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ORIGINAL ARTICLE

No evidence of reproductive senescence within the natural lifespan in resident mountain chickadees (*Poecile gambeli*)

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Abstract

Reproductive aging in vertebrates is commonly characterized by an increase in reproductive performance early in life and a decline in reproductive performance late in life (i.e. senescence). However, some species do not seem to exhibit reproductive senescence, and others even exhibit increased reproductive performance throughout their lifetimes. Our understanding of the mechanisms that underly this variation in different species remains limited, in particular whether these patterns are driven by female or male contributions to reproduction in sexually-reproducing taxa. Here we report results from a longitudinal study on the relationship between age and reproductive performance in a wild, resident songbird. Our dataset included 698 breeding attempts from 551 unique mountain chickadee (*Poecile gambeli*) pairs composed of individuals aged 1 through 9 years old. First egg dates, clutch sizes, and brood sizes varied most with female age, whereas mean fledgling mass was best predicted by male age. Both female and male reproductive performance were positively associated with age, but the processes underlying these patterns differed between the sexes. Long-lived individuals of both sexes exhibited higher reproductive performance than short-lived individuals, but females also showed within-individual improvements in reproductive performance with age. In contrast, individual male reproductive performance remained stable with age, suggesting the observed population-level positive association in males was a result of lower survival of low-quality breeders. Our results reveal a lack of reproductive senescence in mountain chickadees within their naturally-observed lifespans and show that age-related reproductive patterns of both sexes can contribute to the reproductive performance of breeding pairs.

Significance statement

Old age is often associated with reduced reproductive ability, but not all vertebrates show declines in reproduction in old ages. Our understanding of the processes that underly this variation among species is lacking. Here we investigated the relative roles that female and male age play in determining the reproductive performance of breeding pairs of mountain chickadees (*Poecile gambeli*), a small montane songbird in which both parents care for offspring. We found that neither females nor males exhibit reproductive declines within their natural lifespans, and that females even exhibit gradual improvements in reproductive ability as they age. Longer-lived individuals of both sexes exhibited higher reproductive ability, suggesting that differences in individual quality also contribute to reproductive aging patterns in this species.

Keywords Aging · Senescence · Songbird · Paridae · Reproduction · Selective disappearance

Introduction

Aging is a nearly universal process in animals that can shape population dynamics when survival and reproductive performance vary across an individual's lifetime (Williams 1957; McAdam et al. 2007; Jones et al. 2014). Longitudinal studies of marked individuals have revealed that one of the most common aging patterns in vertebrates is characterized

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by an increase in reproductive performance early in life, and senescence of reproductive performance late in life (Nussey et al. 2006; Bouwhuis et al. 2009; Froy et al. 2013; Warner et al. 2016; Žák and Reichard 2021), sometimes separated by stable performance in mid-life (Hayward et al. 2013). Early-life increases in reproductive performance are often ascribed to increased foraging and reproductive experience (Forslund and Pärt 1995; Daunt et al. 2007; Saraux and Chiaradia 2022), whereas reproductive senescence is thought to be associated with processes similar to those underlying actuarial senescence, such as physiological deterioration (Williams 1957; Kirkwood 1977) and accumulation of mutations (Medawar 1952). However, some vertebrates do not appear to exhibit reproductive senescence and may even exhibit increased reproductive performance throughout their lifetimes, at least within observed lifespans in natural conditions (Holmes et al. 2003; Sparkman et al. 2007; Jones et al. 2014; Nisbet et al. 2020).

While our knowledge of the diversity of relationships between age and reproduction is improving, our understanding of the processes that underly senescence patterns in different species remains limited (Nussey et al. 2013; Lemaître and Gaillard 2017; Roper et al. 2021). In particular, one major question that remains to be answered for many sexually-reproducing iteroparous taxa is, when reproductive performance changes with age, is female or male age more important for determining the reproductive success of a breeding pair? Past studies of reproduction and age have focused primarily on females (Nussey et al. 2013; Lemaître and Gaillard 2017), but it is now undeniable for many taxa that age-related changes in male physiology (e.g. sperm quality) and male parental care can affect the reproductive performance of the females they mate with (Pizzari et al. 2008; Dean et al. 2010; Fay et al. 2016).

Socially monogamous songbirds that exhibit biparental care of offspring offer a prime opportunity to examine how sex-specific aging patterns affect pair reproduction. In songbirds, parental care from both parents is typically required to successfully raise young and the different stages of the avian nesting cycle provide insight into the relative roles that female and male age play in determining a pair's reproductive performance (Robertson and Rendell 2001; Brown and Roth 2009; Cooper et al. 2021; Pitera et al. 2021). Early in the nesting cycle, variation in lay date and the number of eggs laid (i.e., clutch size) is traditionally attributed to female physiological quality and female response to environmental conditions (Visser et al. 2009; Husby et al. 2010; Welklin et al. 2023). First egg dates and clutch sizes, however, may also be affected by male traits if females vary their reproductive investment relative to the quality of their social mate (Harris and Uller 2009; Horváthová et al. 2012; Branch et al. 2019a), or if females mate with males suffering from senescence in ejaculate quality (Pizzari et al. 2008; Dean et al. 2010; Evans et al. 2019). Later in the nesting cycle, number of fledglings (brood size) and fledgling mass are attributed to both female and male parental care as altricial songbird nestlings typically rely on feeding from both parents until after leaving the nest and learning to forage for themselves.

