This manuscript is available as a preprint at DOI: 10.32942/osf.io/uepxj

Supplementary material and code: https://github.com/evebcooper/wren-trait-ageing

Title: Ageing and senescence across reproductive traits and survival in superb fairy-wrens (*Malurus cyaneus*)

Abstract

Why do senescence rates of fitness-related traits often vary dramatically? By considering the full ageing trajectories of multiple traits we can better understand how trade-offs and life-history shapes the unique evolution of senescence rates within a population. Here, we examine age-related changes in survival and six reproductive traits in both sexes using a long-term study of a wild population of a cooperatively-breeding songbird, the superb fairy-wren (*Malurus cyaneus*). We compare ageing patterns between traits by estimating standardized rates of maturation, the 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 ageing and senescence patterns between survival and reproduction, and between the sexes. In both sexes, rates of survival started to decline from maturity onwards. In contrast, all reproductive traits showed improvements into early adulthood and many showed little or no evidence of senescence. Male reproductive ageing appeared to be driven by sexual selection, with extra-group reproductive success and sexually-selected plumage phenology showing much greater change with age than did within-group reproductive success. We discuss how the superb fairy-wrens' complex life history may contribute to the disparate ageing patterns in this species.

Introduction

Life-history theory asserts that senescence evolves as a consequence of the declining strength of selection with increasing age. It was on this basis that influential evolutionary biologist George C

Williams posited in his 1957 paper that "*Senescence should always be a generalized deterioration, and never due largely to changes in a single system*"(Williams, 1957). In recent years, it has become possible to characterize this "*generalized deterioration*" by measuring the ageing of multiple fitness-related traits in wild animal populations. However, the empirical evidence to date suggests that, rather than senescing in unison, either the onset of senescence, or the rates of senescent declines often vary between different phenotypic traits (for example, Bouwhuis et al. 2012; Massot et al. 2011; Preston et al. 2011; Froy et al. 2013; Hayward et al. 2013; Berger et al. 2015*a*; Zhang et al. 2015; Hammers et al. 2015; Kervinen et al. 2015; Piper et al. 2017). In a recent review, Bouwhuis and Vedder (2017) show that, amongst longitudinal studies of ageing in wild bird populations, performance declines are most often reported for physiological traits (89% of which show a decline), and less so for traits involved in reproductive performance (67%) or traits associated with sexual selection (50%).

These asynchronous patterns of trait senescence are often interpreted as running counter to Williams's 1957 postulate (Brunet-Rossinni and Austad 2006; Nussey et al. 2009; Hayward et al. 2013, 2015; Bouwhuis and Vedder 2017; Gaillard and Lemaître 2017). Alternatively, a more nuanced interpretation might suggest that his prediction did not necessarily preclude asynchronous patterns of trait-specific senescence if the relative fitness cost of the deterioration differs between traits. In this case, traits with a higher fitness cost should be expected to senescence slower or later, whereas traits with lower implications for survival or reproduction may deteriorate more quickly (Lemaître and Gaillard 2017). However, empirical evidence does not always suggest this to be the case in practice (Brunet-Rossinni and Austad 2006; Bouwhuis and Vedder 2017). Additionally, fitness costs of senescence is not uniform across species, with the hypothetical reproductive value costs of senescence ranging from 1.4 to 62.5% across 13 bird and mammal species (Bouwhuis et al. 2012; Bouwhuis and Vedder 2017). The relative forces of sexual and natural selection are likely to play a key role in determining relative rates of senescence in reproductive and survival-related traits (Bonduriansky et al. 2008; Hooper et al. 2018), which may explain some of these inconsistencies and differences between species. Asynchronies in trait-specific senescence can thus provide unique insight into the evolution of a species' life-history.

One often-ignored factor that may contribute to variation in senescence between traits is variation in the rate of maturation of each trait (Bouwhuis et al. 2012; Lemaître et al. 2015; Lemaître and Gaillard 2017; Cooper and Kruuk 2018). The process of ageing is typically characterized by both a period of early-adulthood improvement (maturation), and a period of later-life deterioration (senescence) (Baudisch 2011; Jones et al. 2014). As for senescence, rates and durations of trait maturation vary between traits. The rate and duration of trait improvement can directly influence the onset and the rate of phenotypic senescence (Gustafsson and Part 1990; Bouwhuis et al. 2010; Kim et al. 2011; Hammers et al. 2013). Investigating the entire lifetime trajectory of a trait, considering both early-adulthood maturation and late-life senescence, may thus offer insights into the potential causes of variability in senescence rates between traits.

A fundamental premise of life-history theory is that trade-offs occur between reproduction and survival, and thus may influence the ageing of these traits. However, annual reproduction and survival probability are correlated to a multitude of other fitness-related traits, from physiology to behavior (Stearns 1980, 1989). Life-history trade-offs often result in the ageing of one trait being interdependent on the ageing of other traits. For example, if the effectiveness of parental care increases with experience, females may shift their optimal allocation to account for the higher survivorship (quality) of their offspring by investing less in offspring quantity with increasing age (Kindsvater et al. 2010; Hayward et al. 2013; Berger et al. 2015). In males, improved reproductive success with age could be a result of greater investment in secondary sexual traits and extra-pair mating (Cleasby and Nakagawa 2012), or, for species with paternal care, improved parental care (Lemaître and Gaillard 2017). A single model of the effect of age on reproductive success may overlook such age-related changes in its components, and the central role of trade-offs in determining ageing (Lemaître and Gaillard 2017). Investigating how a suite of fitness-related traits change with age, rather than only reproduction or survival, may therefore help to elucidate the proximate mechanisms driving patterns of ageing (Nussey et al. 2009; Hayward et al. 2013, 2015).

To better understand how a species' life history influences ageing patterns, we can investigate how differences in life-history between males and females relate to differences in ageing between the sexes. (Lemaître and Gaillard 2017). In polygynous species, sexual selection may lead to a live-fast-die-young strategy in males (Bonduriansky et al. 2008). In some species where males bear costly secondary sexual traits, they appear to senesce more rapidly than females (Loison et al. 1999; Clutton-Brock and Isvaran 2007; Preston et al. 2011). Conversely, high reproductive costs of gestation or maternal care can result in faster female deterioration with age relative to males who do not bear these costs (Lemaître and Gaillard 2017). Further, the ageing of male reproductive success could also in theory be almost entirely driven by female mate choice, if females prefer particular male age classes (Kokko 1997; Promislow 2003; Bonduriansky et al. 2008). For example, female preference for older males may evolve if age is an honest signal of male quality (Akçay and Roughgarden 2007; Hsu et al. 2015). Alternatively, females may prefer younger males if male sperm quality declines with age and this negatively influences offspring fitness (Hansen and Price 1995; Radwan 2003; Velando et al. 2011). Female preferences may also explain why age-dependency of male extra-group paternity success is observed more often than age-dependency of within-group paternity success, on the assumption that extra-group mate choice better reflects female preference (Cleasby and Nakagawa 2012).

Since the trajectories of both maturation and senescence in a species will depend on the ecological context, an understanding of the ultimate and proximate mechanisms of ageing requires analyses of ageing in wild populations. However, this may be difficult to do given the considerable practical constraints and technical issues involved (Monaghan et al. 2008; Nussey et al. 2008). Analysis of ageing in the wild requires that individuals are accurately aged, and (ideally) tracked until their death. In order 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 can take decades to collect (Nussey et al. 2008). Data collection itself may be intensive as a range of important life-history traits must be tracked at many time points in the lifespan of each individual. Additionally, factors influencing the age-structure of each trait which are not a direct consequence of ageing, 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).

