Article Type: Letter

Title: **Polyandry and senescence shape egg size variation in a precocial bird**

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Short Running Title: Reproductive senescence in a polyandrous shorebird

Keywords: ageing, *Charadrius nivosus*, disposable soma, life history, mating system, reproductive investment, reproductive performance, season, snowy plover, trade-off.

Abstract Word Count: 284

Total Word Count: 1254+1973+603+1375 = 5205 (without Abstract)

Abstract (284 words):

Identifying age-dependent trade-offs between reproductive effort and survival in wild organisms is central for understanding the evolutionary mechanisms of senescence. According to the disposable soma theory, early-life energy investments in reproduction compromise late-life investments in somatic maintenance – leading to senescence. Once thought to only be detectable in captive populations, senescence has recently been documented by several longitudinal studies of wild organisms. However, some reproductive traits that are used to quantify senescence may also be shaped by other age-dependent processes such as mating tactics. For instance, polygamy, which is often positively associated with age, may lead to reduced gamete size due to trade-offs between gamete quantity and quality. Here we investigate how mating behaviour and senescence are associated with reproductive trade-offs of female snowy plovers (*Charadrius nivosus*). Snowy plovers are long-lived shorebirds (longevity record: 19 years) that produce several nests each year, with females either being polyandrous and sequentially changing partners between breeding attempts or remaining monogamous between attempts. We examined how age, seasonality, and mating tactics affect within-female variation in egg volume using repeated measures collected over a 14-year period. Our results provide clear evidence for senescence in snowy plover females starting at three years of age. Furthermore, females laid smaller eggs in years when they were polyandrous compared to years when they were monogamous, with early- and late-season clutches having the smallest eggs. We suggest that individual female reproductive performance is regulated by flexible mating tactics and age- and season-dependent effects. Our findings highlight the existence of multiple trade-offs for female reproductive investments that likely shape individual variation in lifetime reproductive success. We encourage future research investigating reproductive senescence of wild populations to incorporate age-dependent reproductive investments in light of mating system dynamics.

Impact Summary (297 words):

Why do organisms senesce at older ages? Life-history theory predicts that early life investments in reproduction compromise future investment opportunities for somatic repair, which leads to senescence. Earlier works assumed that senescence was only observable in captive populations due to the high degree of extrinsic mortality experienced by wild organisms. However, with the expansion of longitudinal studies collecting repeated measures from wild individuals, recent works

have identified key insights into the selective processes driving patterns of senescence in nature. Here, we use a 14-year longitudinal mark-recapture dataset of snowy plovers (*Charadrius nivosus*) breeding in a wild subtropical population in western Mexico to investigate age-dependent trade-offs between female reproductive effort and performance. The snowy plover is a long-lived shorebird characterized by a flexible polyandrous mating system. This rare breeding behaviour represents a unique background for investigating senescence in light of between and within-individual variation in reproductive investment. Our study focused on age-dependent dynamics of egg volume – a convenient measure of a female's intrinsic reproductive investment, particularly in birds with precocial chicks. We explored age-related correlates of within-female egg volume dynamics while controlling for among-female variation and the confounding effect of trait-dependent (dis)appearance of young (or old) females in the population. Our results show that egg volume expresses an early-life increase followed by a late-life decrease, indicative of reproductive senescence. Furthermore, females tended to lay smaller eggs in years during which they were polyandrous than in years when they were monogamous. Notably, polyandry was not associated with age. As expected, egg volume was highly repeatable within females and clutches. We conclude that age-dependent reproductive effort is an important component driving between- and within-individual variation in reproductive performance of facultatively polygamous species. We encourage future works studying reproductive senescence of wild populations to incorporate age-dependent reproductive investment and mating tactics.

Main Text:

INTRODUCTION (1254 words)

The costs of survival and reproduction are considered to be central for the evolution of life history strategies. Life-history theory predicts that fitness trade-offs between current and future reproduction shape inter-specific variation in reproductive strategies observed among iteroparous organisms (Partridge, 1989). To maximize the transfer of their genes to the next generation, individuals adjust their current reproductive investment in light of future reproductive prospects (Jankowiak et al., 2018). The compromise between current and future reproduction enforces trade-offs between investments in reproduction and other competing functions, such as self-maintenance (Stearns, 1977, 1992; Christe et al., 2012).

In many organisms, reproductive productivity is age-dependent (Bouwhuis et al., 2009; Hammers et al., 2012; Lemaître et al., 2015; Zhang et al., 2015; Salguero-Gómez et al., 2016; Jankowiak et al., 2018; Dingemanse et al., 2020): an individual's performance increases over early life to a maximum and is followed by a decline in older ages. This decline in reproductive performance at old age is considered a sign of senescence – a within-individual age-specific decline in reproductive performance paired with an increase in the probability of death caused by the loss of physiological and cellular function (Medawar, 1952; Williams, 1957). Senescence was initially thought to be the result of natural "wear and tear" of body tissues that accumulate throughout an individual's life (Sohal, 1986), but several recent empirical studies using model organisms have identified molecular and evolutionary mechanisms likely responsible for senescence (Rose, 1984; Charlesworth, 1994; Holmes et al., 2001, 2003). Moreover, theoretical works hypothesize that senescence is the evolutionary outcome of weakened selection at older ages due to extrinsic sources of mortality (Medawar, 1952; Williams, 1957; Hamilton, 1966).

A prominent hypothesis explaining the occurrence of senescence is the disposable soma theory (sensu Kirkwood, 1977), which states that individuals are constrained by the amount of resources they have to invest in survival and reproduction (Kirkwood & Austad, 2000). Therefore, senescence is the consequence of age-dependent trade-offs between energy investments in reproduction at the expense of somatic repair (Kirkwood & Rose, 1991; Kirkwood & Austad, 2000; Drenos & Kirkwood, 2005). Thus, an individual's investment in current reproduction may

exacerbate physiological and cellular damage, which might have knock-on effects on their capability for future reproductive investments at older ages – ultimately impairing performance.

Earlier works assumed that senescence was only observable in captive populations due to the high degree of extrinsic mortality experienced by pre-senescent individuals in the wild through predation, disease, or resource shortages (Kirkwood & Rose, 1991; Bronikowski & Promislow, 2005). However, with the expansion of longitudinal studies collecting repeated measures from wild individuals, recent works have identified key insights into the selective processes driving patterns of senescence in nature (e.g., Bowen et al., 2006; Nussey et al., 2006, 2008; Bouwhuis et al., 2009; Schroeder et al., 2012; Zhang et al., 2015; Warner et al., 2016; Dingemanse et al., 2020; Lemaître et al., 2020). A key issue for studying senescence in wild populations is that stochastic extrinsic mortality reduces the frequency of observable individuals in older age classes, hence making it challenging to disentangle among- vs. within-individual age-dependent variation – a phenomenon known as "selective disappearance" (Nussey et al., 2008; van de Pol & Wright, 2009). Investigations using longitudinal data to test for senescence are particularly powerful as they can quantitatively control for the confounding effects of selective disappearance through repeated measures of individuals as they age (Nussey et al., 2008; van de Pol & Wright, 2009; Dingemanse et al., 2020).

