and in molt date will indicate the extent to which female choice is based on molt date.

Methods

Species and Study Site

The population of superb fairy-wrens located in and around the Australian National Botanic Gardens, Canberra, Australia (35°16'S, 149°06'E), has been intensively monitored since 1988 (Cockburn et al. 2003). The study site, approximately 60 ha in area, contains 40–90 territories encompassing between 120 and 230 year-round resident adults. In this study, we used data from the years 1988–2017.

Fairy-wrens are cooperative breeders. Year-round territories are occupied by a single breeding female, a dominant male with which she maintains a social bond, and between zero and five subordinate males. These subordinate males (hereafter referred to as “helpers”) aid the breeding female and dominant male in the provisioning of young and in defense of the territory (Dunn and Cockburn 1996). About half of the helpers (47%) are the sons of the female on the territory (Hajduk et al. 2018). The other half of the helpers are unrelated to the female on the territory, typically as a result of their mother having died and a new female moving into the territory where they reside (Cockburn et al. 2003). Male dominance ranking on a territory is determined entirely by age. When the dominant male on a territory dies, the oldest helper male residing on the territory takes the dominant position (Cockburn et al. 2008b).

Although the female on a territory is pair-bonded to the dominant male, there is an extremely high rate of extrapair mating. Only 39% of offspring are sired by the dominant male, with the rest being sired either by the helper males on the same territory or, much more commonly (95% of the time), by males on other territories (Mulder et al. 1994; Hajduk et al. 2018).

Females typically breed every year starting at the age of one, and both helper and dominant males can sire offspring from age one as well (Cockburn et al. 2003). The breeding season typically lasts from September to February. Throughout a breeding season, a female can successfully raise up to three broods, with broods containing an average of three young (Cockburn et al. 2016). However, because of high rates of nest predation, as many as eight clutches may be initiated in a season (Cockburn et al. 2016).

Shortly after hatching (or, for immigrants, shortly after arrival in the study area), individuals are color-banded, and a blood sample is taken to assign parentage using

single-nucleotide polymorphism genotyping (van de Pol et al. 2020). Many components of life history are continuously tracked for each individual. Nestling trajectories, such as the day of hatching and fledging, are usually known within 1 day. Dates of mortality, immigration, emigration, changes in group composition or territory borders, and male molt from brown winter plumage to blue breeding plumage are known within an accuracy of 1 week or shorter. Emigration from the study area typically occurs only when juvenile females disperse from their natal territories. Males are extremely philopatric, with 72% of adult males remaining on their natal territory their entire life (Cockburn et al. 2008b). Males that do disperse move to an immediately neighboring territory 95% of the time (Cockburn et al. 2008b), so any male dispersal is easily tracked. Females disperse from their natal territory and must establish themselves on a new territory as the dominant female for their first breeding season at the age of one. Females remain on their first breeding territory for their entire lives 80% of the time; in the rare cases that they do subsequently move, it is most common for them to move directly to an adjacent territory (Cockburn et al. 2003; Double et al. 2005). Therefore, disappearance of any individual from the study area (failure to be seen in our year-round weekly censuses) can reasonably be assumed to be a death except in the case of juvenile (aged <1 year) females, which were excluded from the analyses presented here.

The aim of this study was to estimate patterns of aging across a broad variety of traits in the population. We included only individuals of known birth year and death year in analyses. This excluded any individuals that had not died yet or that were born outside of the study area and had immigrated into the study area at an unknown age in adulthood. The cohort (and hence age) of many immigrant females is known precisely, as immigration in the first year is confined to two narrow periods of the year. The effect of age on each trait was modeled using annual measures taken on individuals from the age of one (the age of reproductive maturity) to their death. We analyzed a total of nine traits (survival and reproduction in each sex as well as two additional components of reproduction in females and three additional components of reproduction in males). These are outlined below, and sample sizes for all traits are given in table 1.

Survival (Both Sexes)

We analyzed male and female survival separately. Annual survival for each individual was considered from September 1 (the start of the breeding season) to August 31 of the subsequent year. We treated individuals in their first year of breeding as 1-year-olds, although in actuality first year breeders will vary in age from 6 months to 1 year because

Table 1: Spline and parametric effects describing sex-specific aging in survival- and reproduction-related traits in superb fairy-wrens using generalized additive mixed models

Trait	Model structure	Sample size	Spline terms EDF			Parametric terms (SE)				
			Age	Incubation	Intercept	Longevity	Status/dom	Terminal effect		
Female survival	Bernoulli	1,896 (751)	1.000**	...	59.870** (12.960)	
Male survival	Bernoulli	2,747 (979)	1.001**	...	45.983** (12.419)	
Female breeding start	Gaussian	1,089 (678)	5.555**	...	12.152** (1.414)	-.477 (.353)	-2.714 (1.367)	
Female clutch size	Quasi-Poisson	3,865 (771)	7.828**	5.336**	1.148** (.014)	.003 (.003)005 (.007)	
Female independent offspring	Poisson	1,372 (606)	4.540**374** (.085)	.026 (.016)	-.129 (.188)	
Male molt date	Gaussian	2,116 (1,024)	5.709**	...	-42.588** (3.222)	.777 (.569)	-.856 (1.934)	
Male extragroup offspring	Poisson	2,310 (780)	3.731**	...	-6.303** (.926)	.061 (.051)	.025 (.170)191 (.619)	
Male within-group offspring	Poisson	2,310 (780)	2.019	...	-6.281** (.770)	.052 (.042)	2.017** (.182)	...	-.480 (.414)	
Male total offspring	Poisson	2,310 (780)	3.567**	...	-5.037** (.801)	.057 (.034)	.861** (.115)	...	-.110 (.274)	