The superb fairy-wren (*Malurus cyaneus;* hereafter 'fairy-wren'*)*, a small passerine species endemic to south-eastern Australia, offers an excellent system to investigate sex-specific, trait-specific ageing in the wild. Fairy-wrens are relatively long-lived for a small passerine, with individuals of both sexes reaching a maximum lifespan at over ten years of age. Male and female fairy-wrens have disparate life histories. Females always disperse as juveniles while males will often remain on their natal territory as subordinate 'helpers', helping raise the offspring of their mother in subsequent years into adulthood (Cockburn et al. 2008b). Whilst queuing for reproductive dominance may result in slower ageing in males than in females, males have a costly sexually-selected trait of moulting into blue breeding plumage each season, which could result in the opposite effect, accelerating their ageing over that of females. It is therefore not clear what form of sex-specific ageing patterns we should see in systems where these aspects of life-history exist and interact. Despite accumulating research on trait-specific ageing in wild populations, most work to date has focused on females (Lemaître and Gaillard *2017*), and studies that do investigate trait-specific ageing in both sexes are generally biased towards monogamous systems where the life-histories and senescence of both sexes are generally expected to be more similar (Bonduriansky et al. 2008). Thus despite high levels of polygamy as well as morphological and life-history sexual-dimorphism being common in birds, we are not aware of any other study of trait-specific ageing in both sexes of a bird species with considerably dimorphic life-histories. A 30-year longitudinal study of a wild population of the highly sexually dimorphic fairy-wrens provides a large sample of individuals with extremely detailed data on their reproductive histories and timing of death (Cockburn et al. 2016).

The overall aim of this study was to describe and compare patterns of ageing in an array of traits in fairy-wrens, in order to determine how ageing is shaped by their complex life history. Doing so raises several statistical and philosophical challenges. Ageing trajectories may not follow simple parametric functions and so ideally need to be modelled without constricting the effect of age to a particular functional shape. Further, in order to make quantitative comparisons of ageing between traits, it is necessary to define which features of the ageing function to quantify. In this study we therefore took a two-stage approach of (a) modelling the ageing trajectory across the lifespan of each trait non-parametrically using generalized additive mixed-models (GAMMs) (Wood 2017) and then (b) using standardized estimates from these non-parametric models, we ran a break-point analysis 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 ageing has the potential to be applied across other traits and species. Standardized methods for investigating trait-specific ageing across species are key to improving our understanding of how ageing patterns evolve. For this reason, we provide an annotated code detailing our methodology in the hope of encouraging a standardized approach to ageing research across other wild populations (appendix 1). We also provide life tables of age-specific survival and reproduction in the fairy-wren population in order to highlight how this modelling approach disentangles other sources of heterogeneity in the population, such as social context and environmental variability across years, from the specific influence of age on traits (supplementary section S1).

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 120-230 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 provisioning of young and in defence of the territory (Dunn and Cockburn 1996). About half of helpers (47%) are the sons of the female on the territory (Hajduk et al. 2018) The other half of 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 extra-pair mating in fairy-wrens. 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).

Shortly after hatching (or, for immigrants into the study area, shortly after their arrival), individuals are colour-banded, and a blood sample taken to assign parentage using SNP genotyping (Peñalba et al. 2019). Many components of life-history are continuously tracked for each individual. Nestling trajectories, such as the day of hatching, incubation and fledging are usually known within one day. Dates of mortality, immigration, emigration, changes in group composition or territory borders, and male molt from the brown winter plumage to blue breeding plumage are known within an accuracy of one week or shorter. Emigration from the study area typically only occurs 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. 2008*b*). Males that do disperse move to an immediately neighbouring territory 95% of the time (Cockburn et al. 2008*b*), 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 move subsequently, 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 females, which were excluded from the analyses in this study.

The aim of this study was to estimate patterns of ageing across a broad variety of fitness-related traits in the population. We only included individuals of known birth year and death year in analyses. This excluded any individuals that had not died yet, or that were born outside 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 year old (the age of reproductive maturity), until their death. We analyzed a total of eight traits related to female and male survival and reproduction. 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 1st (the start of the breeding season) to August 31st of the subsequent year. We treat individuals in their first year of breeding as one year olds, although in actuality individuals will vary in age from six months to one year at this point due to variation in birthdate. For results to be comparable with the results for reproductive traits, and since death cannot be differentiated from emigration in juvenile (<1 year old) females, survival was only measured from the age of one onwards. For each individual, annual survival was recorded as a binary variable.

Female Reproductive Traits

Females typically breed every year starting at the age of one (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, due to high rates of predation, as many as eight clutches may be initiated in a season (Cockburn et al. 2016). We measured three components of female reproductive fitness, described below.

- *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 January 1st). In order 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 3, and a range from 1 to 5. Within our dataset, females produced between 1 and 6 clutches within a breeding season. Females start incubation on the day she lays the last egg of her clutch. Clutches that were abandoned or depredated before incubation started were not included in analyses.

- *Female fecundity*. 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 onwards). Across the entire study period, the earliest a chick has been known to reach independence and disperse from their natal territory is five weeks after fledging and so we used the cut-off of four weeks after fledging as a measure of offspring survival to potential independence. This measure of female fecundity was chosen as it encompasses both fertility (the number of offspring produced), and effects of parental care across the breeding season. Breeding seasons where the female died before she could have possibly produced independent offspring (6 weeks after the population-level average breeding start date for the given year) were excluded from the analysis.

Male Reproductive Traits

Males may gain fertilizations from the female with which they share a territory (within-group success), or with females from outside their territory (extra-group success). Both dominant and helper males can sire young as early as at one year old. This success is related to plumage characteristics, in particular the date of their molt from brown eclipse plumage to blue breeding plumage (Cockburn et al. 2008a). Since paternity could only be determined 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; Cockburn unpublished data). We measured three components of males' reproductive fitness, described further below.

- *Molt Date.* Males are seasonally dichromatic, molting from brown plumage to nuptial blue plumage each year for the breeding season. We measured molt date as the Julian date on which a male has completely shed their brown plumage and grown the nuptial blue plumage. There is great variation between individuals in the timing of this molt, from as early as eight months before to as late as three months after the start of the breeding season (Cockburn et al. 2008*a*). Males commence displays and extra-group courtship as soon as they complete molting to blue (Mulder 1997), and males that molt earlier have higher siring success in that year's breeding season (Dunn and Cockburn 1999; Cockburn et al. 2008*a*). We tracked the date that each male completes molt in a rolling census, 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 breeding season and signify a higher quality of the trait.

- W*ithin-group success* 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, via the dominant female on the territory for helpers). Dominant males achieve more than 95% of the within-group paternity on a given territory, with the remainder attributable to the helper males (Mulder et al. 1994; Hajduk et al. 2019). Helpers are disadvantaged with respect to within-group paternity because they are more likely to be directly related to the female on the territory (as her sons, with whom she will not mate), and also because the dominant male will attempt to physically inhibit helper males from mating with the female (Cockburn et al. 2008*b*). For these reasons we excluded helper males from this analysis, and consider only the within-group success achieved by the dominant male.

- *Extra-group success* was measured as the number of offspring a male sired with females residing outside of his own territory. Extra-group siring is the primary route to reproductive success for males, with 61% of offspring in the study area being sired by extra-group males (Mulder et al. 1994; Hajduk 2018). In contrast to within-group success, helpers achieve substantial (33%) of extra-group success by parasitizing the attractiveness of their dominant (Double and Cockburn 2003; Cockburn et al. 2009). Thus, for this measure of male reproductive success we included both dominant and helper males.

Statistical Analysis

We had two aims. First, we modelled the patterns of survival and a variety of reproductive traits 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, onset of senescence, and rates of senescence amongst traits. In the appendix, we provide code which can be used to conduct this two-step analysis, which we hope will be broadly applicable to measuring ageing in any phenotypic trait in a wild population of animals (appendix 1). Additionally, we provide lifetables detailing basic metrics of reproduction and survival at each age for males and female as a point of comparison to our modelled results (supplementary section S1).