Most songbirds are relatively short-lived and often exhibit increased reproductive performance early in life, especially between ages 1 and 2, then exhibit either senescence of reproductive performance (e.g. Robertson and Rendell 2001; Bouwhuis et al. 2009; Dingemanse et al. 2020) or no apparent change in reproduction as they age within their naturally observed lifespans (e.g. Cooper et al. 2021; Scott et al. 2022). To our knowledge, evidence of positive associations between reproductive performance and age in songbirds is limited to studies that lack reproductive data from the oldest individuals of the species (Nol and Smith 1987; Orell et al. 1999; Orell and Belda 2002). For example, Orell et al. (1999) showed that willow tits (*Parus montanus*) exhibit increased reproductive performance from ages 1 through 5, but willow tits commonly live beyond five years (Orell and Belda 2002). Without data from all ages, it is often unclear whether these positive trends continue, stabilize, or reverse in old ages.

Identifying relationships between age and reproductive performance often requires multiple levels of investigation. Correlations between age and reproductive performance can reveal population-level relationships between age and reproduction, but population-level correlations can be explained by within or between-individual effects that lead to different conclusions (van de Pol and Verhulst 2006). For example, a positive correlation between age and reproductive performance could be caused by individuals exhibiting improved reproductive performance as they age, or by between-individual effects such as selective disappearance. Selective disappearance occurs when low-performing breeders live shorter lives than high-performing breeders, resulting in the appearance of a positive correlation between age and reproduction (Cam et al. 2002; Bouwhuis et al. 2009). Failure to test for between-individual effects can lead to faulty conclusions when population-level relationships are assumed to show within-individual change (van de Pol and Verhulst 2006). Support for between versus within-individual effects can be investigated by splitting the age term in a correlational population-level model into two components, one to represent within-individual change, and one to represent between-individual change (e.g. selective disappearance when individuals with poor performance die early while individuals with better performance live longer, but without changing their performance with age), while including individual identity as a random effect (van de Pol and Verhulst 2006; Froy et al. 2017; Murgatroyd et al. 2018).

Here we studied how age-related changes in female and male reproductive performance influence the reproductive success of breeding pairs in a longitudinal study of the mountain chickadee (*Poecile gambeli*), a non-migratory, socially monogamous songbird that exhibits biparental care of altricial young. Previous work on this species suggests that adults (individuals age 2 and older) exhibit higher reproductive performance than first-year breeders (Pitera et al. 2021), but it is unclear how reproductive performance changes throughout an individual's lifetime. We hypothesized that like many short-lived songbirds, including the closely-related great tit (*Parus major*; Bouwhuis et al. 2009), wild mountain chickadees would exhibit improved breeding performance in early ages, then exhibit senescence of reproductive performance in late ages within their naturally observed lifespans. Alternatively, mountain chickadees may exhibit no reproductive senescence, demonstrated by stable reproductive performance in late ages or even improved reproductive performance with age (Fig. 1A). We predicted that both female and male age would contribute to pair reproductive performance since both parents are often required to successfully raise offspring (Pitera et al. 2021). We did not make any a priori predictions for whether females and males would exhibit different rates of reproductive senescence or whether relationships between age and reproductive performance would be explained more by within-individual change or by between-individual change.

Methods

Study system

We followed individually-marked mountain chickadees for 10 years (2013–2022) and measured reproductive performance over 8 breeding seasons (2015–2022) at our long-term study site at Sagehen Experimental Forest (Sagehen Creek Field Station, University of California, Berkeley) in the Sierra Nevada Mountains, California, USA. Study seasons ran from August through July and include both non-breeding (approximately August-April) and breeding periods (approximately May-July). We conducted our study at two elevations: low elevation ranged from 1965 to 2070 m and high elevation ranged from 2380 to 2590 m. While these sites are separated by only 3.5 km in distance and approximately 500 m in elevation, high elevations are harsher and more unpredictable, associated with substantially higher and longer lasting snow cover and stronger and more frequent snowstorms during winter than the low elevations (Kozlovsky et al. 2018; Whitenack et al. 2023). Following short-distance post-natal dispersal during late summer (< 1 km, McCallum et al. 2020; LEW et al. unpubl. data), mountain chickadees are highly resident and remain in these locations for the rest of their lives. Birds were captured using mist nets at established feeders during the autumn and winter and by hand at nest boxes during the breeding season. Our intensive banding efforts resulted in nearly all birds at our study site being banded every year. Nestlings were banded 16 days post-hatch with a metal United States Geological Survey numbered band, and adults were banded with one to two colored plastic bands and an additional colored band with an embedded Passive Integrated Transponder (PIT) tag. Nestlings recaptured after fledging were banded with a PIT tag and a color band.