Note: Random effects of individual and year were included in each model. An observation-level random effect was included in female fecundity and male success models to account for overdispersion. Full details of each model, including the relevant test statistics, the reference degrees of freedom for each spline term, the deviance and adjusted R^2 values, and the variance and number of levels for each random effect, are given in the supplemental PDF, section S4. Sample size is the number of data points included in the model, followed by the number of individuals in parentheses. Sample sizes for females are lower than for males because of the biased adult sex ratio, and sample sizes for some traits (e.g. female breeding start date) are lower than others because of the exclusion of missed or uncertain records of specific life-history events. Longevity is the number of years an individual lived and provides a test of selective disappearance. Status is a binary term specifying whether a male held a dominant (dom) breeding position or a helper position on his home territory in a given year. Terminal effect is a binary term denoting whether it was the individual's final breeding season. Note that parameter estimates for Bernoulli models are on a logit scale and Poisson and quasi-Poisson models are on a log scale. EDF = effective degrees of freedom.

** $P < .01$.

of variation in birth date. For results to be comparable with the results for reproductive traits and since death cannot be differentiated from emigration in juvenile (aged <1 year) females, survival was measured from only the age of one onward. For each individual, annual survival was recorded as a binary variable.

Female Reproductive Traits

Female Independent Offspring. We calculated the annual fecundity of a female as the number of her offspring that reached independence in a given year, calculated for every year that a female was alive (from age one onward). Across the entire study period, the earliest a chick has been known to reach independence and disperse from its natal territory is 5 weeks after fledging, so we used the cutoff of 4 weeks after fledging as a measure of offspring survival to potential independence. If females died before the end of the breeding season, their incomplete record for that season was not included in the analysis.

Breeding Start Date. For every year that a female was alive, the Julian day on which she began incubating her first clutch of the breeding season was determined (number of days counted from Jan. 1). To control for effects of annual weather and food conditions (Lv et al. 2019), the median population-level breeding start date for that given year was subtracted from each breeding start date. Thus, breeding start date was a relative value that compared each breeding female to the population median in that year.

Clutch Size. The number of eggs a female produced in a clutch had a mode of three and a range of one to five. Within our data set, females produced between one and six clutches within a breeding season. Females start incubation on the day that they lay the last egg of their clutches. All clutches were included in analyses except those that were abandoned or depredated before incubation started.

Male Reproductive Traits

Total offspring was measured as the total number of offspring a male sired each year. Since paternity could be determined only in chicks that reached the age at which a blood sample was taken, paternity of chicks that did not survive until bleeding is unknown (23% of chicks, almost entirely due to predation; A. Cockburn, unpublished data). Individual partial breeding seasons, where the male died at any point before the end of the season, were excluded from the analysis. Total offspring is the sum of within-group and extragroup success (see below). Note that our count of male reproductive success does not include the component of survival to independence as for females be-

cause males provide no parental care to the majority of their offspring (i.e., those sired extragroup).

Within-group offspring was measured as the number of offspring a male sired each year via the female with whom he shared a territory (i.e., via his social partner for dominant males and via the dominant female on the territory for helpers). Extragroup offspring was measured as the number of offspring a male sired via females residing outside of his own territory.

Molt date refers to the day on which a male has completely shed his brown plumage and grown the nuptial blue plumage. There is great variation between individuals in the timing of this molt, from as early as 8 months before to as late as 3 months after the start of the breeding season (Cockburn et al. 2008a). Males that molt earlier have higher siring success in that year's breeding season (Dunn and Cockburn 1999; Cockburn et al. 2008a). The date that each male completes molt is tracked via regular censuses of the population to an accuracy within a week. We quantified molt date as the number of days after the median breeding start date of the females in the given year, so that negative values indicate molting before the start of the breeding season and signify a higher quality of the individual.

Statistical Analysis

We had two aims. First, for each of the traits described above, we modeled the patterns of age-related change while controlling for individual and annual heterogeneity, possible selective disappearance, differences in social status, and other extrinsic factors that may influence the effect of age on each trait. Second, using standardized trait measures, we sought to compare rates of maturation (age-related increases), onset of senescence, and rates of senescence (age-related declines) among traits. We provide code that can be used to conduct this two-step analysis, which we hope will be broadly applicable to measuring aging in any phenotypic trait in a wild population of animals (see the code tutorial in the zip file). Additionally, we provide life tables detailing basic metrics of reproduction and survival at each age for males and females as a point of comparison with our modeled results (supplemental PDF, sec. S1; the supplemental PDF is available online).

Characterizing Trait-Specific Aging: Generalized Additive Mixed Models

Aging trajectories may not follow simple parametric functions and ideally need to be modeled without constricting the effect of age to a particular functional shape. For this reason, we used nonparametric smoothing functions, implemented through generalized additive mixed models (GAMMs), to describe patterns of aging in survival and

in each of the reproductive traits (Wood 2017). GAMMs were fit using the *mgcv* package in R version 3.5.0 (R Development Core Team 2018; Wood 2017). GAMMs are an extension of generalized linear mixed models (GLMMs); in addition to the basic parametric terms of GLMMs, GAMMs can include nonparametric terms that are not restricted to conform to any particular parametric function (Wood 2017). In our GAMMs, we modeled age and any other relevant nonparametric terms using penalized thin-plate regression splines. These splines estimate the relationship between the term and the response variable with a number of penalized additive smoothing functions determined by restricted maximum likelihood. The penalized additive value of the number of smoothing functions is the effective number of degrees of freedom for the term. When the effective degrees of freedom value is 1, the relationship is effectively linear (Wood 2017). Thus, using GAMMs allowed us to describe aging patterns across traits without making any a priori assumptions about the overall shape of the trajectory and, in particular, about the existence and onset of trait maturation or senescence (Jones et al. 2008; Nussey et al. 2009).