Characterizing Trait-specific Ageing: Generalized Additive Mixed Models

For each of the eight survival and reproductive traits we used nonparametric smoothing functions, implemented through generalized additive mixed models (GAMMs) to describe patterns of ageing (Wood 2017). All GAMMs were fit using the *mgcv* package in R version 3.5.0 (R Core Team 2018; Wood 2017). GAMMs are an extension of generalized linear mixed models (GLMMs), which, in addition to the basic parametric terms of GLMMs, can also include nonparametric terms that are not forced 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 REML. The penalized additive value of the number of smoothing functions is the effective degrees of freedom for the term. When the effective number of degrees of freedom is 1, the relationship is effectively linear (Wood 2017). Thus, using GAMMs allowed us to describe ageing patterns across traits without making any *a priori* assumptions about the overall shape of the trajectory, and in particular the existence and onset of trait maturation or senescence (Jones et al. 2008; Nussey et al. 2009).

We report a p-value for each non-parametric term from a Wald test, which estimates the probability that the additive value of all the smoothing functions in the spline is 0 (Amodio and Ambrosio 2014). We also report p-values for parametric values in our GAMMs. Due to the high number of terms we tested in this study, we chose the p-value of 0.01 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 first egg laid, centered by the population-level average Julian date for 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, and so a dispersion parameter below 1 is used to model under-dispersed count data. Female fecundity followed a zero-inflated count data structure, as many females failed to gain any reproductive success. We ran a two-stage zero-inflated Poisson model of female fecundity (Greene 1994; Wood et al. 2016). The zero-inflated model fits a mixture of two response variables. One response fits the total number of offspring produced, excluding some zeros in order to meet the assumptions of a Poisson count data distribution; this is fitted with a log link function. The other response variable fits the remaining excess of zeros as a Bernoulli response (fitted with a logit link function). Both male within-group and extra-group mating success also followed a zero-inflated count data structure, similar to the female fecundity data, but with a more right-skewed tail. We modelled these male reproductive traits with zero-inflated Poisson models as well, producing responses for both probability of any offspring, and number of offspring. We confirmed that these three zero-inflated models reasonably fit our data and that the use of the zero-inflated models was appropriate by running 1000 simulations of each GAMM model and plotting predicted variance against the raw data variance for each age (supplementary section S2). 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 (152/2116), males did not fully complete their molt into blue plumage, and so molt date was censored at 10 days past the latest date of molt completion on record. In another 1% of cases (24/2116) 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 September 1st – August 31st; year) as multi-level random effects. These effects controlled for the non-independence 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 modelling of ageing of reproductive traits, the problem of 'selective disappearance' can arise if covariance exists between individual reproductive fitness and lifespan 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 at a within-individual level reproduction does decline 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-year-old), but they do vary considerably in lifespan. Previous studies have found evidence for non-linear relationships between lifespan and reproductive traits (Reid et al. 2003; Nussey et al. 2009), and so lifespan was initially added as a nonparametric spline to each model. In these models lifespan generally had an effective degrees of freedom value close to 1 (supplementary section S3). Since it did not alter our results, we ultimately fitted lifespan as a (linear) parametric effect as this allowed for clear interpretation of the magnitude of the effect.

Since the fairy-wren breeding season can last up to six months of the year (Lv et al. 2019), it is fairly common for an individual to die part way through a breeding season. Death during the breeding season could plausibly lessen the estimate of annual reproductive success of both males and females solely due to the decreased window of time they have to breed in that year, irrespective of any intrinsic decline in reproductive potential. To control for the potentially confounding factor of reduced opportunity to reproduce, we included a binary factor of death during the breeding season (yes/no) in models of male and female reproductive output: this took a value of 'yes' in 9% of records.

In an individual's final year of life, their reproductive investment may differ sharply from their 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 if it was the individual's last year of life. This effect had death during the breeding season (see above) nested within it. Nesting these effects allowed us to differentiate terminal effects caused by changes in inherent quality or investment in the last year of life from the effect death during the breeding season has of reducing the duration of an individual's potential breeding season.

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.

With the exception of within-group reproductive success, 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. In order to compare reproductive ageing and survival of dominants and helpers, these models included a two-level fixed effect denoting 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 modelling 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 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 as 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 ageing 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. Traits modelled by zero-inflated GAMMs were thus modelled by two regressions, for the probability and the count portion of each model. 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 ageing 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 ageing patterns of most traits. We used the 'Segmented' package in R to assess if more than one regression line better described each trait as a function of age, and to then model any segment(s) of the regression (Muggeo 2008). For each regression, we used a Davies test to assess if 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 breakpoint at any age in the regression where the slopes delineated by that breakpoint 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 analysis in this study, we used a p-value threshold of 0.01 to assess significance. For models that did not have a significant breakpoint according to the Davies test, we used the original simple linear regression to describe the ageing pattern of that trait. For models with a significant breakpoint, 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 breakpoint 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 breakpoints were modeled. As a result, traits were represented by either 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 lifespan (excluding individuals that died before maturity) was 3.44 years (± 2.22 SD) for males and 2.97 years (± 1.73 SD) for females. Maximum adult lifespan 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 age 5 (sample sizes for each age in figure 1a,b).

Characterizing trait-specific ageing

There was substantial variation between traits in their changes across the life-span. GAMMs described how each of the eight different traits changed across age in fairy-wrens while controlling for individual and environmental confounding variables, including selective disappearance, terminal effects, dominance status in males, and variability between individuals and years (table 1, figure 1). Both male and female survival declined linearly from age one onwards (figure 1a,b). In contrast, most reproductive traits exhibited non-linear relationships with age. The one exception to this was male within-group success, which was the only trait that showed no statistically significant correlation with age, in either the probability of producing offspring, or the number of offspring (figure 1g,h).

We tested the effect of social dominance (whether a male occupied a dominant or a helper position on his territory) on extra-group reproductive success, molt date and survival (table 1). There was no effect of dominance on extra-group success, though all males beyond the age of 7 are dominants. Dominant males did have an earlier molt date (table 1). The effect of dominance on survival was negative, but non-significant (table 1, p = 0.06).

We included longevity as a covariate in each of our reproductive trait models in order to control for any selective disappearance. There was no support for any effect of longevity in any model of reproductive fitness in either male or female fairy-wrens.