Most individuals that were not banded as nestlings were aged as first-year or adult (age 2 or greater) using multiple plumage characteristics (Pyle 2022; validated in our study system using recaptures of nestlings banded in the nest). Individuals in their first year of age were considered first-year breeders and assigned age 1, whereas individuals past their first breeding season were considered adults and assigned age 2. New individuals with unknown histories were assumed to be first-year and assigned age 1 considering that we exhaustively band birds (both during breeding and non-breeding seasons) and that mountain chickadees are highly philopatric following the post-natal dispersal (Branch et al. 2019b; Heinen et al. 2021; Pitera et al. 2021). Across 10 years of our study, approximately 31% of males and females were included in this unknown history category. Thus, there is a small hypothetical possibility that a small subset of individuals may be older than reported, but in no cases was an individual younger than their assigned age. However, to be sure these individuals did not influence our conclusions, we also analyzed relationships between age and breeding using a reduced dataset that did not include these birds with unknown histories (see supplemental results). The oldest bird ever recorded in our population was 11 years old but very few individuals live past 7 years of age: of 322 first-year and adult birds banded in our first two years, only 2.5% lived longer than 7 years. Therefore, our range of demographic data includes female and male breeders from ages 1 through 9 and covers the majority of ages in our population.

Mountain chickadees nest in secondary cavities, including nest boxes, allowing for monitoring of all stages of the nesting cycle. We monitored breeding at approximately 350 (number varied slightly among the years) nest boxes across both elevations from May through July of each year and measured reproductive performance through measurement of first egg dates, clutch sizes, brood sizes, and mean fledgling mass (Sonnenberg et al. 2023; Whitenack et al. 2023). Brood size (number of fledglings) and fledgling mass (g)