We report a *P* value for each nonparametric term from a Wald test, which estimates the probability that the additive value of all of the smoothing functions in the spline is 0 (Amodio and Ambrosio 2014). We also report *P* values for parametric values in our GAMMs. Because of the high number of terms we tested in this study, we chose the *P* value of .01 as a conservative threshold against which to assess the strength of evidence in all models.

We ran each GAMM using the appropriate error distribution for the response trait. Female and male survival each followed a Bernoulli distribution (fitted with a logit link function). Female breeding start date was measured as the Julian date of the first egg laid and centered by the population-level average Julian date for the first egg laid for the given year, resulting in a normal distribution. Clutch size was modeled using a quasi-Poisson distribution (with a log link function), which differs from a Poisson distribution model only in that the dispersion parameter is not fixed at 1 so a dispersion parameter below 1 is used to model underdispersed count data. Female independent offspring, male total offspring, male within-pair offspring, and male extrapair offspring were each modeled using a Poisson distribution (with a log link function). The data in these models were overdispersed, so we included an observation-level random effect to model the extra-Poisson variation present in the data (Harrison 2014). To include an observation-level random effect in these models, we used *gamm4*, an extension of the *mgcv* package that has improved performance when fitting GAMMs with a large number of random effect levels (Wood 2017). The data in each model were also zero inflated. To confirm that these four Poisson

models reasonably fit our data despite the zero inflation, we ran 1,000 simulations of each GAMM and plotted the predicted variance against the raw data variance for each age (supplemental PDF, sec. S2). In addition, we modeled female independent offspring and male total offspring using Poisson zero-inflated model distributions, which allowed further partitioning of reproductive output into two components for each sex: (i) probability of reproduction (vs. not) and (ii) amount of reproductive success (described in further detail in the supplemental PDF, sec. S3). In brief, zero-inflated models are principally used in the case where there are two types of zero values present in the data set; in the fairy-wrens, this could reflect either a complete failure to reproduce (a definite zero) or reproducing with a failure of offspring surviving to fledging (a zero resulting from extrinsic environmental stochasticity). Male molt date was measured as the number of days after the median population-level breeding start date for the given year that a male entirely completed his molt into blue plumage. This resulted in a normal distribution for molt date. In 7% of cases (152/2,116), males did not fully complete their molt into blue plumage, so molt date was censored at 10 days past the latest date of molt completion on record. In another 1% of cases (24/2,116), males kept their blue plumage from the previous season without ever returning to brown plumage, and we censored these males to a value 10 days earlier than the earliest molt date on record.

All models included individual identity (ID) and the breeding year of measurement (running from Sept. 1 to Aug. 31; year) as multilevel random effects. These effects controlled for the nonindependence of repeated measures on the same individual across years and for annual variation in the trait mean associated with differences in environmental conditions, respectively.

In the modeling of aging of reproductive traits, the problem of selective disappearance can arise if covariance exists between individual reproductive fitness and life span or age at maturity (van de Pol and Verhulst 2006). For example, if individuals that have higher reproductive performance tend to live longer on average, then in later age classes, as poorer-quality individuals die out, the population-level reproductive performance could appear to be increasing, even if within-individual level reproduction declines at these ages (van de Pol and Verhulst 2006). Fairy-wrens reach sexual maturity and are capable of reproducing in their first breeding season (age one), but they vary considerably in life span. Previous studies have found evidence for nonlinear relationships between life span and reproductive traits (Reid et al. 2003; Nussey et al. 2009), so life span was initially added as a nonparametric spline to each model. In these models, life span generally had an effective degrees of freedom value close to 1 (supplemental PDF, sec. S4). Since it did not alter our results, we ultimately fitted life span as a

(linear) parametric effect, as this allowed for clear interpretation of the magnitude of the effect.

In an individual's final year of life, reproductive investment may differ sharply from reproduction in previous years. In some species, the final year of life results in a sharp increase in reproductive performance (referred to as "terminal investment"; Weladji et al. 2010; Froy et al. 2013), while in others, the final year of life is associated with decreased reproduction (Coulson and Fairweather 2001; Reed et al. 2008). We controlled for any terminal effects in all our models of reproductive traits by adding a two-level fixed effect denoting whether it was the individual's last year of life.

Clutch size in fairy-wrens tends to vary throughout the breeding season, with smaller clutches at the beginning and end and the largest clutches in the middle of the breeding season. To control for this temporal variation, we added a spline term of Julian date of clutch incubation to the model of clutch size, which took a roughly quadratic form.

All models of male traits included both dominant and helper males. The dominance status of an individual is typically stable within a year but can be transient between years, with helpers moving to dominant breeding positions. To compare reproductive aging and survival between dominants and helpers, these models included a two-level fixed effect denoting an individual's social status (dominant or helper) in the year of observation.

Standardized Rates of Maturation and Senescence

In a second stage of analysis, we used the estimates produced from the GAMM of each trait to assess standardized rates of maturation, onset of senescence, and rates of senescence for each trait using simple linear regression. For each GAMM, we extracted the predicted mean estimate and standard error of the age term for each age. For zero-inflated models of reproductive success in either sex, this resulted in two sets of age effect estimates and standard errors: one for the probability of producing any offspring and the other for the number of offspring. We standardized each estimate in two steps. First, we subtracted the mean predicted value of the effect of age from the estimate so that all trait values were centered to zero. Second, we divided the centered estimate by the range of values predicted by all terms together in the GAMM to control for the variance explained by the age term relative to other variables in the GAMM. Estimates were increased by one order of magnitude for ease of interpretability. For molt date and breeding start date, the signs of the values were reversed so that an increasing value denoted trait improvement across all traits. This process of standardization allows for direct comparison of aging patterns between different traits (Schielzeth 2010).