Mating strategies may also be an important factor that shape reproductive traits and senescence. Conventional sex roles are thought to emerge from initial anisogamy between the sexes – females produce large gametes and provide more parental investment, whereas males produce several small gametes and compete vigorously for access to females (Trivers, 1972; Schärer et al., 2012). Male-male competition through combat can lead to increased somatic deterioration or damage (Bonduriansky et al., 2008). Hence, in polygynous species, strong sexual selection and intrasexual competition are thought to accelerate senescence and may lead to high mortality rates in males (Clutton-Brock & Isvaran, 2007; Bonduriansky et al., 2008; Maklakov & Lummaa, 2013; Greiner et al., 2014; Beirne et al., 2015; Tidière et al., 2015; but see Lemaître et al., 2020). Conversely, in monogamous species where sexual selection is not as intense, senescence acts similarly on both males and females (Clutton-Brock & Isvaran, 2007) or shows only moderate biases towards either sex (e.g., Lecomte et al., 2010; Froy et al., 2017; Tompkins & Anderson, 2019). If sexual selection

leads to high senescence one should expect to detect senescence among females in sex-role-reversed species – yet, senescence of females in sex-role-reversed species has remained understudied.

In oviparous organisms, egg size represents a fundamental measure of female reproductive investment (Kaplan, 1980; Fox, 1994; Williams, 1994, 2012; Starck & Ricklefs, 1998; Moran & Emlet, 2001; Xu et al., 2019) and is shown to be related to inter- and intra-specific variation in several life history traits. For example, egg size is associated with developmental mode with precocial species typically producing larger eggs than altricial species (Deeming & Reynolds, 2015). Egg size may also depend on the mating strategy with polyandrous females typically laying smaller eggs than monogamous ones (Liker et al., 2001; Andersson, 2004). Within individuals, variation in egg size is shown to be highly repeatable (Christians, 2002), but notably, there is no clear association between egg size and female condition (Christians, 2002). Age-dependent changes in egg or clutch size are often consistent with senescence although complicated by considerable among-individual variation (Beamonte-Barrientos et al., 2010; Dingemanse et al., 2020).

Among oviparous animals, shorebirds (part of the order Charadriiformes) produce some of the largest eggs in relation to body mass due to the needs of their precocial nidifugous young (Lack, 1968; Rahn et al., 1975). As a clade, shorebirds also exhibit a disproportionately high prevalence of polyandry (Oring, 1986; Colwell, 2010). Sexual and natural selection presumably act divergently on egg size with natural selection on offspring viability favouring larger eggs with more nutrients to enhance offspring survival (Blomqvist et al., 1997; Starck & Ricklefs, 1998; Williams, 2012) whereas sexual selection favours smaller egg sizes as females need to partition finite resources among several consecutive clutches (Liker et al., 2001; Andersson, 2004).

Here, we investigate age-dependent egg size variation using a 14-year longitudinal mark-recapture dataset of snowy plovers (*Charadrius nivosus*) breeding at Bahía de Ceuta – a wild sub-tropical population in western Mexico. The snowy plover is a long-lived shorebird (Colwell et al., 2017) exhibiting a rare breeding behaviour characterized by sex-role reversal including facultative sequential polyandry (Eberhart-Phillips et al., 2017; Kupán et al., 2019). The prominent variation

175 of reproductive investment within the same sex provides a highly suitable study system to
176 investigate how senescence and mating strategy shape female reproductive output in a species with
177 non-conventional sex roles. We examined whether age-related dynamics in egg size follow a
178 pattern typical for senescence and/or selection on polyandry. We hypothesized that an early-life
179 increase in egg size, followed by a peak maximum, and a decline thereafter, would indicate
180 senescence being responsible for age-related changes in egg volume. By contrast, we hypothesized
181 that a linear decrease of egg size over age would indicate that selection on polyandrous females is
182 driving age-dependent variation.
183
184 Our study sheds light on the ecological implications of reproductive senescence in a wild open
185 population and provides important information on the intrinsic and extrinsic selective forces
186 affecting egg size variation. This in turn provides valuable insights for our understanding of how
187 senescence and mating strategy may condition reproductive performance differently at the
188 individual and population level.
189
190 MATERIALS AND METHODS (1973 words)
191 *Data collection*
192 We studied the reproductive effort of female snowy plovers at Bahía de Ceuta – an important
193 breeding site located on the coast of Sinaloa, northwest Mexico (23º54'N, 106º57'W). Details on
194 the study site and population are provided elsewhere (e.g., Cruz-López et al., 2017; Eberhart-
195 Phillips et al., 2020a). In brief, we annually monitored breeding birds from mid-April until early
196 July, and collected mark-recapture data following the methods described in Székely et al., (2008).
197 We exhaustively searched for nests using telescopes and mobile hides to minimize disturbance.
198 Upon finding a nest, we measured each eggs' length and width to the nearest tenth of a mm to
199 determine egg size. Using these egg dimensions, we calculated egg volume following Hoyt (1979)
200 as:

201 Eq. 1 $$egg\ volume = K \times length \times width^2,$$

202 where K is 0.486, a volume-index constant for snowy plovers determined by Székely et al. (1994)
203 through the use of an egg volumeter (Hanson, 1954). The modal clutch size of snowy plovers is
204 three (87%) and is the maximum number of eggs we have observed in this population (Eberhart-
205 Phillips et al., 2020b). We regularly checked incomplete nests until the clutch was completed and

assigned the age of these nests according to the lay date of the last egg laid (Plaschke et al., 2019). If the clutch was complete upon discovery, we determined its lay date by floating the egg and estimating the stage of embryonic development (Székely et al., 2008).

We identified nesting adults that had been previously marked based on their unique colour ring combination. We captured unmarked adults on their nests during incubation using funnel traps and assigned a unique colour combination for subsequent recognition (Hall & Cavitt, 2012). Because snowy plovers have circadian sex roles during incubation (Vincze et al., 2017), we generally targeted females for captures during the day and males during the night. In the rare circumstance when we were unable to identify parents before hatching, we attempted capturing parents whilst they tended chicks. As snowy plovers only show a small degree of sexual dimorphism (Küpper et al., 2009), we determined sex of all captured plovers in the field through a combination of plumage characteristics (Argüelles-Ticó et al., 2016), time of capture, and other behavioural cues (e.g., sex-specific brood care; Kupán et al., 2019). Furthermore, we confirmed sex molecularly from DNA extracted from blood samples through PCR amplification of Z and W specific DNA regions with two sex-typing markers: P2/P8 and Calex-31 (Griffiths et al., 1998; Küpper et al., 2007; Dos Remedios et al., 2010).

We visited known active nests every four or five days to determine the status of the nest (e.g., active, abandoned, predated) until the 20th day and thereafter daily until the eggs hatched or the nest failed. We marked hatched chicks with an alphanumeric metal and a single colour ring for subsequent identification in the chance that these individuals recruited into the breeding population as adults in future years.