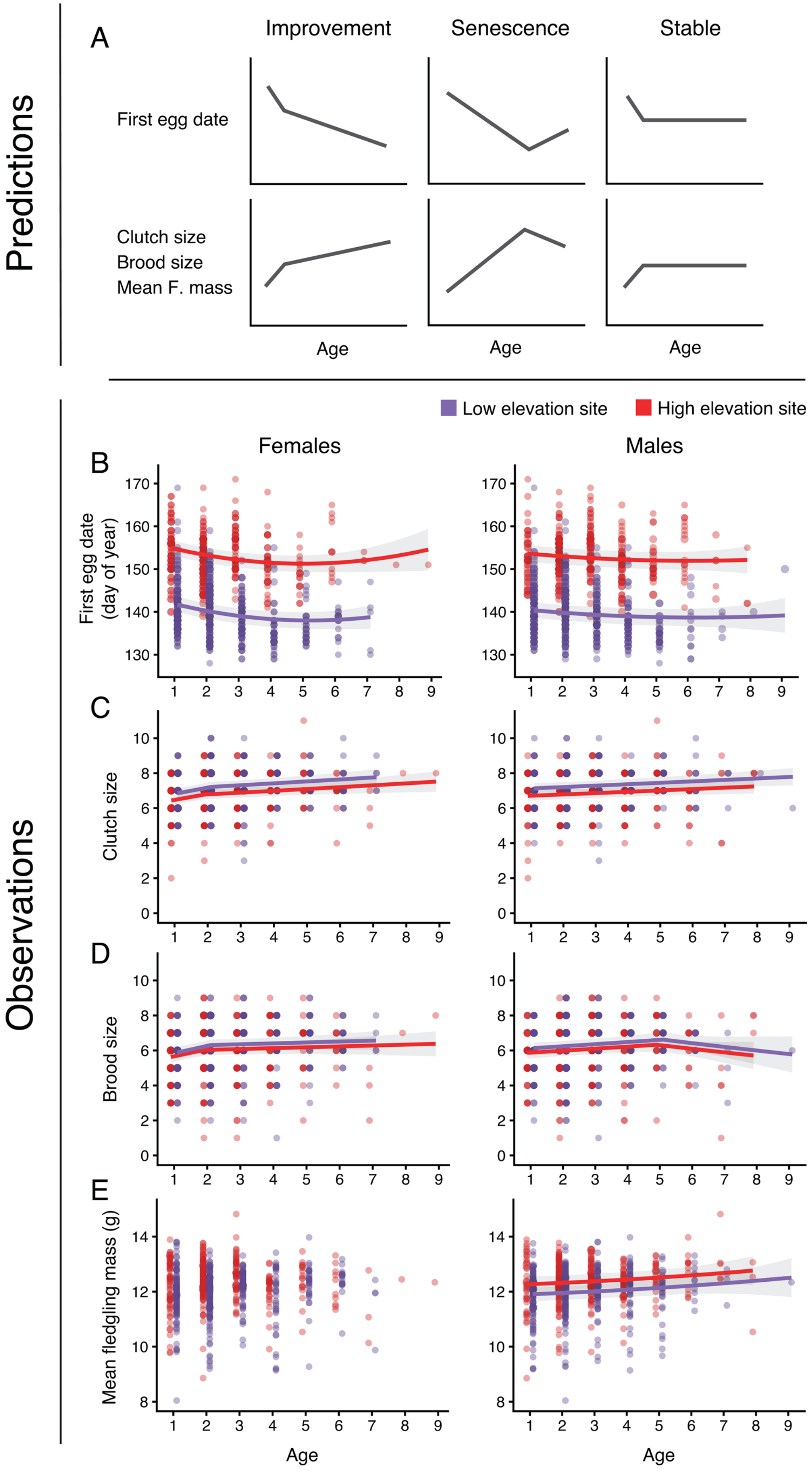

Fig. 1 Population-level relationships between age and reproductive performance for female and male mountain chickadees. **A**) Predictions for each reproductive performance variable. Improvement with age would be characterized by an overall negative correlation between age and first egg date and by an overall positive correlation between age and the remaining variables. Senescence would be characterized by an increase in first egg date and a decline in the remaining variables in late ages. Following panels show the observed relationships between female and male age and **B**) first egg date, **C**) clutch size, **D**) brood size, and **E**) mean fledgling mass from the combined-sex models. Brood size was included as a fixed effect when modeling mean fledgling mass. Lines represent model predictions and 95% confidence intervals of statistically significant relationships ($p < 0.05$). Points show raw data and the lines and points are colored relative to their respective elevation

were measured on day 16. Nestlings typically fledge the nest between day 20 and 24 (Grundel 1987), but nearly all young alive at day 16 fledge successfully as we check all nest boxes after fledging (VVP personal observation). Thus, brood size at day 16 represents the number of fledglings. Breeding pair composition was identified through observations of color-banded pairs interacting with nest boxes and via PIT-tag reads at nest boxes equipped with Radio Frequency Identification (RFID) antennas (Bridge et al. 2019). We identified the sex of breeding birds based on the following well-established characteristics: only females incubate, females are the only sex of this species with brood patches, and only males have large cloacal protuberances during breeding. We analyzed data from initial nests only, as second nests are rare (Whitenack et al. 2023). It was not possible to record data blind because our study involved focal animals in the field.

Age and reproductive performance

We first examined relationships between age and reproductive performance separately for males and females to determine how each sex's age related to each reproductive performance variable (van de Pol and Verhulst 2006; Froy et al. 2017; Murgatroyd et al. 2018). Reproductive performance variables were modeled separately by constructing multiple candidate models for each variable that included reproductive performance (first egg date, clutch size, brood size, or mean fledgling mass) as the response, elevation (high or low) as a fixed effect, and individual identity and year as random effects. Age was included as a linear, quadratic, or single threshold fixed effect. Threshold models test for different slopes on either side of a specified breakpoint and are especially useful for determining the age at which reproductive senescence begins (Berman et al. 2009; Froy et al. 2017; Murgatroyd et al. 2018). Ages ranged from 1 to 9 years in our dataset, so seven threshold models were constructed with breakpoints at each age from ages 2 through 8. We also constructed a null model for each reproductive performance variable that included no age term in the model.

In total, we compared the ability of 10 candidate models to explain the relationship between each sex's age and each reproductive variable using AICc (Hurvich and Tsai 1989). We considered models within 2 AICc values to have equal support, and when the model with the linear function was within 2 AICc values of the top model, we report results from the model using the linear function. Otherwise, we report the model with the lowest AICc score. We tested whether the slopes of the relationships between age and reproduction differed between the high and low elevation sites by testing whether an interaction between age and elevation improved the model using a likelihood ratio test. When the interaction did not improve the model, we modeled both elevations together, using elevation as a fixed effect. It is possible the known improvement in breeding performance between the first and second years of age (Pitera et al. 2021) could dominate the threshold models, possibly obscuring a threshold later in life associated with senescence. To account for this potential issue, we repeated these analyses for a dataset that did not include one-year-old individuals.

First egg date and mean fledgling mass were modeled using the gaussian distribution in the R package 'lme4' (Bates et al. 2015). Clutch size and brood size were modeled using the Generalized Poisson distribution and a log link in the R package 'glmmTMB' to account for underdispersion and to improve residual fit (Joe and Zhu 2005; Brooks et al. 2017). We tested the residual fit of all models using the R package 'DHARMa' (Hartig 2018) and all model assumptions were met. All analyses were conducted in R version 4.1.1 (R Core Team 2021).

Importance of female versus male age for pair breeding success

We tested the relative importance of female and male age on pair reproductive performance by combining the top female and male age functions into a single model for each reproductive performance variable. These combined-sex models included elevation as a fixed effect, with year, female identity, and male identity included as random effects. We tested whether female or male age explained more variation in each reproductive performance variable by removing the female or male age fixed effects from each model and calculating the difference in AICc compared to the full model (ΔAICc; Froy et al. 2017).