We then ran a simple linear regression for each trait as a function of age, using only these standardized estimates of age. In the regressions, we weighted each data point by the inverse of the standard error for that age predicted by the GAMM. Weighting the data points ensured that estimate precision was accounted for while at the same time not allowing the much larger sample size at lower ages in the GAMMs to entirely drive the regression prediction.

Since aging is commonly characterized by early-life trait increases (maturation) and late-life trait declines (senescence; Jones et al. 2008, 2014), a single linear regression may not be adequate in describing the aging patterns of most traits. We used the segmented package in R to assess whether more than one regression line better described each trait as a function of age and to model any segments of the regression (Muggeo 2008). For each regression, we used a Davies test to assess whether the trait would be better described by two linear regressions of age rather than one (Davies 1987, 2002; Cheng 2017). The null hypothesis of the Davies test is that there is no break point at any age in the regression where the slopes delineated by that break point would be significantly different from each other (Davies 2002). Thus, a significant Davies test result indicates that the relationship between age and the trait is better represented by two linear regressions rather than one. As with all previous analyses in this study, we used a *P* value threshold of .01 to assess significance. For models that did not have a significant break point according to the Davies test, we used the original simple linear regression to describe the aging pattern of that trait. For models with a significant break point, we used the segmented function in R to create two regressions of the trait of interest as a function of age. This method implements a bootstrap restarting algorithm described in Wood (2001) to assess the break point of the model and then estimates the two resulting linear regressions. Since there can be a period of plateau between trait maturity and trait senescence, we also tested for a second break point in segmented models. In models with a second significant Davies test, two break points were modeled. As a result, traits were represented by one of the following: a single continuous linear regression with one slope representing the entirety of adult life, a segmented linear regression with two slopes representing early adulthood and late life, or a segmented linear regression with three slopes representing early adulthood, mid-life, and late life.

Results

Mean adult life span (excluding individuals that died before maturity) was 3.44 years (± 2.22 SD; 979 individuals) for males and 2.97 years (± 1.73 SD; 751 individuals) for females. Maximum adult life span observed in the study

was 12 years in males and 10 years in females, although only 19% of males and 13% of females survived to 5 years (sample sizes for each age in fig. 1A, 1B). There was substantial variation between traits in their changes across the life span, described further below. Detailed results for each GAMM, including R^2 values, relevant test statistics, and the variance explained by each random effect are available in the supplemental PDF (sec. S5).

Survival

Both female and male survival appeared to decline linearly in the GAMMs (fig. 1A, 1B), and as such, there was no

support for any break point in the models of female or male survival, with survival declining across adulthood in both sexes (fig. 2A, 2B; table 2). The rate of decline, based on the linear models, was similar in males and females (male slope: -0.51 ; female slope: -0.56 ; table 2). However, the male survival GAMM had a greater intercept than that of the female model (male intercept: 0.73 ± 0.10 ; female intercept: 0.60 ± 0.10), and in a post hoc analysis, a GLMM of the effect of sex on annual survival probability (sample size: 4,792 individual years; random effects of year and individual) indicated that, overall, males had a higher chance of survival than females (log odds ratio = 0.29 ± 0.06), despite the similar rates of