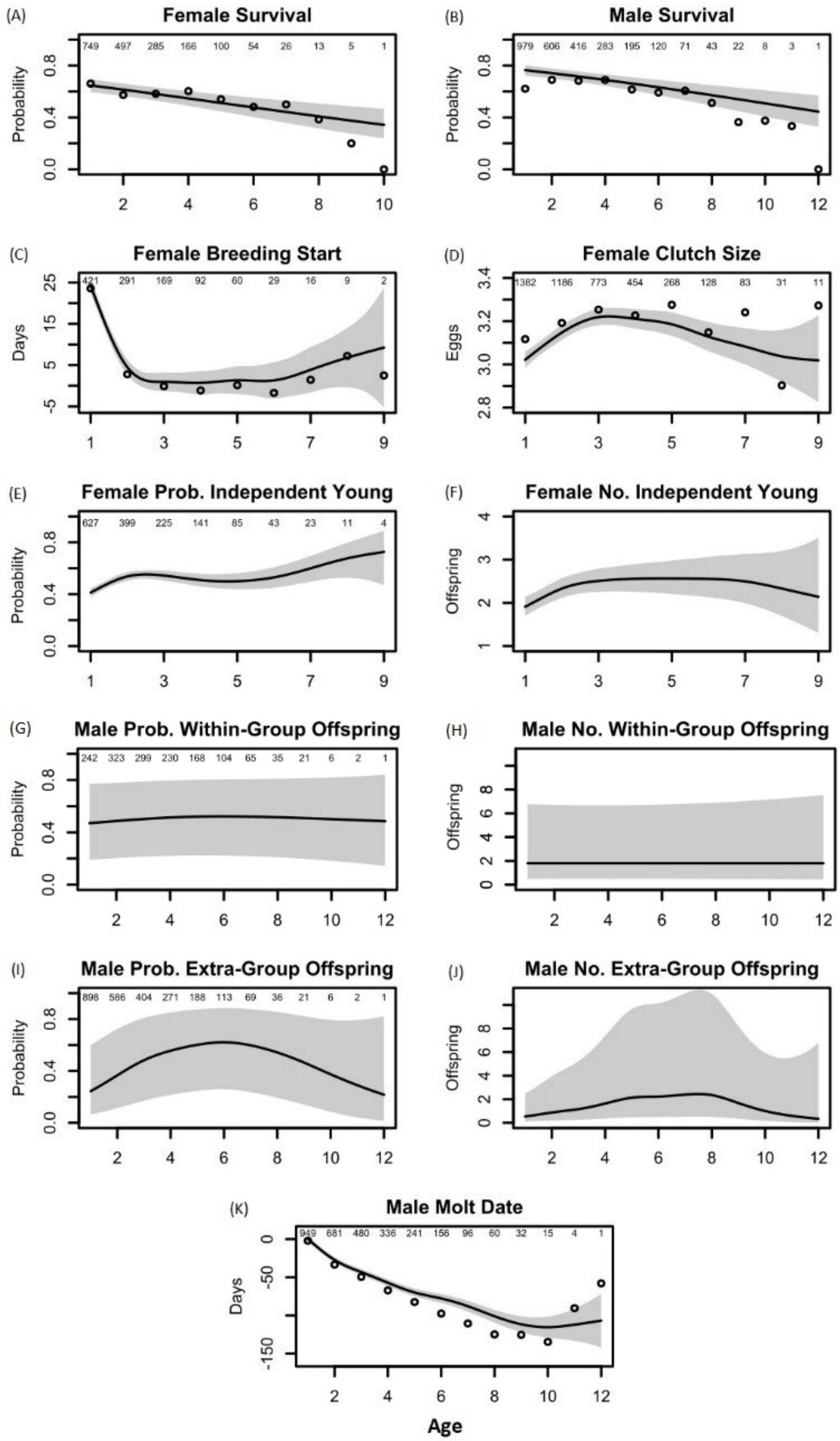

(A)
Female Survival
Probability
749 497 285 166 100 54 26 13 5 1
0.0 0.4 0.8
2 4 6 8 10
(B)
Male Survival
Probability
979 606 416 283 195 120 71 43 22 8 3 1
0.0 0.4 0.8
2 4 6 8 10 12
(C)
Female Breeding Start
Days
421 291 169 92 60 29 16 9 2
-5 5 15 25
1 3 5 7 9
(D)
Female Clutch Size
Eggs
1382 1186 773 454 268 128 83 31 11
2.8 3.0 3.2 3.4
1 3 5 7 9
(E)
Female Prob. Independent Young
Probability
627 399 225 141 85 43 23 11 4
0.0 0.4 0.8
1 3 5 7 9
(F)
Female No. Independent Young
Offspring
1 2 3 4
1 3 5 7 9
(G)
Male Prob. Within-Group Offspring
Probability
242 323 299 230 168 104 65 35 21 6 2 1
0.0 0.4 0.8
2 4 6 8 10 12
(H)
Male No. Within-Group Offspring
Offspring
0 2 4 6 8
2 4 6 8 10 12
(I)
Male Prob. Extra-Group Offspring
Probability
898 586 404 271 188 113 69 36 21 6 2 1
0.0 0.4 0.8
2 4 6 8 10 12
(J)
Male No. Extra-Group Offspring
Offspring
0 2 4 6 8
2 4 6 8 10 12
(K)
Male Molt Date
Days
949 681 480 336 241 156 96 60 32 15 4 1
-150 -50 0
2 4 6 8 10 12
Age

Figure 1 Generalized additive mixed models (GAMMs) for 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), female probability of having any offspring (E), and total number of offspring that reach the age of independence (F), male probability of siring any offspring within his territory (G) , and total number of offspring sired within his territory (H), male probability of siring any offspring outside of his territory (I), and total number of offspring sired outside his territory (J), and molt date, measured as the number of days relative to the median start of female breeding that males complete their molt into breeding plumage (K). Shaded area represents ±2 standard errors from the estimate, including the uncertainty about the overall mean. Number of data points are denoted for each age at the top of each graph. Paired graphs of probability and number of offspring (for females and males) are the results of a single zero-inflated model (E-J, see Methods for details). Empty circles represent the means of raw data values. Raw mean values and sample sizes are not included for zero-inflated models since, as mixture models, we cannot ascribe the zeros to either the binary or the conditional parts of the model.

Table 1 Spline and parametric effects describing ageing in eight traits in superb fairy-wrens using generalized additive mixed-models (GAMMs). Terms where $p < 0.01$ are in bold. Random effects of individual and year were included in each model. Full details of each model for the eight traits, 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 tables S3 – S10.

Trait	Model/ distribution	Sample size	Spline terms EDF		Parametric terms (SE)				
			Age	Incubation	Intercept	Longevity	Status [dom]	Final breed	Death [yes]
Female survival	Bernoulli	1896 (751)	**1.000**	-	**59.870 (12.960)**	-	-	-	-
Male survival	Bernoulli	2747 (979)	**1.001**	-	**45.983 (12.419)**	-	-0.191 (0.103)	-	-
Female breeding start	Gaussian	1089 (678)	**5.555**	-	**12.152 (1.414)**	-0.477 (0.353)	-	-2.714 (1.367)	-
Female clutch size	Quasi-Poisson	3865 (771)	**7.828**	**5.336**	**1.148 (0.014)**	0.003 (0.003)	-	0.005 (0.007)	-
Female fecundity	Zero-inflated	1558 (678)							
Probability	- Bernoulli		**4.417**	-	0.063 (0.110)	0.035 (0.024)	-	-0.246 (0.299)	-0.759 (0.321)
Number	- Poisson		**3.325**	-	**0.793 (0.077)**	0.017 (0.015)	-	-0.006 (0.184)	-0.114 (0.097)
Male within-group success	Zero-inflated	1440 (530)							
Probability	- Bernoulli		2.593	-	**-2.772 (0.693)**	-0.006 (0.045)	-	-0.240 (0.427)	-0.968 (0.554)
Number	- Poisson		1.005	-	**0.593 (0.183)**	0.020 (0.035)	-	-0.491 (0.460)	-0.328 (0.581)
Male extra-group success	Zero-inflated	2511 (898)							
Probability	- Bernoulli		**3.486**	-	**-4.251 (0.782)**	0.030 (0.047)	0.172 (0.164)	0.324 (0.358)	**-1.194 (0.460)**
Number	- Poisson		**4.962**	-	**1.026 (0.186)**	-0.051 (0.034)	-0.245 (0.125)	-0.417 (0.294)	0.060 (0.213)
Male molt date	Gaussian	2116 (1024)	**5.709**	-	**-42.588 (3.222)**	0.777 (0.569)	**-4.193 (1.588)**	-0.856 (1.934)	-

Note: Sample size is the number of data points included in the model, followed by the number of individuals in brackets. Sample sizes for females are lower than for males due to the biased adult sex-ratio, and sample sizes for some traits (e.g. female breeding start date) are lower than others due to exclusion of missed or uncertain records of specific life-history events. EDF is the effective degrees of freedom for the spline term. 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. Final breed is a binary term denoting whether or not it was the individual's final breeding season. Death is a binary term specifying if the individual died before the end of the breeding season in a given year which is nested within Final breed (see Methods for more details). Note that parameter estimates for Bernoulli models are on a logit scale and for Poisson and Quasi-Poisson models are on a log scale.