For the years 2006 to 2016 all longitudinal data collected has been compiled as part of the *CeutaOPEN* project – an open-access database for individual-based field studies in evolutionary ecology and conservation biology (Eberhart-Phillips et al., 2020a). We accessed these data directly from the open source repository (Eberhart-Phillips et al., 2020b) and supplemented them with data from three additional field seasons: 2017, 2018, and 2019. The *CeutaOPEN* database is composed of five tables that correspond to our routine data collection in the field. Here we used the "Captures", "Resights", and "Nests" tables. The "Captures" and "Resights" tables contain

information about all the individuals captured and observed, whereas the "Nests" table contains the morphometric and spatiotemporal information related to each nest monitored. Please refer to our RMarkdown vignette that connects to *CeutaOPEN* and reproduces all analytical methods and results discussed below (Supplementary File 1).

Statistical Analyses

Age estimation of individuals with unknown origin—Investigating senescence requires information on the age of individuals. However, marked populations in the wild are often composed of a mix of individuals that are of known or unknown age (Colchero et al., 2012) – with the former being individuals initially marked at birth (i.e., 'uncensored'), and the latter being immigrants of unknown age or those that were born before the study's first marking occasion (i.e., 'left-truncated'). To estimate the ages of unknown individuals in our marked population we employed a capture-mark-recapture analysis using the 'Bayesian Survival Trajectory Analysis' (BaSTA) package in R (v1.9.4, Colchero et al., 2012), which uses a Bayesian hierarchical framework to fit parametric survival functions of the marked population while accounting for imperfect detection. BaSTA derives birth year estimates of left-truncated individuals from the population mean of the projected survival function. As snowy plovers show prominent sex differences in survival (Eberhart-Phillips et al., 2017, 2018), we estimated female-specific survival functions for our population. Due to high natal dispersal we could not confidently determine the fate of juveniles marked in our population. To acknowledge this uncertainty, our capture-mark-recapture sample only included individuals that survived to their first breeding season, i.e. we constrained first-year survival probability to 1.

In total, our capture-mark-recapture data comprised of 400 uniquely marked females, of which 41 hatched locally and subsequently recruited into the adult population as known-age individuals (Fig. 1a), and the remaining 359 individuals were adults of unknown age and origin. Over the 14-year study period we monitored the presence or absence of marked individuals annually by recapturing or observing them in the field, amounting to a total of 811 post-birth detections of the 400 females in our sample (median detections per adult = 2; mean = 2.13 ± 1.49 SD). In short, BaSTA determined that a logistic bathtub-shaped mortality model best fit our data – revealing that female mortality rate increased until age 5 years, after which it became constant (Fig. 1a; see Appendix

S1 for detailed methods). From this model, we extracted the point estimate and 95% credible interval birth year for each individual in the capture-mark-recapture sample.

Modelling individual variation in egg volume—To ensure that we appropriately captured within-individual variation in reproductive effort over age, we limited our analysis of egg volume to a subset of females in our population that had at least three years of repeated egg volume observations. This restricted our sample for studying egg volume dynamics to 51 females that included ten individuals that we marked as hatchlings but later recruited as breeding adults in subsequent years (i.e., known age; Fig. 2a) and 41 individuals that were initially marked as adults (i.e., unknown age; Fig. 2b). Note that three individuals (one first encountered as an adult [CA1579] and two local recruits [CA2036 and CA1526]; Fig. 2) had been already marked two years prior to the start of our monitoring period (i.e., pre-2006) and were thus added to our sample after running BaSTA on the 2006–2019 capture-mark-recapture data.

We followed common statistical approaches to investigate senescence in birds (e.g., Bouwhuis et al., 2009, 2010; Schroeder et al., 2012; Herborn et al., 2016; Graham et al., 2019; Dingemanse et al., 2020) by fitting linear and quadratic age to model age-specific trends in egg volume. Our senescence model controlled for selective appearance and disappearance of females differing in average egg volume by fitting 'first observed age' and 'last observed age' as fixed effects – this accounts for between-individual age effects introduced by selective disappearance and appearance (van de Pol & Verhulst, 2006; Dingemanse et al., 2020), and allows us to interpret the remaining "age" effect as a close estimate of a within-individual age effect. We modelled age effects on egg volume by fitting a univariate mixed-effect model, in which our global model included age, age squared, first observed age, last observed age, and observed polyandry as fixed covariates. We also included lay date and lay date squared as fixed covariates to account for seasonal variation in egg volume as several shorebird studies report a seasonal decrease in egg volume (Dittmann & Hötker, 2001; Skrade & Dinsmore, 2013; Kwon et al., 2018; Kubelka et al., 2020; Verhoeven et al., 2020). We standardized lay date according to year so that breeding season phenology was comparable across years. Observed polyandry was a binomial variable that scored an individual as polyandrous or monogamous in a given year based on the number of mates we observed (see Fig. 2 for sampling distribution). To assess the relationship between polyandry and age, we fitted a

binomial linear mixed effects model that tested the likelihood of polyandry predicted by age. We compared model fit of this model it to a null model, while controlling for selective (dis)appearance. To ensure that intercepts of our models represented the reproductive performance for the earliest age at reproduction (i.e., age 1 in snowy plovers, Page et al., 2009), we fitted age as '*age* – 1' – otherwise it would represent reproduction as age 0, which is an empirically meaningless estimate. All models included random intercepts for nest, individual, and year, and assumed a Gaussian error distribution of egg volume.

Our model set included seven candidate models that we hypothesized to explain variation in egg volume (Table 1). All models had the same random-effect structure to permit comparisons of model fit and all age-dependent models included the 'first observed age' and 'last observed age' fixed effects to acknowledge selective (dis)appearance. We ranked models according to *AIC* and evaluated model support by inspecting the top model's Akaike weight (w) and the second-ranked model's ΔAIC (Burnham & Anderson, 2002). Furthermore, for each model we assessed the relative contributions to variance of the random and fixed effects by calculating conditional and marginal R^2 (Nakagawa & Schielzeth, 2013).

We employed the "lme4" (Bates et al., 2015) and "arm" (Gelman, 2011) packages in R (R Core Team, 2013) to conduct our statistical modelling and assessed homoscedasticity by visually examining the residuals (see Fig. S2). Uncertainty in our parameter estimates of the top model was evaluated by extracting the 95% CIs of each parameter's posterior distribution from 5,000 simulations using the "arm::sim" function (Gelman, 2011). We bounded the simulation such that iterations drawing nonsensical values were discarded and re-simulated (e.g., quadratic effects with maxima outside our observed age range of 1 to 13). We deemed an effect 'strongly supported' if the 95% CI did not include zero, and 'moderately supported' if the mean estimate was skewed away from zero but its 95% CI overlapped zero. We concluded 'no effect' if the point estimate of a variable was centred around zero.

Determining the age at peak performance—To pinpoint when egg volume starts to senescence in snowy plovers, we followed Dingemanse et al. (2020) by decomposing the quadratic within-individual age effect with an a priori planned post hoc 'peak performance' analysis of the top

model determined from the *AIC* model selection (Table 1). The peak performance analysis estimates the age when the trait is at its peak as:

Eq. 2 $$peak\ age = {-\beta_{age}}/{(2 \times \beta_{age^2})}$$

and the value of the trait associated with the peak age as:

Eq. 3 $$peak\ egg\ volume = \beta_0 - \left[{\beta_{age}}^2 / (4 \times \beta_{age^2})\right]$$

We acknowledged the uncertainty of these derived parameters by taking forward the simulated posteriors of each fixed-effect parameter (see above), thus calculating 5,000 peaks. As quadratic age effects can arise due to pre-peak age-dependent increases and/or post-peak age-dependent decreases (i.e., senescence), we split the quadratic age effect of the original model into a two-level fixed effect called 'pre-peak' that binned all pre-peak ages as '0' and all post- peak ages as '1'. This way our post hoc peak performance model had the same structure as the original model except that the quadratic age term was replaced with the 'pre-peak' fixed effect and an interaction between 'age' and 'pre-peak'. From the model estimates we derived the pre-peak age effect as the main effect of age (i.e., it was specified as the reference level of the 'pre-peak' factor), and we derived the post-peak age effect as the sum of the pre-peak age effect and the interaction effect.