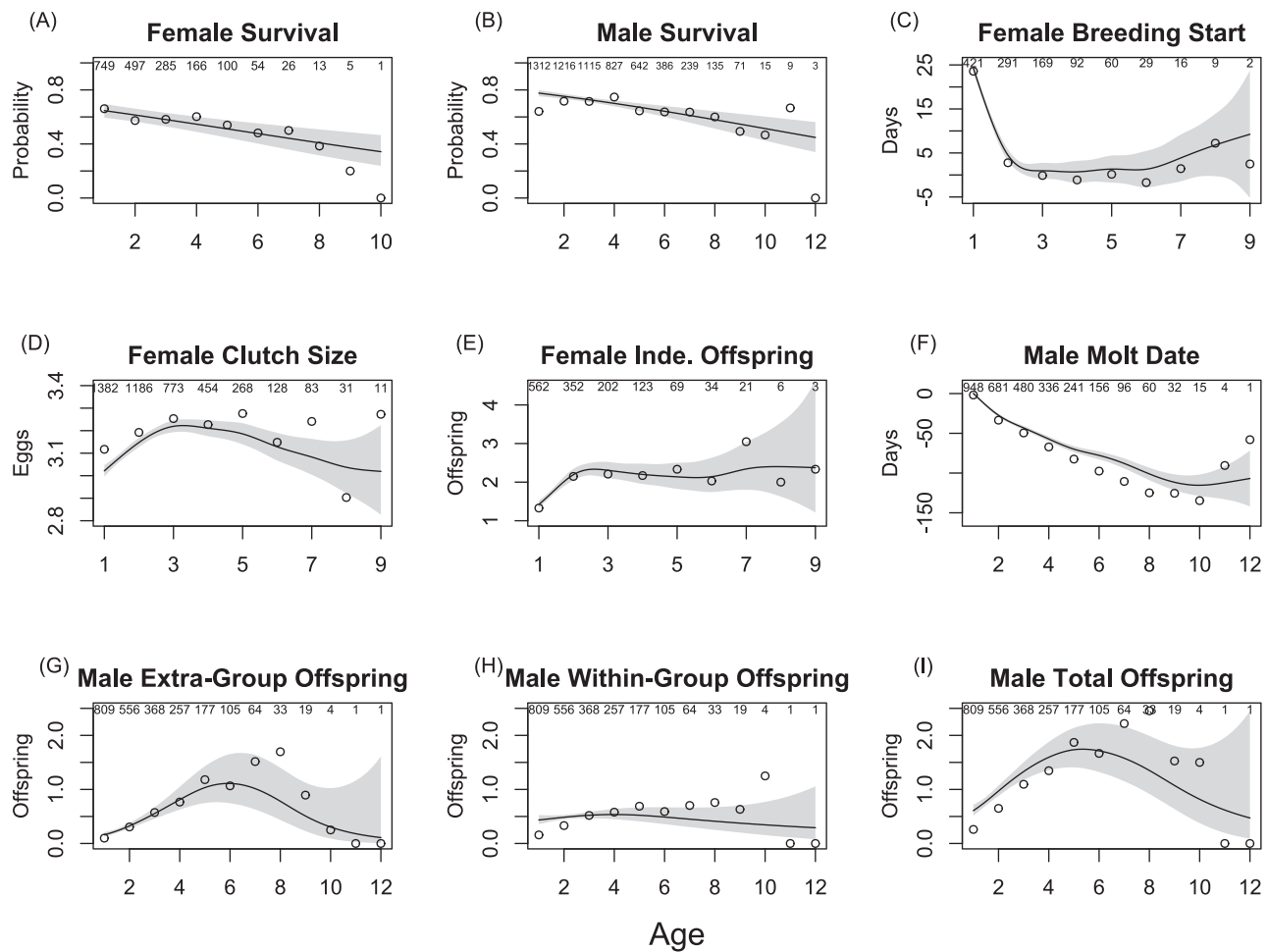


Figure 1: Superb fairy-wren aging patterns as predicted by generalized additive mixed models for female survival (A), male survival (B), breeding start date measured as the day females lay their first clutch relative to the population average date (C), female clutch size (D), number of independent offspring reared for females (E), molt date measured as the number of days relative to the median start of female breeding that males complete their molt into breeding plumage (F), offspring sired outside the territory (extragroup) for males (G), offspring sired within the territory (within-group) for males (H), and total offspring sired for males (I). Shaded area represents ± 2 SEs from the estimate, including the uncertainty about the overall mean. Number of data points is denoted for each age at the top of each graph. Circles represent the means of raw data values.