Between versus within-individual effects

The statistical models described above represent an analysis of the population-level relationships between female and male age and reproductive performance (e.g. performance of all observed individuals as a function of their age). However, individual aging trajectories can differ from population-level trends if individuals with poor performance die early whereas individuals with better performance live longer (van de Pol and Verhulst 2006). Therefore, we tested whether within-individual aging trends matched those of the population level or whether the population-level trend was explained by between-individual variation using the within-group centering approach introduced by van de Pol and Verhulst (2006). We focused these analyses on the sex whose age function best explained each reproductive performance variable in the combined sex models, as measured by ΔAICc.

Each reproductive performance variable was modeled separately and models included the same terms as the single-sex models described previously, but here we replaced the age function with two new fixed effects. ‘Age last measured’ (ALM) was included to represent the contribution of between-individual variation in phenotypic quality because it represents differences in years lived between individuals. Use of age last measured rather than lifespan allowed us to use our entire dataset rather than a reduced dataset of birds with known lifespans. However, to be complete, we also conducted the same analysis for individuals with known lifespans (i.e. individuals who had not been captured, resighted via color bands at nest boxes, or detected at our smart RFID feeders for two years (Welklin et al. 2024)). The difference between age and ALM (age - ALM) was included to represent the contribution of within-individual change in reproductive performance to population-level trends (van de Pol and Verhulst 2006). Values for this variable are mostly negative and increase as individuals age, ending at zero when each individual’s age last measured is subtracted from itself. We tested the statistical significance of each age term using likelihood ratio tests and compared the relative importance of each effect by calculating the change in AICc when the fixed effect was removed from the model (ΔAICc). We did not include any analysis of between versus within-individual effects at the beginning of life because our observations suggest that all mountain chickadees in our population begin breeding at age 1. We also ran this analysis on a dataset that did not include one-year-old individuals to account for known improvements in reproductive performance between ages 1 and 2 (Pitera et al. 2021).

Results

Age and reproductive performance

We observed 698 breeding attempts from 551 unique mountain chickadee pairs at two elevations (300 nests from 242 unique pairs at high elevation and 398 nests from 309 unique pairs at low elevation) over eight breeding seasons (range 59–108 nests per season). Our dataset included 362 females and 377 males that bred in an average of 1.9 seasons (range = 1–6 for females and range = 1–7 for males; supplemental Fig. S1). 46% (166/362) of females and 45% (170/377) of males bred in multiple seasons. Ages ranged from 1 to 9 years old and female and male age were positively correlated within breeding pairs (Pearson’s correlation: $N = 698$ pairings, $P < 0.001$, $r = 0.32$). Interactions between age and elevation did not improve the fit of any models (likelihood ratio tests: all $P > 0.05$), so we report results from models including both elevations as the absence of an interaction between age and elevation suggests no differences in age-related reproductive performance at both elevations in our study.

Both female and male age were associated with pair reproductive performance, but reproductive variables were influenced by each sex’s age in different ways (Table 1; Figs. 1, S2 – S4). Changes in first egg date with age were

Table 1 Population-level associations between female and male age and pair reproductive performance

Response variable	*N* (breeding attempts)	Sex	*N* (ind)	Function	Age term	Estimate	SE	t score or z score	*P*	ΔAICc
First egg date	698	F	362	Quadratic	Age	-29.615	6.078	-4.87	< 0.001	41.35
					Age^2	16.062	5.129	3.13	0.002	
		M	377	Quadratic	Age	-13.573	5.906	-2.30	0.022	12.71
					Age^2	5.070	5.278	0.96	0.337	
Clutch size	692	F	362	Threshold	Age $\leq$ 2	0.051	0.013	3.86	< 0.001	28.41
					Age $\geq$ 2	0.015	0.005	2.79	0.005	
		M	375	Linear	Age	0.011	0.004	2.81	0.005	5.85
Brood size	632	F	337	Threshold	Age $\leq$ 2	0.069	0.022	3.16	0.002	10.76
					Age $\geq$ 2	0.008	0.008	0.97	0.332	
		M	358	Threshold	Age $\leq$ 5	0.019	0.008	2.41	0.016	2.29
					Age $\geq$ 5	-0.034	0.023	-1.47	0.142	
Mean fledgling mass	622	F	336	Quadratic	Age	0.676	0.882	0.77	0.444	1.89
					Age^2	-1.240	0.809	-1.53	0.126	
		M	355	Quadratic	Age	2.367	0.894	2.65	0.008	5.65
					Age^2	0.299	0.800	0.37	0.709	

Estimates for female and male age fixed effects from combined-sex models that used the top age function (linear, quadratic, or threshold) are presented for each sex. Each model included elevation as a fixed effect, with year and female and male identity as random effects. Brood size was included as a fixed effect when modeling mean fledgling mass. t-scores are presented for first egg date and mean fledgling mass, and z-scores are presented for clutch size and brood size. ΔAICc shows the change in AICc score when the female or male age term(s) were removed from the model to determine which sex’s age better explained pair reproductive performance. Full model selection results based on AICc scores are available in supplemental Table S3 and full model results for each of the presented models are available in supplemental Table S4