RESULTS (603 words)

We collected measurements from 775 eggs, originating from 270 clutches of 51 repeatedly measured females over a 14-year period. Based on BaSTA's estimated birth year, 20 of the 41 unknown-age females in our sample were first observed nesting at age 1 (49%), 20 at age two (49%), and one at age three (2%; Fig. 2). Of the ten locally hatched females, six first nested at age one (80%), one was first observed nesting at age two (10%), and two were first observed nesting at age three (20%; Fig 2). The average tenure of all females in the sample was 5.2 years (± 2.29 SD) with an average age span of 3.43 years (± 1.85 SD, median: 4, range: 3 to 13 years) and an average of 3.8 years of observed ages per female (± 1.25 SD, median: 3, range: 3 to 8 age-specific observations; Fig. 2). Females in our sample were typically observed nesting every consecutive year since their first observation, however, some individuals skipped years (average yearly interval between nesting attempts = 1.17 ± 0.30 SD). 59% of females were polyandrous at least once

throughout the observation period (Fig. 2), however, polyandry was not related to age (1.6 *AIC* units less than null model) with seven (14%) females being polyandrous during their first breeding season and 13 (25%) females being polyandrous during their last breeding season.

Egg volume variation was best explained by our model containing quadratic age, quadratic lay date, and mating strategy (Table 1). Support for the top model was overwhelming despite the only difference being the inclusion of mating strategy (top model *AICw* = 0.99, second-best model Δ*AIC* = 8.48; Table 1). Overall, mixed effects accounted for 66% of variation in egg volume, with fixed effects explaining 7% of this variation (Table 1).

Females were highly repeatable in their egg volumes across years: adjusted individual cross-year repeatability (r) was 0.5 ([0.42, 0.58] 95%CI; Fig. 3). Furthermore, eggs within the same clutch were also fairly repeatable in volume (r = 0.17; Fig. 3). We detected no evidence for selective appearance of individuals according to egg volume, as the effect of 'first observed age of reproduction' was not strongly supported (Fig. 3). However, we found moderate support for a selective disappearance (i.e., 'last observed age of reproduction') effect of individuals with large eggs (Fig. 3).

Reproductive senescence of egg volume

Egg volume was greatest for 3-year-olds ('age at peak': 3.51; Figs. 3 and 4). Prior to peak age, we found moderate support for an increase in egg volume of 25 mm^3 per year of age ('pre-peak age effect'; Figs. 3 and 4). After peak age, we found strong support indicating that egg volume decreased by 36 mm^3 per year ('post-peak age effect'; Figs. 3 and 4). The results were qualitatively unchanged when we removed the outlying nests of two females that we observed breeding beyond nine years of age (Figs. S3 and S4).

Effects of season and mating strategy on egg volume variation

Egg volume was overall positively associated with lay date; however, this trend was non-linear: individuals nesting at the start and end of the season laid smaller eggs than individuals nesting in the middle of the season (Figs. 3 and 5). Furthermore, polyandrous mating behaviour was associated with lay date such that early- and late-season nests were more likely to be from

individuals that exhibited polyandry in a given season, whereas monogamous nesting attempts were more likely to occur shortly before the season's midpoint (Figs. 3 and 5). This result means that females laid smaller eggs when they were polyandrous in a given year than when they were monogamous.

DISCUSSION (1375 words)

Identifying age-dependent trade-offs between reproductive effort and survival in wild organisms is central for understanding of the evolutionary mechanisms of senescence (Lemaître et al., 2015). Here we show that senescence, mating strategy, and seasonal constraints all jointly affect egg size in a facultatively polyandrous snowy plover population. Consistent with previous work (Christians, 2002), we found that egg size was highly repeatable for individual females. Yet, an individual's egg size dynamics exhibited age-dependent changes that were consistent with reproductive senescence: the within-female relationship between age and egg size had a negative quadratic shape. Egg size peaked in individuals between three and four years of age with a moderate increase in egg size before peak performance and a strong decrease in egg volume thereafter.

Several studies of oviparous organisms have observed age-dependent variation in egg size, with some studies finding a positive relationship (Cooch et al., 1992; Flint & Sedinger, 1992; Robertson et al., 1994; Warner et al., 2016; Verhoeven et al., 2020) and others observing a negative relationship (Reid, 1988; Potti, 1993; Ito, 1997). However, several of these studies failed to account for selective disappearance (e.g., Cooch et al., 1992; Flint & Sedinger, 1992; Potti, 1993) and thus complicate the interpretation of individual- vs. population-level effects. Similar to our results, recent longitudinal studies document an increase in egg size in early life, followed by peak and then a late-life decline (Bouwhuis et al., 2009; Jankowiak et al., 2018). The early-life increase in egg size may indicate individual improvement through more efficient foraging abilities, better mate choice, or improved predator avoidance (Forslund & Pärt, 1995). Another explanation for the early-life increase could be that females engage in reproduction before their physiological development is completed. We recorded females first breeding as early as 10 months after hatching (Eberhart-Phillips et al., 2020b) – an age at which females might not be fully mature and consequently unable to invest heavily into reproduction. Consistent with an early life trade-off

between reproductive effort and survival, snowy plover females have a lower survival rate than males, which is especially pronounced during the first year of life (Eberhart-Phillips et al., 2017).

The observed post-peak decline (average 36 mm^3 per year, Fig. 4) appears moderate at first sight (0.5% of egg volume) although it was statistically well supported. Importantly, the observed senescence effect was robust to the removal of the outlier nests of two females that were still reproducing after an age of nine (Fig. S3). In fact, when we excluded the outlier clutches of these two females, we observed that both the post-peak senescence effect and the quadratic relationship became stronger (Figs. S3 and S4). This could be indicative that these two longer-lived "outlier" females might be of higher quality, as the senescence effect seems to appear earlier for the majority of the female population. Another possibility is that immigrant females are actually older than what was estimated through our survival trajectory analysis – making the early appearance of senescence an artefact of methodological limitations to accurately age unknown birds. Regardless, the quadratic effect of age on egg volume was robust in both scenarios.