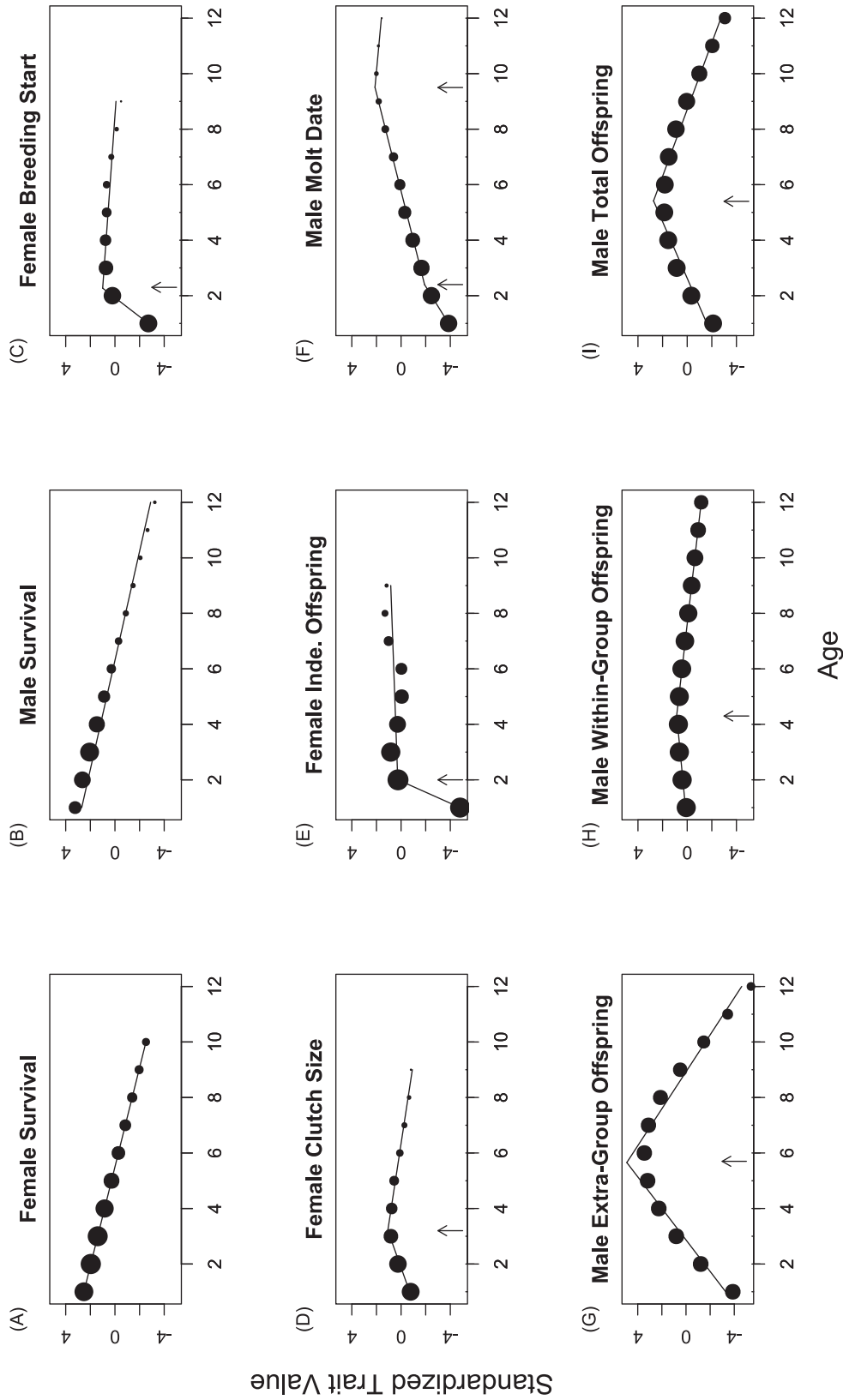


Figure 2: Standardized aging patterns with segmented or continuous linear regressions estimating the effect of age on female survival (A), male survival (B), breeding start date measured as the day females lay their first clutch relative to the population average date (C), female clutch size (D), the number of independent offspring reared for females (E), molt date measured as the number of days relative to the median start of female breeding that males complete their molt into breeding plumage (F), offspring sired outside the territory (extragroup) for males (G), offspring sired within the territory (within-group) for males (H), and total offspring sired for males (I). Circles represent the raw data, which are the estimates for each age predicted from the corresponding generalized additive mixed model (GAMM) and z transformed to allow direct comparisons between traits. The size of the circle represents the inverse of the standard error associated with the GAMM estimate. Regressions are weighted by these inverse standard errors. Regressions that are continuous did not have a significant break point (A and B), and the regression with two break points (C) had a second significant break point ($P < .01$). Arrows denote locations of break points. Note that female breeding start date and male molt date have been multiplied by -1 for consistency with the other traits so that higher values indicate earlier dates.

Table 2: Estimates for the effect of age on each trait in a linear regression or a segmented linear regression (when significant break points were found)

Trait	Across-life slope (99% CI)	Early-adulthood slope (99% CI)	First break point age (99% CI)	Midlife slope (99% CI)	Second break point age (99% CI)	Late-life slope (99% CI)
Female survival	-.560** (-.560 to -.560)
Male survival	-.511** (-.511 to -.511)
Female breeding start date	...	2.921** (2.132 to 3.710)	2.2 (2.1 to 2.5)	-.160 (-.336 to .015)
Female clutch size803** (.513 to 1.093)	3.2 (2.9 to 3.6)	-.344** (-.497 to -.191)
Female independent offspring	...	5.046** (2.675 to 7.418)	2.0 (1.7 to 2.3)081 (-.380 to .542)
Male molt date	...	1.395** (1.033 to 1.756)	2.4 (2.0 to 2.8)	.567** (.504 to .630)	9.5 (8.9 to 10.1)	-.208 (-.651 to .235)
Male extragroup offspring	...	1.760** (1.072 to 2.447)	5.7 (5.0 to 6.3)	-1.501** (-1.967 to -1.035)
Male within-group offspring214** (.140 to .288)	4.3 (4.0 to 4.7)	-.259** (-.287 to -.232)
Male total offspring981** (.552 to 1.410)	5.4 (4.7 to 6.1)	-.831** (-1.109 to -.554)

Note: Data values analyzed in these models were the mean values for each age as predicted by the respective generalized additive mixed model (table 1) centered on the mean trait value and divided by the range of trait values (see "Methods"). Each data point was weighted by the inverse of its standard error. CI = confidence interval.

** $P < .01$.

decline. There was a nonsignificant negative effect of being a dominant male (compared with a helper) on male annual survival (table 1; $P = .06$).

Female Reproductive Traits

The three female reproductive traits—*independent offspring*, *breeding start date*, and *clutch size*—all had periods of trait maturation that ended around the age of two or three (table 2). Of the three female reproductive traits, only *clutch size* showed evidence of senescence after the initial period of trait improvement (table 2).

In the zero-inflated model of independent offspring (supplemental PDF, sec. S3), while the probability of any independent offspring showed a nonsignificant positive trend across the total female life span (slope: 0.320; confidence interval [CI]: -0.040 to 0.681), the (non-zero-inflated) total number of offspring showed early-life improvements (slope: 1.370; CI: 1.061 to 1.678) and late-life senescence beyond age 6.6 (slope: -0.523 ; CI: -0.885 to -0.161).

In each GAMM of the reproductive traits, we included longevity to test for any selective disappearance and a two-level factor of final year of breeding to test for any terminal effects. There was no support for either an effect of longevity or terminal effects in any model of female reproductive performance (table 1).

Male Reproductive Traits

Male reproductive traits exhibited periods of trait maturation, but the duration of maturation varied between traits. We found evidence of senescence for all male traits with the exception of *molt date* (table 2). Extragroup success reached its peak about 1.5 years later than within-group success (table 2; break point of 4.3 vs. 5.7). Extragroup success demonstrated a rate of maturation approximately eight times greater and a rate of senescence approximately six times greater than the age-related changes for within-group success (table 2). As expected, male total success had a break point and aging rates that roughly averaged the values of the within-group and extragroup estimates, with a slight bias toward the estimates of the extragroup (fig. 2) since 61% of paternity is achieved extragroup (Hajduk et al. 2018). *Molt date* was the only trait to have two break points, with a steep rate of maturation up until age 2.4 followed by a relatively shallower rate of improvement to age 9.5, after which there was no change with age (table 2; fig. 2).

There was no effect of social status (dominant or helper position) on extragroup success, but dominant males did have substantially higher within-group success, which re-

sulted in a positive effect of dominance on total offspring (table 1). Dominant males also had an earlier molt date (table 1). Similarly to females, there was no support for either an effect of longevity or terminal effects in any model of reproductive performance for males (table 1).