Table 2 Relative contribution of between versus within-individual variation to patterns of reproductive performance

Response variable	Sex	Fixed effect	Estimate	SE	t score or z score	*P*	ΔAICc
First egg date	F	ALM	-0.890	0.165	-5.39	< 0.001	24.63
		Age - ALM	-0.922	0.204	-4.51	< 0.001	16.45
Clutch size	F	ALM	0.024	0.004	5.52	< 0.001	27.67
		Age - ALM	0.026	0.006	4.71	< 0.001	19.97
Brood size	F	ALM	0.025	0.006	3.92	< 0.001	13.35
		Age - ALM	0.025	0.009	2.73	0.006	5.34
Mean fledgling mass	M	ALM	0.074	0.023	3.29	0.001	2.65
		Age - ALM	0.037	0.034	-1.09	0.275	-5.78

Estimates for age last measured (ALM), representing between-individual variation in lifespan, and the difference between age and ALM, representing within-individual change are shown for the sex whose age best explained each reproductive variable. Elevation was included as a fixed effect and individual identity and year were included as random effects in all models. t-scores are presented for first egg date and mean fledgling mass and z-scores are presented for clutch size and brood size. ΔAICc shows the change in AICc score when the fixed effect was removed from the model. A negative ΔAICc value means removing the fixed effect from the model resulted in a lower (better) AICc score, suggesting the fixed effect was not important for predicting the response variable. Sample sizes match those presented in Table 1. Full model results for each of the presented models are available in Table S5

defined by a positive quadratic relationship for both female and male age, but this relationship was more pronounced in females in which 1-year-old females and females age 6 and older exhibited slight delays in first egg dates compared to females aged 2–5 (Table 1; Fig. 1B). Clutch size showed an overall positive association with female and male age, but the threshold effect of female age was marked by a more dramatic increase between ages 1 and 2, then a smaller but still positive and statistically significant slope beyond age 2 (Table 1; Fig. 1C). Brood size showed a similar relationship to female age as clutch size, but the positive slope after the threshold was not statistically significant (Table 1; Fig. 1D). Male age was associated with increasing brood sizes between ages 1 and 5, then a non-significant decline in brood size starting at age 5 (Table 1; Fig. 1D). Female age was not a statistically significant predictor of mean fledgling mass, but male age was positively associated with mean fledgling mass, suggesting that older males raised heavier offspring (Fig. 1E). The observed lack of reproductive senescence remained when improvements in reproductive performance between ages 1 and 2 were excluded from the dataset (Table S6). Analysis of the reduced dataset that did not include individuals with unknown histories also produced similar results as those presented in Table 1 (Table S7).

Importance of female versus male age for pair breeding success

After accounting for substantial effects of year and elevation on reproductive performance, first egg date, clutch size, and brood size were more strongly associated with female age than male age, whereas mean fledgling mass was primarily associated with male age, as measured by change in AICc score (Table 1).

Between versus within-individual effects

Comparison of between and within-individual effects revealed that the relationships between female age and first egg date, clutch size, and brood size were driven by both between and within-individual variation. Age last measured, representing between-individual variation in lifespan, was negatively associated with first egg date, and positively associated with clutch and brood size (Table 2), suggesting that long-lived females nested earlier, laid more eggs, and raised more offspring than short-lived females. However, the difference between female age and ALM was also negatively associated with first egg date, and positively associated with clutch and brood size (Table 2), suggesting that individual females also exhibited increasing reproductive performance as they aged. Between-individual effects (ALM) consistently explained more variation in female reproductive performance than did within-individual improvement (age - ALM), as measured by change in AICc, but both effects were statistically significant predictors of female reproductive performance. In contrast, the difference between male age and age last measured was not a statistically significant predictor of mean fledgling mass, but age last measured was positively associated with mean fledgling mass (Table 2), suggesting that long-lived males raised heavier offspring than short-lived males, resulting in the overall positive association between male age and fledgling mass. Analysis of the dataset that did not include one-year-old individuals returned similar results (Table S8), and the same analysis conducted for individuals with known lifespans detected less evidence for within-individual improvement with age but still showed no evidence of reproductive senescence (Table S9).