Given that we have observed females still breeding at an age of 14 years (i.e., ten years after the peak; Fig. 2), the cumulative decline would tally up to a 5% reduction of peak egg volume. Such a decrease becomes relevant when considering the developmental mode of snowy plovers. For plovers with their nidifugous chicks, small egg volume differences can have significant ramifications for chick survival (Starck & Ricklefs, 1998), as chicks are not fed by the parents but rather must forage for themselves immediately after hatching. Moreover, chicks of polyandrous females are typically cared for solely by their father, forcing them to rely more on their intrinsic reserves than the added benefits of biparental care. Consequently, comparatively small differences in egg size could have large knock-on effects for chick survival (Williams, 1994; Starck & Ricklefs, 1998). Yet, females need to trade-off the survival benefits of increased egg size for their offspring with their own resources required for maintenance and future reproductive investments, particularly when they attempt to maximize their reproductive output through polyandry. In snowy plovers, a completed clutch equals approximately 60% of a female's body mass (Page et al., 2009): representing a substantial investment. Furthermore, snowy plover females incubate the clutch jointly with their male partner but desert soon after hatching to seek a sequential breeding attempt with a different male (Warriner et al., 1986; Eberhart-Phillips, 2019). Consistent with theoretical

assumptions and previous empirical findings, we found that in years when females were polyandrous, they laid smaller eggs than in years when they were monogamous, suggesting a trade-off with between gamete size and number (Andersson, 2004). Contrary to our prediction, we found no effect of female age on polyandry.

Most studies conducted on temperate or high latitude breeding shorebirds have found a negative association between time of the season and egg size (Byrkjedal & Kalas, 1985; Sandercock et al., 1999; Kubelka et al., 2020) although in polyandrous red-necked phalaropes (*Phalaropus lobatus*) egg size increased across the breeding season (Kwon et al., 2018). However, most investigations of seasonal egg size dynamics did not disentangle whether the observed changes were due to within- or among-individual effects. For example, laying schedules associated with female quality and/or age could be responsible for much of the observed seasonal variation in egg size. A study including 15 arctic shorebirds suggested that indeed among-individual variation may account for more of the seasonal variation in egg size than within-individual variation (Weiser et al., 2018). We observed a quadratic effect of time of season on egg size: early and late season clutches had smaller eggs than those nesting at the middle of the season. Our observed seasonal variation in egg size might be explained by a combination of mating strategy and environmental constraints. Polyandrous females generally produced early- and late-season clutches (Fig. 5) while also laying smaller eggs. This indicates that polyandrous females trade-off egg quantity with size. The seasonal variation could represent a trade-off between a female's capacity to build up adequate energy reserves for egg volume investment while also attempting to breed early enough in order to allow time for sequential mating opportunities later in the season. At the end of the season, late nesting females are under a tight schedule for producing sequential clutches rapidly before impending high tides and precipitation flood the breeding grounds (Plaschke et al., 2019). Notably, chick survival is especially high at the beginning of the season when resources are plentiful (Cruz-López et al., 2017; Kupán et al., 2019), which would support the notion that monogamous females breeding in the middle of the season may account for resource constraints by producing larger eggs to enhance chick survival.

One limitation of our study is that some snowy plover females show high breeding dispersal and can produce sequential nests hundreds of kilometres apart (Stenzel et al., 1994; D'Urban Jackson

et al., 2020). As our population is open to immigration and emigration, we have likely missed documenting polyandrous breeding attempts at unmonitored neighbouring nesting sites – meaning that we underestimate the true extent of polyandry. Yet, our observed clutch laying distribution (Fig. 5) suggests that this unavoidable limitation is not a major concern because we would have otherwise expected a larger share of seemingly monogamous females breeding at the beginning and end of the breeding season – instead we see that monogamous breeders tend to nest in the middle of the season.

In conclusion, we show that individual variation in egg size of snowy plovers is modulated by age, mating strategy, and time of season. Our results suggest that senescence is a major driver of age-dependent dynamics of egg size – consistent with the disposable soma theory. Yet, we also show that the mating strategy, which is not related to age in this system, has an impact on egg size, a reproductive trait that is commonly used to detect senescence. We suggest that future research should explore whether and how polygamy and senescence interact to affect the reproductive output and what consequences these factors have on offspring survival. Studying patterns of senescence in wild populations with flexible mating systems may help shed light on how variation in mating strategies shape individual life history trajectories and lifetime reproductive success.

ACKNOWLEDGEMENTS

We dedicate this article to our colleague and friend René Beamonte-Barrientos who tragically passed away in March 2016. René worked on senescence in birds including snowy plovers and inspired us to conduct this study. We thank Salvador Ángel del Gómez, Miguel Guevara-Medina and Ivan Guardado for assistance with fieldwork, and Daniel Galindo-Espinosa for logistic support. We also thank Niels Dingemanse for his advice and for sharing the R code to conduct the pre- and post-peak trait analysis. Fieldwork was conducted under permit from SEMARNAT (SGPA/DVGS/2631/19). A full list of funding for fieldwork is provided on www.chorlito.org. AH was funded by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 793077. MCL was supported by a doctoral grant from CONACyT (248125/378124) and the Cornell Lab of Ornithology 'Coastal Solutions Fellowship'. CK was supported by the Max Planck Society. LJEP was funded by the German Science Foundation (DFG Eigene Stelle grant: EB 590/1-1).

AUTHOR CONTRIBUTIONS

CK, JS, and LJEP: conceived and supervised the study

LF, CK, MCL, EGM, and LJEP: collected the data

LF, AH, and LJEP: conducted the analysis and wrote the accompanying RMarkdown document (Supplementary File 1)

LF, AH, CK, and LJEP: interpreted the results

LF, CK, and LJEP: wrote the manuscript

All authors helped to revise the manuscript and approved the final version.

DATA ACCESSIBILITY

We provide all computer code and documentation as a html vignette written in Rmarkdown (File S1) together with all of the raw datasets needed to reproduce our modeling and analyses – these files can be found in this project's Open Science Framework repository: doi.org/10.17605/OSF.IO/TE76U

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TABLES AND FIGURES

Table 1. Model selection results describing egg volume dynamics of snowy plovers. Competing fixed effects included 'Age' (i.e., linear age trend), 'Senescence' (i.e., quadratic age trend), 'Quadratic lay date' (i.e., lay date + lay date^2), and 'Polyandry' (i.e., polyandry or monogamy). All models included the 'first observed age' and 'last observed age' as fixed effects to control for selective (dis)appearance and random intercepts for nests nested within individual, and year. *k:* number of modelled parameters; Δ*AIC:* difference in Akaike's information criterion (*AIC*) between a given model and the top model; *w:* relative Akaike weight, $R^2_{conditional}$*:* total variance explained by random and fixed effects; $R^2_{marginal}$*:* marginal variance explained solely by fixed effects. AIC value of top model was 11105.52.