Discussion

We investigated fairy-wren aging patterns by measuring annual survival and reproductive success in each sex as well as two components of reproductive success for females (*clutch size* and *breeding start date*) and three for males (*extragroup offspring*, *within-group offspring*, and *molt date*). The aging of these traits was highly asynchronous, with variable rates and durations of both early-adulthood improvements and late-life declines, some traits not showing any period of maturation in early adulthood, and others not showing any evidence of senescence. Our results add to the growing body of empirical evidence that traits do not senescence synchronously within an individual (Nussey et al. 2009; Froy et al. 2013; Hayward et al. 2013, 2015; Zhang et al. 2015; Piper et al. 2017; Tompkins and Anderson 2018). They also show that senescence is not ubiquitous across all traits. Below, we discuss the insights that our results provide for understanding aging in wild animal populations and consider how the distinctive ecological and evolutionary forces faced by this species may be driving these patterns.

Survival

Annual survival probability declined at similar rates in males and females from their first year of adult life (table 2). As with other small passerines, the days immediately after fledging are the most dangerous time for both sexes (A. Cockburn, unpublished data). Survival is unlikely to peak until after the attainment of a breeder or helper position at age one, so this age is likely to be an accurate estimate of senescence onset.

Although males display a costly secondary sexual trait (Peters 2000; McQueen et al. 2017), this did not appear to cause a faster rate of survival senescence in males relative to females, and a post hoc analysis indicated that females had lower annual survival overall compared with males. Our results indicate that the association between strong intrasexual selection and more rapid male senescence in mammals may not be broadly applicable to intersexual selection in birds in relation to dramatic plumage coloration. The life-history factors that mold senescence are complex and can be interacting. Although the annual molt into nuptial plumage may increase mortality risk in males (Peters 2000; McQueen et al. 2017), other aspects of male

life history in fairy-wrens may decrease their mortality, such as cooperative breeding delaying peak reproductive performance (Promislow 2003).

The onset of survival senescence in the first year of breeding is aligned with the classic evolutionary aging theory prediction that selection on somatic maintenance should decline from the age of sexual maturity (Williams 1957; Hamilton 1966). However, it is contrary to most empirical evidence of survival senescence in iteroparous birds and mammals, which shows that survival senescence is most commonly delayed until some years after the age of sexual maturity (Jones et al. 2008; Péron et al. 2010; Gaillard and Lemaître 2017). One rationale explaining the delayed survival senescence in these other species is that, when the actual possibility of reproductive success occurs some time after the physiological possibility of reproductive success (sexual maturity), there could be strong selective pressure to continue to invest heavily in somatic maintenance beyond sexual maturity, delaying the onset of survival senescence (McElligott et al. 2002; Brunet-Rossinni and Austad 2006). In female fairy-wrens, reproductive success is relatively likely from age one (supplemental PDF, table S1), so the onset of survival senescence at this age makes intuitive sense. In contrast, in male fairy-wrens, young adults are more likely to be helpers, as they queue for dominance on their territory by age, which substantially lowers their within-group reproductive success at age one. However, by controlling for dominance status in our male survival model, we have modeled the effect of age on survival independent of any delayed social maturity caused by being a helper. Thus, our results represent the effect of age on survival while controlling for plasticity in senescence that is driven by how social circumstances lead to changes in life history with age. This may be why our results align more closely with the classic aging theories, which did not take into account life-history trade-offs. It is important to note, however, that survival rates measured in the wild are a consequence of both extrinsic and intrinsic sources of mortality. As a result, the observed age-related changes in survival may also be influenced by changes in life history or behavior, which impact extrinsic mortality risk rather than intrinsic senescence per se.

Reproduction

The effects of age on female and male reproductive traits were considerably different from those on survival. Unlike survival, all reproductive traits experienced some period of early-adulthood improvement, and not all traits demonstrated senescence. There were also some notable differences in aging patterns among the reproductive traits.

For females, the number of independent offspring increased dramatically from age one to two, after which point

there was no change with age. Although there was no change in reproductive fitness contribution for females at these later ages, the zero-inflated model revealed that this lack of overall change was a consequence of counteracting changes in the probability and the (non-zero-inflated) total number of independent offspring produced. The probability of producing any independent offspring slowly increased across all ages ($P = .017$), while the (non-zero-inflated) number of independent offspring increased in early adulthood before plateauing and demonstrating senescence at late ages (supplemental PDF, sec. S3). This decline in total number of independent offspring may be driven in part by the senescence of clutch size but not breeding start date (table 2; fig. 2). The improvement in probability of independent offspring may indicate an improvement in maternal care abilities with age. Disentangling different components of reproduction in female fairy-wrens has illustrated that, underlying a lack of overall reproductive aging, there can be dynamic and counteracting shifts in traits related to physiological fertility and postnatal maternal effects.

The early-adulthood improvement and subsequent late-life declines in male total reproductive success appeared to be entirely driven by the dramatic age-related changes in extragroup success (figs. 1G–1I, 2G–2I). The effects of age on within-group offspring in both the GAMM and the standardized regression were much weaker or nonexistent. These results suggest that sexual selection, specifically intersexual selection, plays an important role in reproductive aging, as male extragroup success in fairy-wrens is primarily driven by female mate choice (Double and Cockburn 2000). We believe that it is likely that female precopulatory mate choice specifically and not other avenues of intersexual selection, such as sperm competition or cryptic (postcopulatory) female choice, are driving male reproductive aging. If these other modes of sexual selection did play a role, we would expect to see similar age-related changes in within-group success. Thus, it appears that female preference for middle-aged males is driving both male reproductive improvement in early adulthood and male reproductive senescence in late life.