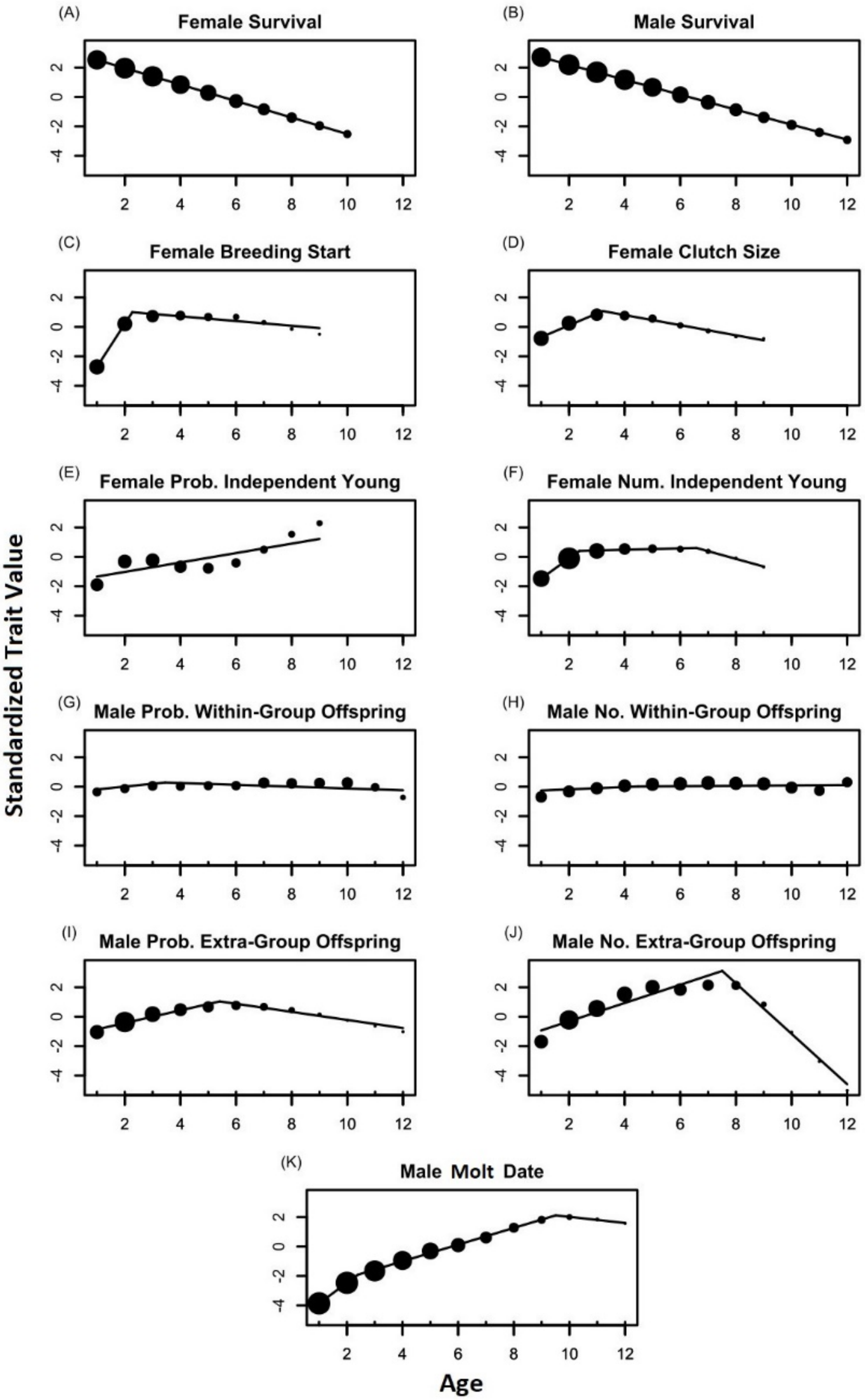
Standardized Linear Regressions

We used linear models of standardized predictions for each age in order to quantify and compare between traits the rates of maturation, the onset of senescence, and the rates of senescence. We found considerable variation between traits in all three of these components of ageing (table 2, figure 2).

There was no support for any breakpoint in the models of female or male survival, with survival declining across adulthood in both sexes, suggesting that the onset of senescence is at the age of one year, when the birds become reproductively competent.

Female reproductive traits demonstrated variable extents of trait maturation, and only some demonstrated senescence. With the exception of female probability of independent young, which improved from age one onwards (slope approaching significance with p = 0.017, table 2), the other female reproductive traits, breeding start date, clutch size, and number of independent young, all had periods of trait maturation that ended before the age of four (table 2). Both female number of independent offspring and clutch size demonstrated senescence, but with variable onset. Female number of offspring plateaued after maturation, with senescence not beginning until age 6.6, whereas clutch size showed senescence from age 3.2 (table 2). There was no evidence of senescence for female breeding start date and probability of independent offspring (table 2).

Male reproductive traits also all exhibited periods of trait maturation, and we found evidence of senescence for all male traits with the exception of molt date (table 2). Both measures of male extra-group reproductive success (probability and number of offspring) improved to mid-ages (ages 5.4 and 7.5 respectively), followed by senescent declines (table 2). Although within-group reproductive success probability and number also improved and then declined after middle ages as well, the rates of these changes were considerably smaller than any of the other significant slopes in the 9 traits measured (table 2, figure 2). Molt date had the steepest rate of maturation of any trait up until age 2.4, followed by a shallower rate of improvement to age 9.5, after which there was no change with age (table 2).



(A)
Female Survival
(B)
Male Survival
(C)
Female Breeding Start
(D)
Female Clutch Size
(E)
Female Prob. Independent Young
(F)
Female Num. Independent Young
(G)
Male Prob. Within-Group Offspring
(H)
Male No. Within-Group Offspring
(I)
Male Prob. Extra-Group Offspring
(J)
Male No. Extra-Group Offspring
(K)
Male Molt Date
Standardized Trait Value
Age
2
0
-2
-4
2
4
6
8
10
12

Figure 2 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), female probability of having any offspring reaching the age of independence (E), and total number of offspring that reach the age of independence (F), male probability of siring any offspring within his territory (G) , and total number of offspring sired within his territory (H), male probability of siring any offspring outside his territory (I), and total number of offspring sired outside his territory (J), and molt date, measured as the number of days relative to the median start of female breeding that males complete their molt into breeding plumage (K). Filled circles represent the raw data, which are the estimates for each age predicted from the corresponding 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 (which will be determined by sample size at that age). Regressions are weighted by these inverse standard errors. Regressions which are continuous did not have a significant break point and regressions with two break points (F and K) had a second significant break point ($p < 0.01$).

Table 2 The estimates for the effect of age on each trait in a linear regression, or a segmented linear regression (when significant breakpoint(s) in the model were found). The data values analyzed in these models were the mean values for each age as predicted by the respective GAMM model (table 2), 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. Terms where $p < 0.01$ are in bold

Trait	Across-life slope (99% CI)	Early-adulthood slope (99% CI)	First Breakpoint age (99% CI)	Mid-life slope (99% CI)	Second Breakpoint age (99% CI)	Late-life slope (99% CI)
Female survival	**-0.560 (-0.560, -0.560)**	-	-	-	-	-
Male survival	**-0.511 (-0.511, -0.511)**	-	-	-	-	-
Female breeding start date	-	**2.921 (2.132, 3.710)**	2.2 (2.1, 2.5)	**-**	-	-0.160 (-0.336, 0.015)
Female clutch size	-	**0.803 (0.513, 1.093)**	3.2 (2.9, 3.6)	-	-	**-0.344 (-0.497, -0.191)**
Female fecundity						
- *probability of offspring*	0.320 (-0.040, 0.681)	-	-	-	-	-
- *number of offspring*	-	**1.370 (1.061, 1.678)**	2.4 (2.2, 2.5)	0.048 (-0.085, 0.181)	6.6 (6.1, 7.1)	**-0.523 (-0.885, -0.161)**
Male molt date	**-**	**1.395 (1.033, 1.756)**	2.4 (2.0, 2.8)	**0.567 (0.504, 0.630)**	9.5 (8.9, 10.1)	-0.208 (-0.651, 0.235)
Male within-group success						
- *probability of offspring*	-	**0.192 (0.134, 0.250)**	3.4 (3.1, 3.8)	-	-	**-0.062 (-0.081, -0.043)**
- *number of offspring*	-	**0.078 (0.072, 0.084)**	4.5 (4.0, 4.9)	-	-	**0.013 (0.009, 0.017)**
Male extra-group success						
- *probability of offspring*	-	**0.431 (0.290, 0.571)**	5.4 (4.7, 6.1)	-	-	**-0.275 (-0.441, -0.110)**
- *number of offspring*	-	**0.621 (0.318, 0.925)**	7.5 (6.7, 8.3)	-	-	**-1.714 (-2.866, -0.562)**

Discussion

We investigated ageing patterns across survival and six reproductive traits in female and male fairy-wrens. The ageing of these traits was highly asynchronous, with variable rates and durations of both early-adulthood improvements and late-life declines, with some traits not showing any period of maturation in early adulthood, and others not showing 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). Below we discuss how the patterns of ageing in fairy-wrens fit with theory and empirical research on ageing, and consider how the distinctive ecological and evolutionary forces faced by this species may be driving these patterns.