Predictors of egg volume	*k*	*w*	Δ*AIC*	$R^2_{conditional}$	$R^2_{marginal}$
Senescence + Quadratic lay date + Polyandry	11	0.99	0.00	0.66	0.07
Senescence + Quadratic lay date	10	0.01	8.48	0.66	0.07
Age + Season + Polyandry	10	0.00	23.25	0.66	0.07
Age + Quadratic lay date	9	0.00	31.41	0.66	0.06
Quadratic lay date + Polyandry	7	0.00	48.59	0.65	0.02
Quadratic lay date	6	0.00	56.94	0.65	0.02
Null	4	0.00	93.62	0.65	0.00

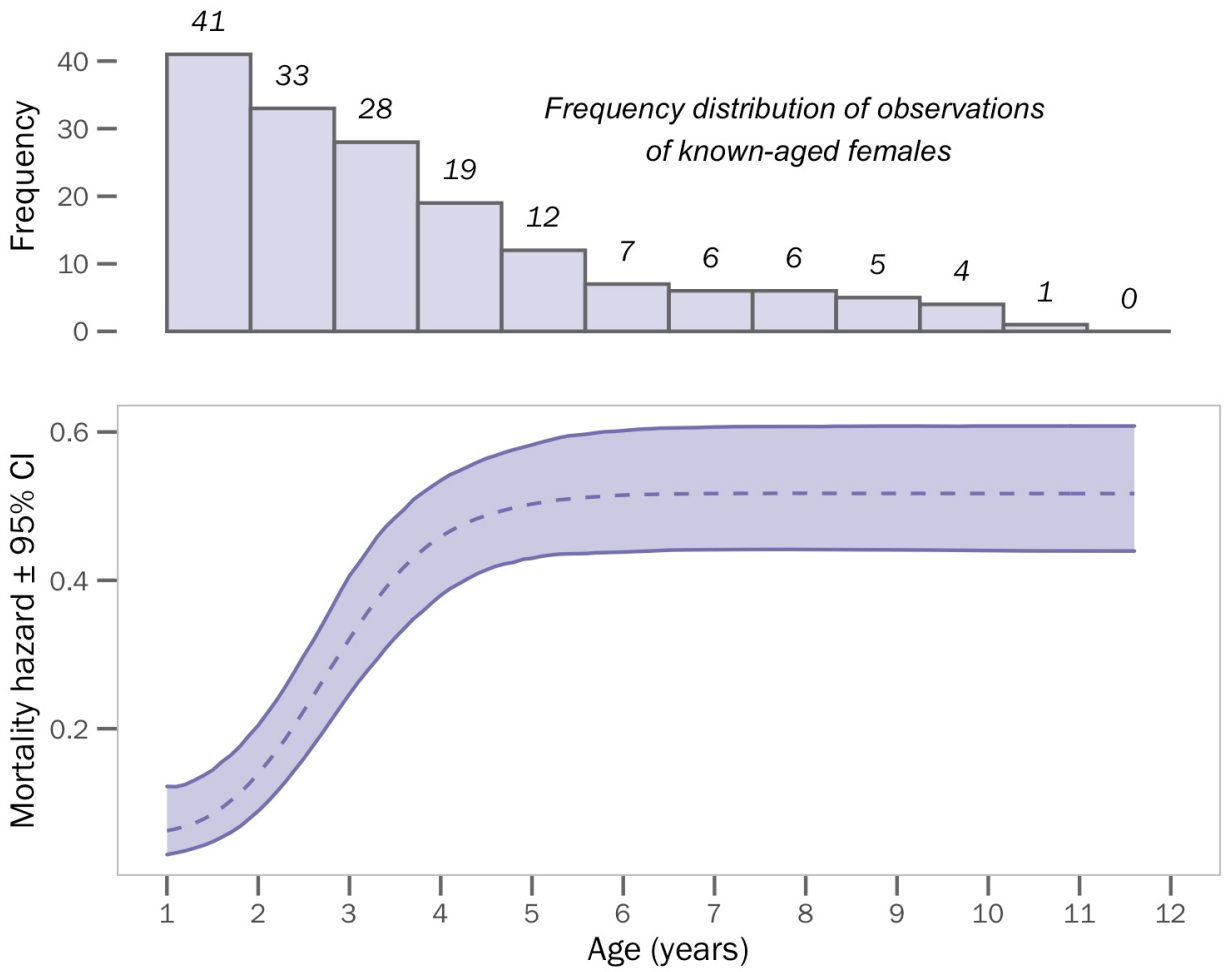

Figure 1. Logistic-bathtub mortality function for snowy plover females: a) frequency distribution of observations of known-aged females and b) age-dependent mortality hazard.

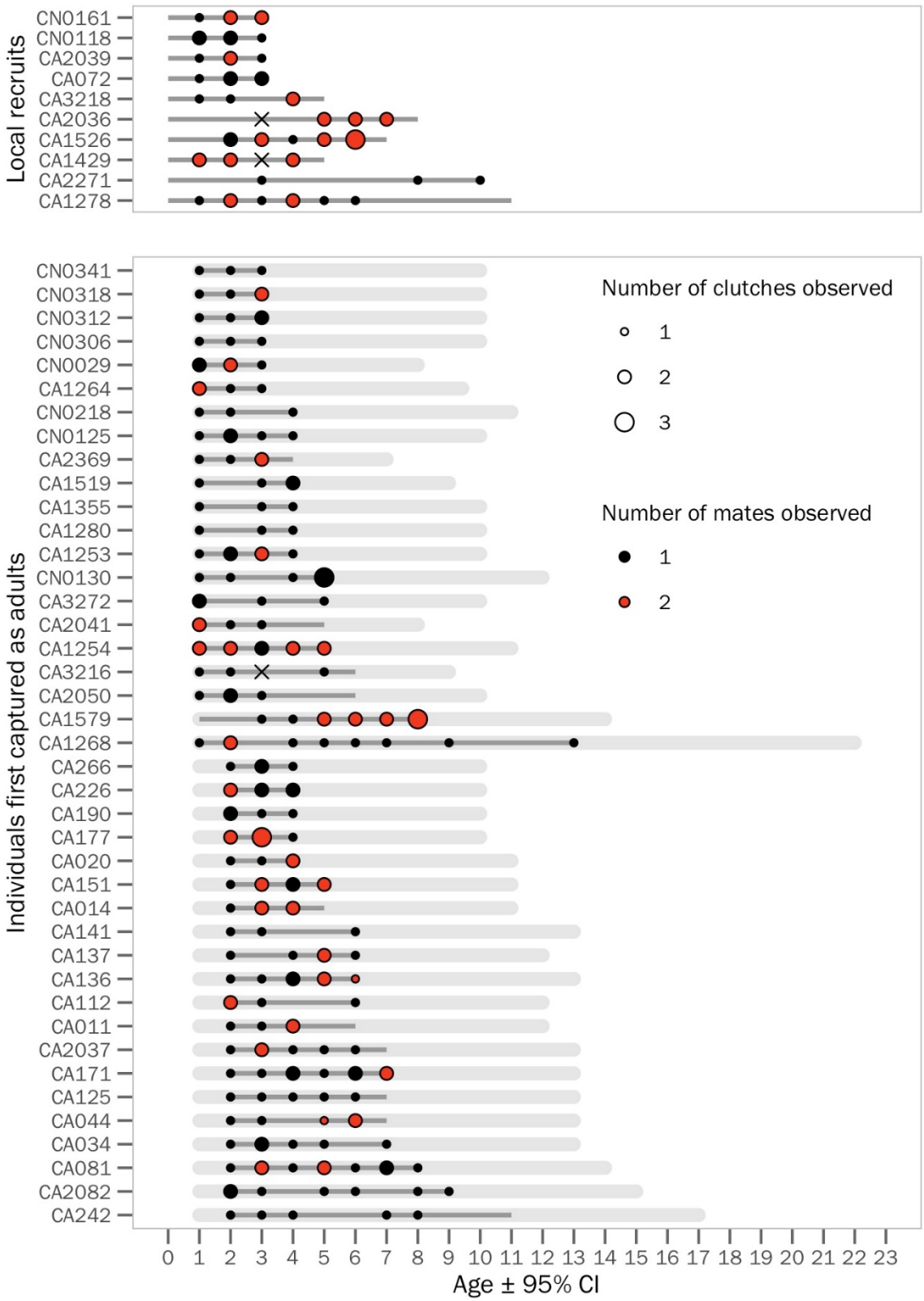

Figure 2. Mating strategy and clutch number of female snowy plovers according to age. Each row shows an individual female in the population for which we have at least three years of observations.