In addition to the larger change with age in extragroup reproductive success (compared with within-group success) in males, the extragroup success also reached its peak at later ages when compared with both male within-group success and female independent offspring (1.4 and 3.7 years later, respectively; table 2). Only 5% of adult males survive to age six, the point at which they would have reached peak extragroup reproductive success. Selection for an earlier reproductive peak in males is expected to break down when reproductive success is reliant on an age-dependent sexually selected trait (Bonduriansky et al. 2008), which may explain the peak of male extragroup success relatively

later in life seen here. Earlier molt date is a signal of high male quality and a strong predictor of male reproductive success (Dunn and Cockburn 1999; Cockburn et al. 2008a). Since molt date steadily improved by shifting earlier with age until very old ages (table 1; fig. 1F), this pattern is likely a major contributor to the observed pattern of increase in male extragroup success. To investigate this prediction further, we added molt date as an additional explanatory variable to the GAMM of extrapair success and compared the rates of maturation in the subsequent segmented regressions with the rates estimated by our model, which did not control for molt date. We found that there was still early-life improvement in extrapair success when controlling for molt, but the rate of maturation was reduced by approximately half (supplemental PDF, sec. S6). This indicates that the improvement in molt date with age does indeed play a considerable role in driving early-life improvements in extragroup success.

That molt date continuously shifts to earlier dates and shows no real evidence of senescence may seem counter-intuitive given the evidence in this study of significant survival senescence from the onset of adulthood. Given that the production of costly secondary sexual traits is generally expected to be condition dependent (Zahavi 1975; Andersson 1986), one might predict that these traits deteriorate as a part of the general somatic deterioration associated with survival senescence. It may be possible to make sense of this phenomenon by viewing it through the lens of life-history theory. With increasing age, expected future fitness (residual reproductive value) declines, resulting in increases in the relative value of current reproduction (Kirkwood and Rose 1991). Thus, increased investment in secondary sexual traits, which improve reproductive success within the current breeding season, should be increasingly favored over investment in somatic maintenance and future reproduction. Game theory models have predicted that progressive increases in costly secondary sexual trait expression with age are evolutionarily stable in iteroparous organisms (Kokko 1997). Additionally, this theory is supported by empirical evidence, as continued improvement in ornamental traits into old age classes, despite senescence in both reproductive success and survival, appears to be a common finding in longitudinal animal studies (Nussey et al. 2009; Evans et al. 2011; Preston et al. 2011; Potti et al. 2013). Similar to these studies, extrapair mating success in the fairy-wrens displays senescence at ages where molt date continues to improve, suggesting that other factors unrelated to molt date are also influencing extrapair success in late life. Since sperm quality is known to decline with age (Hansen and Price 1995; Radwan 2003; Preston et al. 2011; Velando et al. 2011; Cornwallis et al. 2014), this could be contributing to the expedited senescence of extragroup success in old males. The considerable

variation in reproductive aging seen in both females and males illustrates the complexity of reproductive aging, where different reproductive traits can be driven by differing ecological and evolutionary forces, resulting in a variety of different aging patterns.

Individual Variability in Aging

We controlled for any potential correlation between life span and performance by adding a fixed effect of longevity to all of the models of reproductive traits. Longevity was not significant in any model. Thus, there is no evidence that longer-lived individuals have inherently different reproductive investment strategies or face different reproductive constraints. In addition, for most of the fairy-wren traits, the random effect of individual identity explained a very small amount of the variance compared with, for example, the random effect of year, which in most models explained several orders of magnitude more variance (see details of the models in the supplemental PDF, sec. S5). This suggests that variation in performance in the population is more driven by extrinsic conditions than by variation in intrinsic quality. The one exception to this was molt date, where the variance explained by individual identity was relatively large. To further explore this, we fit an additional model for molt date with the inclusion of a random effect of identity as an interaction term with age to test for between-individual variation in aging rates of molt date. The variation explained by the ID \times age term in this additional model was significant in a Wald test ($P < .001$), which suggests that males vary in the shapes of their molt aging patterns. We plan to further investigate how both genes and the environment contribute to this individual-level variation in molt aging in future work (Charmantier et al. 2014).

Conclusions

Within our study population of superb fairy-wrens, we found marked differences between aging trajectories of survival and reproductive traits and between individual aspects of reproduction within the sexes. Despite strong declines in survival from age one in both sexes, senescence was detected in only four of the seven models of reproductive traits and, for males, only at later ages to which only 13% of individuals survive. It is likely that these instances of reproductive senescence could be identified only because of the magnitude of our sample sizes and longevity of the study. This finding highlights the difficulty in confidently assessing late-life aging patterns in wild animal populations. Continuing long-term data collection from individual-based studies is thus especially

valuable for investigating senescence patterns in the wild (Charmantier et al. 2014).

Our study adds to the increasing body of literature that demonstrates that traits do not age in unison and suggests that the pattern of aging in each trait will be molded by unique selection pressures. The exact nature of these selection pressures may be difficult to infer because of the complexity of potential evolutionary and ecological forces acting on any one trait. Key to making progress in this field is the ability to compare aging across traits, populations, and studies. We have presented here a comprehensive analytical approach to quantifying aging patterns in traits that follow very different aging trajectories and to assessing differences in the key parameters of early-adulthood rates of maturation, onset of senescence, and later-life rates of senescence. This approach could be used for multitrait comparisons within other populations and for comparisons across populations. To facilitate this, we have provided annotated code of our methods (see the code tutorial in the zip file) with the hope of increasing the number of future studies that use standardized aging analyses.

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Statement of Authorship

H.L.O. and A.C. collected the data. L.E.B.K. and E.B.C. planned the analysis. E.B.C. analyzed the data and drafted the manuscript. E.B.C., L.E.B.K., A.C., and T.B. revised the manuscript. All authors approved the final manuscript.

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