Survival

In both sexes annual survival probability declined from their first year of adult life at similar rates (table 2). Similar to other small passerines, the first days immediately after fledging are the single most dangerous time for both sexes (Cockburn, *unpublished data*). Survival therefore 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.

Given the highly divergent life-histories of the two sexes, it was initially surprising that there was no apparent difference in survival senescence. However *post-hoc* analysis (supplementary section S5) indicated that there was no difference in survival probability between the sexes. Williams (1957) predicted that survival senescence should be more rapid in the sex with the higher mortality risk, so the comparable rates of survival senescence are therefore in line with this part of Williams' theory. Life-history factors which mold annual mortality risk are complex and can be interacting. Although the annual molt into nuptial plumage increases mortality risk in males, other aspects of male life-history may decrease their mortality, such as cooperative breeding delaying peak reproductive performance.

The onset of survival senescence in the first year of breeding is also aligned with the classic evolutionary ageing 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 this delayed survival senescence in these other species is that, when the actual possibility of reproductive success occurs sometime 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 (supplementary table S1), and 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 modelled 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 ageing theories, which did not take into account life-history trade-offs. It is also worth noting that differences related to which life-history factors are controlled for within any given study may also explain some of the disparity in ageing patterns seen between species more broadly.

Reproduction

The effects of age on 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 ageing patterns amongst the reproductive traits. For female fecundity, the standardized regressions showed evidence that the probability of any independent young slowly increased across all ages ($p = 0.017$), whilst the (non-zero-inflated) number of independent young increased in early adulthood, before plateauing and demonstrating senescence at late ages (table 2). These differences between probability and number of independent young suggest that females may shift their reproductive strategies with age, investing more in quality and less in quantity in later life.

For males, our results suggest that sexual selection plays an important role in reproductive ageing. There were dramatic age-related changes in both the probability and the number of extra-group offspring, whereas the effects of age on within-group offspring in both the GAMM and standardized regressions were much weaker or non-existent. In the fairy-wren system, extra-group mating success is almost entirely driven by female choice, while within-group success is dependent largely on social circumstances such as the presence of helpers or the relatedness between the females and the adult males in her social group (Double and Cockburn 2000). These differences between extra- versus within-group success indicate that male reproductive ageing may be predominately driven by sexual selection, as a female preference for middle-aged males could drive the improvements in extra-pair success in early-adulthood, followed by declines in late-life.

In addition to the larger change with age in extra-group reproductive success (compared to within-group success) in males, the two measures of extra-group success also reached their peaks at later ages than did the within-group success measures, by 2 and 3 years for probability and number of offspring, respectively (table 2). 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 extra-group success so late in life seen here. Earlier molt date is a signal of male quality and a strong predictor of male reproductive success (Dunn and Cockburn 1999; Cockburn et al. 2008*a*). Since molt date steadily improved by shifting earlier with age until very old ages (table 1, figure 1K), this pattern is likely a major contributor to the observed pattern of increase in male extra-group success. To investigate this prediction further, we added molt date as an additional explanatory variable to the GAMM of extra-pair success and compared the rates of maturation in the subsequent segmented regressions to the rates estimated by our model which did not control for molt date. We found that there was still early-life trait improvement when controlling for molt, but the rate of improvement was reduced by approximately half for the number of extra-pair young (supplementary section S6). This indicates that the improvement in molt date with age does indeed play a considerable role in driving early-life improvements in extra-group success.

That molt date continuously shifts to earlier dates and shows no real evidence of senescence may seem counterintuitive given the evidence in this study of significant survival senescence from the onset of adulthood. Given that the production of 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 potential reproduction (Kirkwood and Rose 1991). Thus, increased investment in secondary sexual traits which improve reproductive success within the 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, in the fairy-wrens, extra-pair mating success displays senescence at ages where molt date continues to improve, suggesting that other factors, unrelated to molt date, are also influencing extra-pair 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 extra-group success in old males.

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

Individual Variability in Ageing

We controlled for any potential correlation between lifespan 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 higher or lower annual fitness, and there is no indication of selective disappearance in the population. In a recent collation of studies reporting correlations between lifespan and reproductive fitness, Vedder and Bouwhuis (2018) found that a lack of any association is not uncommon, as no such correlations were found in five out of 14 species of bird. In line with the a lack of consistent differences in quality between individuals, in the models of most of our traits the random effect of individual identity explained a very small amount of the variance in comparison with, for example, the random effect of year, which in most models explained several orders of magnitude more variance (supplementary section S4). This suggests that variation in performance in the population is more driven by extrinsic conditions rather than variation in intrinsic quality. The one exception to this was moult 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. The variation explained by the ID x age term was significant in a Wald test ($p < 0.001$), which suggests that males vary in the shapes of their molt ageing patterns. We plan to further investigate how both genes and the environment contribute to this individual-level variation in molt ageing in a future paper.

Conclusions

Within our study population of superb fairy-wrens, we found marked differences between ageing trajectories of survival and reproductive traits, between male and female reproduction, and between individual aspects of reproduction within the sexes. Despite strong declines in survival from age one in both sexes, senescence was only detected in five of the nine models of reproductive traits, and only at later ages between 2.4 and 7.5 years of age. It is likely that these instances of reproductive senescence could only be identified due to the sheer scale of the study’s sampling effort. This finding highlights the difficulty in confidently assessing late-life ageing 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.

Our study adds to the increasing body of literature that demonstrates that traits do not age in unison, and suggests that the pattern of ageing in each trait will be molded by unique selection pressures. The exact nature of these selection pressures may be difficult to infer due to 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 ageing across traits, populations, and studies. We have presented here a comprehensive analytical approach to quantifying ageing patterns in traits that follow very different ageing 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 multi-trait comparisons within other populations, and also for comparisons across populations. To facilitate this, we have provided annotated code of our methods (appendix 1), in the hopes that we can increase the number of future studies that use standardized ageing analyses.

Acknowledgements

We are grateful to the Australian National Botanic Garden for permission to work at the study site and for logistical support. We also thank the many field assistants who contributed to data collection over the years. Our research was licensed by the Australian National University Animal Experimentation Ethics Committee. We thank Daniel Nussey and Jacob Moorad for helpful discussions. We thank the Australian Research Council for long-term funding of the superb fairy-wren project via grants to AC and LK, of which the most recent grant for the data in this study was DP150100298.

References

Akçay, E., and J. Roughgarden. 2007. Extra-pair paternity in birds: Review of the genetic benefits. Evolutionary Ecology Research 9:855–868.

Amodio, S., and A. D. Ambrosio. 2014. On concurvity in nonlinear and nonparametric regression models. Statistica 74:81–94.

Andersson, M. 1986. Evolution of Condition-Dependent Sex Ornaments and Mating Preferences : Sexual Selection Based on Viability Differences. Evolution 40:804–816.

Baudisch, A. 2011. The pace and shape of ageing. Methods in Ecology and Evolution 2:375–382.

Berger, V., J. F. Lemaitre, D. Allaine, J.-M. M. Gaillard, A. Cohas, J.-F. Lemaître, D. Allainé, et al. 2015*a*. Early and adult social environments have independent effects on individual fitness in a social vertebrate. Proceedings of the Royal Society B: Biological Sciences 282:20151167.

Berger, V., J. Lemaître, J. Gaillard, A. Cohas, V. Berger, J. Lemaître, J. Gaillard, et al. 2015*b*. How do animals optimize the size — number trade-off when aging ? Insights from reproductive senescence patterns in marmots. The Ecological Society of America 96:46–53.