Panel a) shows known-aged females which were born locally, whereas b) shows females that were initially captured as adults and are therefore of unknown age. Points illustrate the age at which we collected observations of egg volume, with the size of the point corresponding to the number of clutches measured at a given age, and the colour indicating if we observed the female mating with one or two distinct males (i.e., in case of multiple clutches at a given age). The light grey buffer around unknown-age females indicates the 95% CI of the ages for an individuals' observed period (i.e., lower limit indicates the minimum age the individual could have entered the population and the upper limit indicates the maximum age of an individual's last observation). The dark grey lines indicate the period for which an individual was observed alive (i.e., in some cases we encountered an individual in the field and confirmed its survival, but we did not observe its nest to be able to measure the eggs. Note also that the age at first encounter of all known-aged individuals is 0). X's correspond to three cases in which we noted the individual nesting, but we were unable to collect data on egg volume.

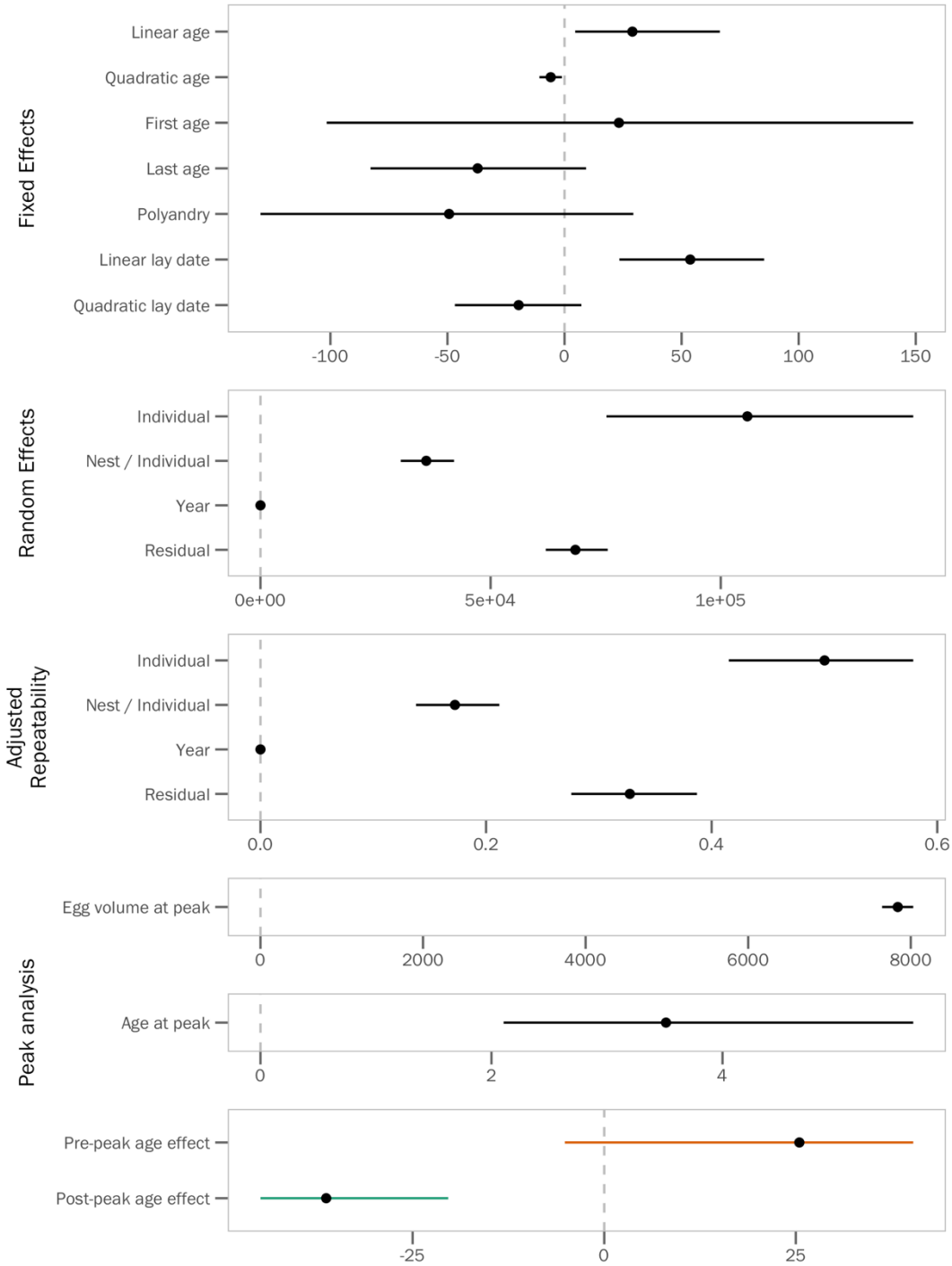

Figure 3. Predictors of variation in egg volume of snowy plovers. Effect sizes and 95% credible intervals correspond to predictors shown in Table 2. Note: orange and green credible intervals of the peak analysis (bottom panel) correspond to those shown in the pre- and post-peak age effects of Fig. 4.