Discussion

Age and reproductive performance

While many vertebrates exhibit reproductive senescence in late ages, even under natural conditions where most individuals rarely live to the limit of their potential lifespan (Nussey et al. 2013), our study of wild mountain chickadees revealed no evidence of reproductive senescence within the naturally observed lifespan. Analysis at the population level revealed that female reproductive performance was either positively associated or was not associated with age, depending on the reproductive variable of interest. Similarly, male age was positively correlated with mean nestling mass. Only the relationship between female age and first egg date showed possible senescence with an increase in first egg dates in the latest ages, but the biological significance of this result is unclear. Early first egg dates are often associated with increased survival and recruitment of offspring (Nilsson and Smith 1988; Ringsby 1998), including in mountain chickadees (LEW et al. unpubl. data), but timing of breeding is also influenced by interactions between intrinsic and extrinsic factors that could lead to variation in laying dates among different ages, such as the ability to match peaks in insect abundance (Visser et al. 2010). Despite large environmental differences between our high and low elevations (Whitenack et al. 2023) and despite elevation-related differences in annual survival (Benedict et al. 2020) and annual recruitment into the breeding population (Branch et al. 2019b), the observed age-related reproductive patterns were similar at both elevations.

Between versus within-individual effects

Population-level correlations between age and reproductive performance do not always reveal within-individual trends as a positive association between age and performance could also arise due to selective disappearance of individuals with poor performance and longer lifespan of better performing individuals (van de Pol and Verhulst 2006). Splitting the age term into between and within-individual components revealed that the positive correlations between age and reproductive performance in females were driven by both between and within-individual effects. Longer-lived female chickadees exhibited higher reproductive performance at all ages, but individual females also exhibited improved reproductive performance with age regardless of their lifespan. Such improvements may have been associated with increased breeding experience and improved foraging efficiency that improved female physiological ability to lay earlier and lay more eggs (Desrochers 1992; Forslund and Pärt 1995; Daunt et al. 2007; but see Nol and Smith 1987). At the population level, older males were associated with heavier fledglings, but splitting the age term into between and within-individual components revealed no evidence for within-individual improvements in the mass of fledglings males raised. Instead, long-lived males raised heavier offspring than short-lived males, suggesting the positive population-level trend was driven by an association between survival ability and reproductive performance instead of within-individual improvement. Such selective disappearance of low-quality breeders who live shorter lives may be common in vertebrates (Forslund and Pärt 1995; Hayward et al. 2013) and can even partly mask senescence when within-individual effects are not accounted for (Bouwhuis et al. 2009). Reproductive senescence did not appear to be masked in this instance because the male within-individual fixed effect still exhibited a positive, but non-significant slope, showing no evidence for age-related senescence.

Importance of female versus male age for pair breeding success

Both female and male reproductive performance can change with age, but for many sexually-reproducing species it is not clear whether changes in pair reproductive output are attributable to female or male age. Female age was a better predictor of pair first egg dates, clutch sizes, and brood sizes in mountain chickadees, whereas male age was weakly associated with these variables but was the primary parental predictor of variation in mean fledgling mass due to longer-lived males raising heavier offspring. Female age explained no variation in fledgling mass, suggesting that male phenotypic quality could play an important role in determining a pair's reproductive success as heavier songbird fledglings typically exhibit greater survival (Perrins 1965; Magrath 1991; Ringsby et al. 1998), including in this system (LEW et al. unpubl. data). The importance of male versus female age for fledgling mass may be explained by previous reports of male mountain chickadees bringing greater volumes of food to fledglings than females (Grundel 1987).

The importance of female age for determining first egg dates, clutch sizes, and brood sizes is not surprising given only females lay eggs, but male age was a statistically significant predictor of each of these reproductive measures, even if it was less important than female age. Male age could influence first egg dates and clutch sizes indirectly by influencing female investment (Harris and Uller 2009; Horváthová et al. 2012), possibly through male provisioning of females prior to egg laying (Nisbet 1973; Galván and Sanz 2011). Indeed, previous work in this system suggests that in some environmental conditions, females adjust the number of eggs they lay relative to their paired male's spatial cognitive ability, an ability involved in food caching which is critical for over-winter survival (Branch et al. 2019a). If the longest-lived males have the best spatial cognition (Heinen et al. 2021; Welklin et al. 2024), females may invest more when paired with older, 'smart' males and produce more young with better spatial abilities considering that these abilities are highly heritable (Branch et al. 2022; Semenov et al. 2024).

Our ability to attribute variation in pair reproductive performance to female versus male age is complicated by the common problem that female and male age were positively correlated within breeding pairs. However, our results do suggest that within-individual female improvements with age and both female and male phenotypic quality contribute to a lack of reproductive senescence and even improvements in reproductive performance for some reproductive measures in this species. This result differs from observations of some other species when the effect of both sexes' ages has been investigated. In alpine swifts (*Tachymarptis melba*), female reproductive performance declined in old ages, but male reproductive performance remained stable (Moullec et al. 2023). Nearly the opposite pattern occurs in white-tailed eagles (*Haliaeetus albicilla*; Murgatroyd et al. 2018) and wandering albatross (*Diomedea exulans*; Fay et al. 2016), yet in other species both females and males show reproductive senescence (Robertson and Rendell 2001; Froy et al. 2017). In our study, older pairs of mountain chickadees raised the most and the heaviest offspring, thus both sexes may benefit from pairing with an old mate (Brooks and Kemp 2001).