Bonduriansky, R., A. Maklakov, F. Zajitschek, and R. Brooks. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. Functional Ecology 22:443–453.

Bouwhuis, S., A. Charmantier, S. Verhulst, and B. C. Sheldon. 2010. Individual variation in rates of senescence: Natal origin effects and disposable soma in a wild bird population. Journal of Animal Ecology 79:1251–1261.

Bouwhuis, S., R. Choquet, B. C. Sheldon, and S. Verhulst. 2012. The Forms and Fitness Cost of Senescence: Age-Specific Recapture, Survival, Reproduction, and Reproductive Value in a Wild Bird Population. American Naturalist 179:E15–E27.

Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings of the Royal Society B-Biological Sciences 276:2769–2777.

Bouwhuis, S., and O. Vedder. 2017. Avian Escape Artists? Patterns, Processes and Costs of Senescence in Wild Birds. Pages 156–174 *in* R. P. Shefferson, O. R. Jones, and R. Salguero-Gómez, 1st eds. The Evolution of Senescence in the Tree of Life. Cambridge University Press, Cambridge.

Bowers, E. K., A. M. Forsman, B. S. Masters, B. G. P. Johnson, L. S. Johnson, S. K. Sakaluk, and C. F. Thompson. 2015. Increased extra-pair paternity in broods of aging males and enhanced recruitment of extra-pair young in a migratory bird. Evolution 69:2533–2541.

Brunet-Rossinni, A. K., and S. N. Austad. 2006. Senescence in Wild Populations of Mammals and Birds. Pages 243–266 *in* Handbook of the Biology of Aging (6th ed.). Academic Press, London.

Cheng, R. 2017. Non-standard parametric statistical inference. Oxford University Press, Oxford.

Cleasby, I. R., and S. Nakagawa. 2012. The influence of male age on within-pair and extra-pair paternity in passerines. Ibis 318–324.

Clutton-Brock, T. H., and K. Isvaran. 2007. Sex differences in ageing in natural populations of vertebrates. Proceedings of the Royal Society B. 274:3097–104.

Cockburn, A., L. Brouwer, N. Margraf, H. L. Osmond, and M. Van de Pol. 2016. Superb fairy-wrens: making the worst of a good job. Pages 133–149 *in* W. D. Koenig and J. L. Dickinson, 1st eds. Cooperative breeding in vertebrates: studies of ecology, evolution and behavior. Cambridge University Press.

Cockburn, A., A. H. Dalziell, C. J. Blackmore, M. C. Double, H. Kokko, H. L. Osmond, N. R. Beck, et al. 2009. Superb fairy-wren males aggregate into hidden leks to solicit extragroup fertilizations before dawn. Behavioral Ecology 20:501–510.

Cockburn, A., H. L. Osmond, and M. C. Double. 2008*a*. Swingin' in the rain: condition dependence and sexual selection in a capricious world. Proceedings of the Royal Society B: Biological Sciences 275:605–612.

Cockburn, A., H. L. Osmond, R. A. Mulder, M. C. Double, and D. J. Green. 2008*b*. Demography of male reproductive queues in cooperatively breeding superb fairy-wrens Malurus cyaneus. Journal of Animal Ecology 77:297–304.

Cockburn, A., H. L. Osmond, R. A. Mulder, D. J. Green, and M. C. Double. 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren Malurus cyaneus. Journal of Animal Ecology 72:189–202.

Cooper, E.B. and Kruuk, L.E.B. 2018 Ageing with a silver-spoon: A meta-analysis of the effect of developmental environment on senescence. Evolution Letters 2: 460-471.

Cornwallis, C. K., R. Dean, and T. Pizzari. 2014. Sex-Specific Patterns of Aging in Sexual Ornaments and Gametes. The American Naturalist 184:E66–E78.

Coulson, J. C., and J. A. Fairweather. 2001. Reduced reproductive performance prior to death in the

Black-legged Kittiwake: Senescence or terminal illness? Journal of Avian Biology 32:146–152.

Davies, R. B. 1987. Hypothesis Testing when a Nuisance Parameter is Present Only Under the Alternatives. Biometrika Trust 74:33–43.

Descamps, S., S. Boutin, D. Berteaux, J. Gaillard, and S. Boutin. 2008. Age-Specific Variation in Survival , Reproductive Success and Offspring Quality in Red Squirrels: Evidence of Senescence 117:1406–1416.

Double, M. C., and A. Cockburn. 2003. Subordinate superb fairy-wrens (Malurus cyaneus) parasitize the reproductive success of attractive dominant males. Proceedings of the Royal Society B: Biological Sciences 270:379–384.

Double, M. C., R. Peakall, N. R. Beck, and A. Cockburn. 2005. Dispersal , Philopatry , and Infidelity : Dissecting Local Genetic Structure in Superb Fairy-Wrens (Malurus cyaneus). Evolution 59:625–635.

Double, M., and A. Cockburn. 2000. Pre-dawn infidelity: Females control extra-pair mating in superb fairy-wrens. Proceedings of the Royal Society B: Biological Sciences 267:465–470.

Dunn, P., and A. Cockburn. 1999. Extrapair Mate Choice and Honest Signaling in Cooperatively Breeding Superb Fairy-Wrens. Evolution 53:938–946.

Dunn, P. O., and A. Cockburn. 1996. Evolution of Male Parental Care in a Bird with Almost Complete Cuckoldry. Evolution 50:2542–2548.

Evans, S. R., L. Gustafsson, and B. C. Sheldon. 2011. Divergent patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. Evolution 65:1623–1636.

Froy, H., R. A. Phillips, A. G. Wood, D. H. Nussey, and S. Lewis. 2013. Age-related variation in reproductive traits in the wandering albatross: evidence for terminal improvement following senescence. Ecology Letters 16:642–649.

Gaillard, J.-M., and J.-F. Lemaître. 2017. The Williams' legacy: A critical reappraisal of his nine predictions about the evolution of senescence. Evolution 71:1–61.

Greene, J. 1994. Accounting for Excess Zeros and Sample Selection in Poisson and Negative Binomial Regression Models. NYU Working Paper No. EC-94-10 9:265–265.

Gustafsson, L., and T. Part. 1990. Acceleration of senescence in the collared flycatcher ficedula-albicollis by reproductive costs. Nature 347:279–281.

Hajduk, G.K. 2019. Interplay between inbreeding, infidelity and social environment in a cooperatively-breeding bird. PhD Dissertation, The University of Edinburgh.

Hajduk, G.K, A. Cockburn, N. Margraf, H.L. Osmond, C.A. Walling, and L.E.B. Kruuk. 2018. Inbreeding, inbreeding depression, and infidelity in a cooperatively breeding bird. Evolution 72:1500-1514.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Hammers, M., S. A. Kingma, K. Bebbington, J. van de Crommenacker, L. G. Spurgin, D. S. Richardson, T. Burke, et al. 2015. Senescence in the wild: Insights from a long-term study on Seychelles warblers. Experimental Gerontology 71:69–79.

Hammers, M., D. S. Richardson, T. Burke, and J. Komdeur. 2013. The impact of reproductive investment and early-life environmental conditions on senescence: support for the disposable soma hypothesis. Journal of Evolutionary Biology 26:1999–2007.

Hansen, T. F., and D. K. Price. 1995. Good genes and old age: Do old mates provide superior genes? Journal of Evolutionary Biology 8:759–778.

Hayward, A. D., J. Moorad, C. E. Regan, C. Berenos, J. G. Pilkington, J. M. Pemberton, and D. H. Nussey.

2015. Asynchrony of senescence among phenotypic traits in a wild mammal population. Experimental Gerontology 71:56–68.

Hayward, A. D., A. J. Wilson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2013. Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. Functional Ecology 27:184–195.

Hooper, A. K., J. Lehtonen, L. E. Schwanz, and R. Bonduriansky. 2018. Sexual competition and the evolution of condition-dependent ageing. Evolution Letters 2:37–48.