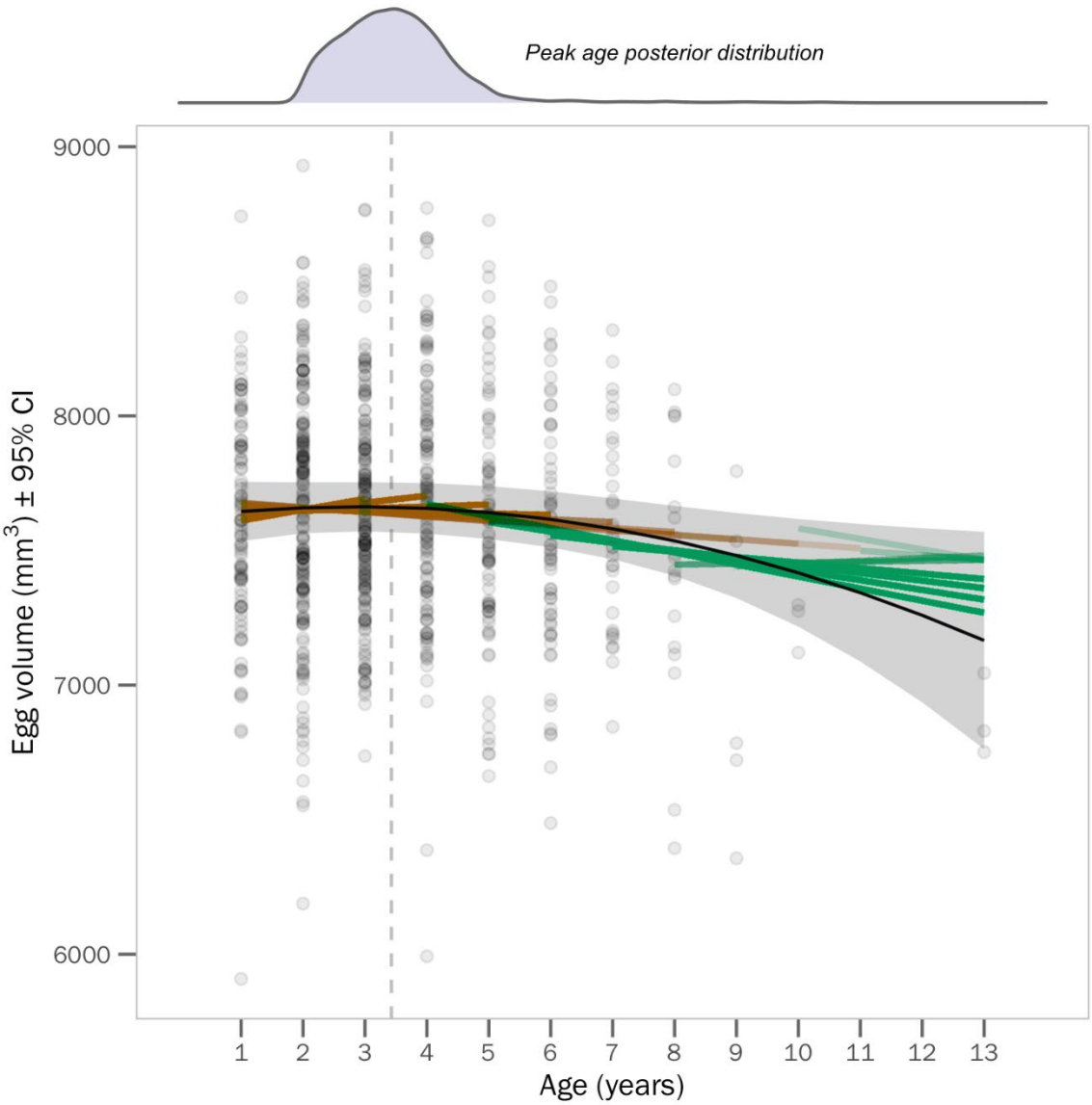

Figure 4. Senescence in egg volume. The black trend line visualizes the average within-individual age pattern of egg volume with the grey shaded area representing the 95% credible interval of the trend derived from the analysis presented in Table 2. The orange and green lines visualize the pre- and post-peak trends, respectively, of the 5,000 simulated posteriors. The vertical dashed line represents the median peak age of the posterior distribution, shown at the top of the figure. Points are the raw data from the 51 females shown in Fig. 2.

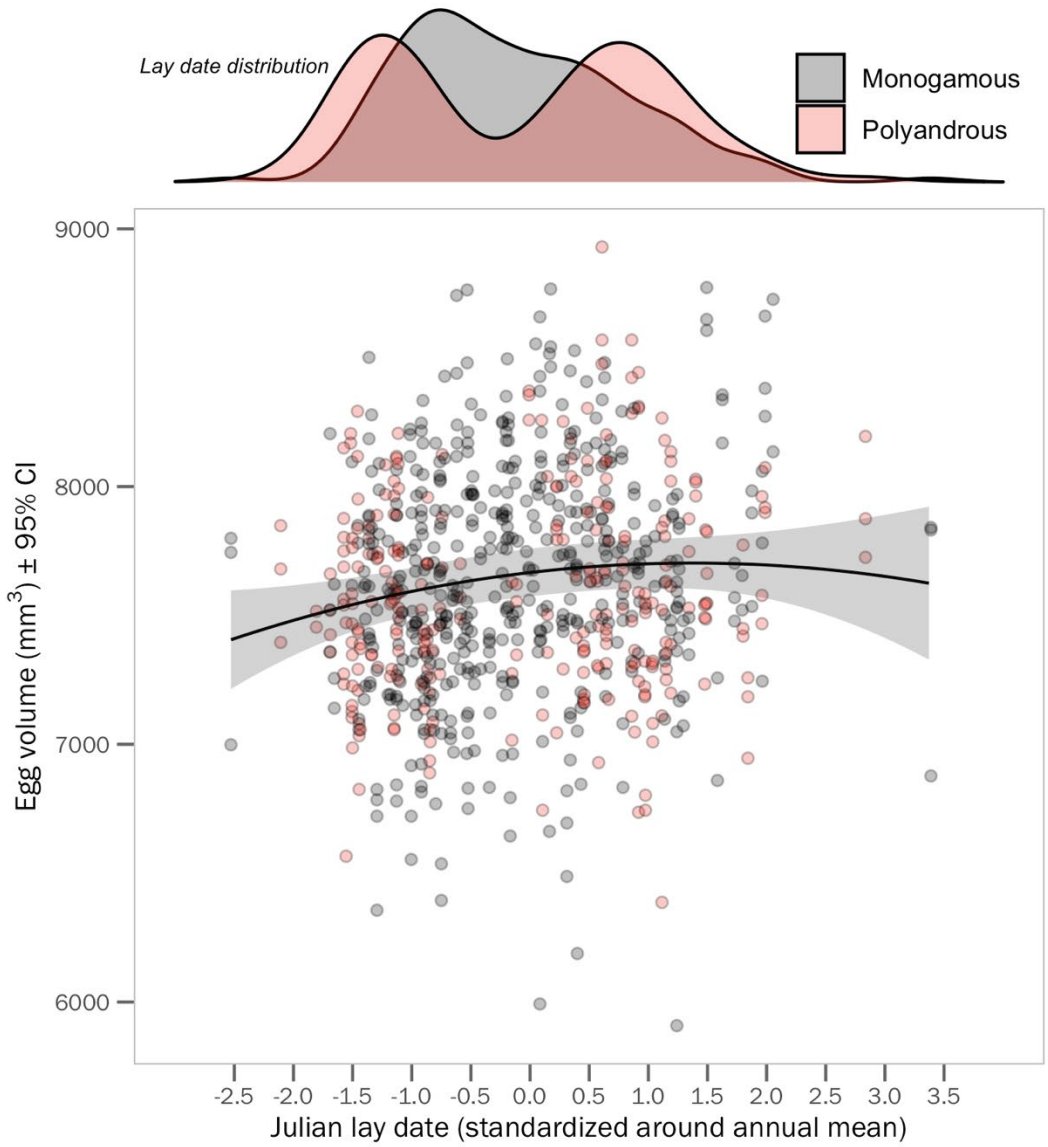

Figure 5. Egg volume variation in response to time of the season and mating strategy. The black trend line visualizes the average within-individual relationship between lay date and egg volume with the grey shaded area representing the 95% credible interval of the trend derived from the analysis presented in Table 2. The red and grey distributions visualize the densities of monogamous and polygamous nests according to lay date. Points are color-coded according to mating tactic and represent the raw data from the 51 females shown in Fig. 2. Note, lay date is mean centred according to year so that annual variation in breeding phenology is standardized.