Delayed reproductive senescence

In mountain chickadees, as well as most other animals that exhibit no reproductive senescence within their natural lifespans, a more accurate term for this phenomenon could be 'delayed reproductive senescence' (Sanz and Moreno 2000), since all organisms are expected to reproductively senesce if they live long enough lives (Nussey et al. 2013). Our findings do not show that mountain chickadees are immune to reproductive senescence, only that reproductive senescence does not appear to occur within the natural lifespan of individuals in the wild. Similar reports of delayed reproductive senescence occur in a few other songbirds, including superb fairywrens (*Malurus cyaneus*; Cooper et al. 2021) and bobolinks (*Dolichonyx oryzivorus*; Scott et al. 2022), but most passerine birds exhibit senescence of reproductive performance late in life (Robertson and Rendell 2001; Holmes et al. 2003; Bouwhuis et al. 2009). Indeed, females of the closely-related great tit exhibit declining brood sizes and a reduction in offspring recruited after age 3 (Bouwhuis et al. 2009). In contrast, but similar to our study, the closely-related willow tit, also a food-caching species, was reported to exhibit increased reproductive performance from ages 1 through 5 (Orell et al. 1999), however as previously described, this species commonly lives beyond 5 years (Orell and Belda 2002). Interestingly, spatial cognitive abilities used for food cache recovery in food caching species such as mountain chickadees and willow tits, also do not show age-related senescence in our study system (Heinen et al. 2021). Our dataset including individual mountain chickadees up to 9 years of age offers greater coverage of our study species' potential lifespan, but few studies of songbirds approach the 48-year study on great tit reproductive senescence, even though that species shows clear senescence at an age where we have large sample size, yet no evidence of senescence (Bouwhuis et al. 2009). However, our sample size is still smaller than that of Bouwhuis et al., meaning the possibility of a type 2 error influencing our findings still exists. Our smaller dataset may explain our failure to detect the expected negative relationship between age and reproductive output in late ages, thus it is possible that more years of data could reveal reproductive senescence in extremely old ages that few individuals attain under natural conditions. However, even with our smaller sample size, our data suggest that such senescence was significantly delayed as we detected significant improvements, rather than declines in reproductive performance throughout most of the naturally observed lifespan in females and no evidence of reproductive senescence in males.

Why the reproductive aging trajectory of mountain chickadees differs so extremely from great tits, one of their close relatives, is currently unclear. A phylogenetic comparison of life-history traits to the presence or absence of reproductive senescence may be revealing, but such a study would require long-term field data from many closely related species in order to first determine which species do or do not exhibit reproductive senescence. Alternatively, it is possible that a commonly measured life-history trait such as lifespan could stand in for presence or absence of reproductive senescence in such an analysis, but lifespan itself as a life history trait does not appear to determine whether a species senesces or not (Sparkman et al. 2007; Moorad et al. 2019; Péron et al. 2019). Further, actuarial and reproductive senescence are often not linked (Hayward et al. 2015). Clearly, more research is required to understand why closely-related species can exhibit such different reproductive senescence trajectories (Jones et al. 2008; Berman et al. 2009; Froy et al. 2017).

Conclusion

\nOur results show that both female and male age contribute to a breeding pair's reproductive performance in mountain chickadees, but instead of reproductive performance declining in old ages, mountain chickadees exhibited no detectable reproductive senescence within their natural lifespans under natural conditions. Instead, females at both elevations exhibited gradual improvement in reproduction, and long-lived individuals of both sexes exhibited higher reproductive performance than short-lived individuals, suggesting a phenotypic link between survival ability and breeding ability. Few individuals attain the oldest ages, but a lack of reproductive senescence in the wild may allow long-lived chickadees to contribute greatly to population growth. Indeed, lifespan will positively correlate with lifetime reproductive success in most animals, but when reproductive senescence is strong, each additional year of life past the peak breeding age will contribute fewer and fewer offspring to differences in lifetime reproduction. However, when reproductive senescence is weak or non-existent, long-lived individuals may sire many more offspring than short-lived individuals, meaning lifespan will more strongly correlate with lifetime reproduction. The lack of reproductive senescence we observe in mountain chickadees may help explain why we observe such strong selection on traits related to lifespan if longer-lived individuals do produce many more offspring (Welklin et al. 2024). Combined, our results emphasize the importance of investigating relationships between age and reproduction for both sexes to fully understand how reproductive aging patterns are likely to influence pair and therefore individual reproduction.\n

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Data availability The data for this study and the scripts to analyze the data are available through Figshare at: https://doi.org/10.6084/m9.figshare.23193494.

Declarations

Ethical approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. All methods and procedures were approved by the University of Nevada Reno (UNR) Institutional Animal Care and Use Committee (IACUC) in accordance with UNR IACUC protocols 20-11-1103, 20-06-1014, 20-08-1062, under California Department of Fish and Wildlife Permit SC-193630001-20007-001.

Conflict of interest The authors declare that they have no conflict of interests.

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