Hsu, Y. H., J. Schroeder, I. Winney, T. Burke, and S. Nakagawa. 2015. Are extra-pair males different from cuckolded males? A case study and a meta-analytic examination. Molecular Ecology 24:1558–1571.

Jones, C. G., P. M. Thompson, J. Brommer, R. McCleery, M. A. C. Nicoll, J.-M. Gaillard, S. Tuljapurkar, et al. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. Ecology Letters 11:664–673.

Jones, O. R., A. Scheuerlein, R. Salguero-Gómez, C. G. Camarda, R. Schaible, B. B. Casper, J. P. Dahlgren, et al. 2014. Diversity of ageing across the tree of life. Nature 505:169–73.

Kervinen, M., C. Lebigre, R. V. Alatalo, H. Siitari, and C. D. Soulsbury. 2015. Life-History Differences in Age-Dependent Expressions of Multiple Ornaments and Behaviors in a Lekking Bird. The American Naturalist 185:13–27.

Kim, S. Y., A. Velando, R. Torres, and H. Drummond. 2011. Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird. Oecologia 166:615–626.

Kindsvater, H. K., S. H. Alonzo, M. Mangel, and M. B. Bonsall. 2010. Effects of age- and state-dependent allocation on offspring size and number. Evolutionary Ecology Research 12:327–346.

Kirkwood, T. B. L., and M. R. Rose. 1991. Evolution of Senescence: Late Survival Sacrificed for Reproduction. Philosophical Transactions of the Royal Society B: Biological Sciences 332:15–24.

Kokko, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. Behavioral Ecology and Sociobiology 41:99–107.

Lemaître, J.-F., V. Berger, C. Bonenfant, M. Douhard, M. Gamelon, F. Plard, and J.-M. Gaillard. 2015. Early-late life trade-offs and the evolution of ageing in the wild. Proceedings. Biological sciences B: The Royal Society 282:20150209.

Lemaître, J.-F., and J.-M. Gaillard. 2017. Reproductive senescence: new perspectives in the wild. Biological Reviews 92:2182-2199.

Loison, A., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and J. M. Jullien. 1999. Age-specific survival in five populations of ungulates: Evidence of senescence. Ecology 80:2539–2554.

Lv, L., Y. Liu, H. L. Osmond, A. Cockburn, and L. E. B. Kruuk. 2019. When to start and when to stop: Effects of climate on breeding in a multi-brooded songbird. Global Change Biology 00:1–15.

Massot, M., J. Clobert, L. Montes-Poloni, C. Haussy, J. Cubo, and S. Meylan. 2011. An integrative study of ageing in a wild population of common lizards. Functional Ecology 25:848–858.

McCleery, R. H., C. M. Perrins, B. C. Sheldon, and A. Charmantier. 2008. Age-specific reproduction in a long-lived species: The combined effects of senescence and individual quality. Proceedings of the Royal Society B: Biological Sciences 275:963–970.

McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (Dama dama). Proceedings of the Royal Society B: Biological Sciences 269:1129–1137.

Monaghan, P., A. Charmantier, D. H. Nussey, and R. E. Ricklefs. 2008. The evolutionary ecology of senescence. Functional Ecology 22:371–378.

Muggeo, V. M. R. 2008. segmented: an R Package to Fit Regression Models with Broken-Line Relationships.

Mulder, R. A. 1997. Extra-group Courtship Displays and Other Reproductive Tactics of Superb Fairy-wrens. Australian Journal of Zoology 45:131–143.

Mulder, R. A., P. O. Dunn, A. Cockburn, K. A. Lazenby-Cohen, and M. J. Howell. 1994. Helpers Liberate Female Fairy-Wrens from Constraints on Extra-Pair Mate Choice. Proceedings of the Royal Society B: Biological Sciences 255:223–229.

Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J. M. Gaillard. 2008. Measuring senescence in wild animal populations: Towards a longitudinal approach. Functional Ecology 22:393–406.

Nussey, D. H., L. E. B. Kruuk, A. Morris, M. N. Clements, J. M. Pemberton, and T. H. Clutton-Brock. 2009. Inter- and Intrasexual Variation in Aging Patterns across Reproductive Traits in a Wild Red Deer Population. American Naturalist 174:342–357.

Péron, G., O. Gimenez, A. Charmantier, J. M. Gaillard, and P. A. Crochet. 2010. Age at the onset of senescence in birds and mammals is predicted by early-life performance. Proceedings of the Royal Society B: Biological Sciences 277:2849–2856.

Piper, W. H., K. M. Brunk, J. A. Flory, and M. W. Meyer. 2017. The long shadow of senescence: age impacts survival and territory defense in loons. Journal of Avian Biology 48:1062–1070.

Potti, J., D. Canal, and D. Serrano. 2013. Lifetime fitness and age-related female ornament signalling: Evidence for survival and fecundity selection in the pied flycatcher. Journal of Evolutionary Biology 26:1445–1457.

Preston, B. T., M. Saint Jalme, Y. Hingrat, F. Lacroix, and G. Sorci. 2011. Sexually extravagant males age more rapidly. Ecology Letters 14:1017–1024.

Promislow, D. 2003. Mate choice, sexual conflict, and evolution of senescence. Behavior Genetics 33:191–201.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Vienna, Austria.

Radwan, J. 2003. Male age, germline mutations and the benefits of polyandry. Ecology Letters 6:581–586.

Reed, T. E., L. E. B. Kruuk, S. Wanless, M. Frederiksen, E. J. A. Cunningham, and M. P. Harris. 2008. Reproductive Senescence in a Long-Lived Seabird: Rates of Decline in Late-Life Performance Are Associated with Varying Costs of Early Reproduction. The American Naturalist 171:E89–E101.

Reid, J. M., E. M. Bignal, S. Bignal, D. I. McCracken, and P. Monaghan. 2003. Age-specific reproductive performance in red-billed choughs Pyrrhocorax pyrrhocorax: patterns and processes in a natural population. Journal of Animal Ecology 72:765–776.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Schroeder, J., T. Burke, M. E. Mannarelli, D. A. Dawson, and S. Nakagawa. 2012. Maternal effects and heritability of annual productivity. Journal of Evolutionary Biology 25:149–156.

Stearns, S. C. 1980. A new view of life-history evolution. Oikos 35:266–281.

Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. Functional Ecology 3:259–268.

Tompkins, E. M., and D. J. Anderson. 2018. Sex-specific patterns of senescence in Nazca boobies linked to mating system. Journal of Animal Ecology 88:986–1000.

van de Pol, M., and S. Verhulst. 2006. Age - Dependent Traits : A New Statistical Model to Separate Within - and Between - Individual Effects. The American Naturalist 167:766–773.

Vedder, O., and S. Bouwhuis. 2018. Heterogeneity in individual quality in birds: overall patterns and insights from a study on common terns. Oikos 127:719–727.

Velando, A., J. C. Noguera, H. Drummond, and R. Torres. 2011. Senescent males carry premutagenic lesions in sperm. Journal of Evolutionary Biology 24:693–697.

Weladji, R. B., O. Holand, J. M. Gaillard, N. G. Yoccoz, A. Mysterud, M. Nieminen, and N. C. Stenseth. 2010. Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? Oecologia 162:261–271.

Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. Evolution 11:398–411.

Wood, S. N. 2001. Minimizing Model Fitting Objectives That Contain Spurious Local Minima by Bootstrap Restarting. Biometrics 57:240–244.

Wood, S.N. 2017. Generalized Additive Models: An Introduction with R (2nd edition). Chapman and Hall/CRC.

Wood, S. N., N. Pya, and B. Säfken. 2016. Smoothing Parameter and Model Selection for General Smooth Models. Journal of the American Statistical Association 111:1548–1563.

Zahavi, A. 1975. Mate selection - A selection for a handicap. Journal of Theoretical Biology 53:205–214.

Zhang, H., O. Vedder, P. H. Becker, and S. Bouwhuis. 2015. Age-dependent trait variation: the relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. Journal of Animal Ecology 84:797–807.