Article Type: Original Article

Title: **Egg size variation and breeding phenology in a long-lived sequentially polygamous shorebird**

Short Running Title: Egg size variation in a polygamous shorebird

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AUTHOR CONTRIBUTIONS

LJE-H, CK, and JS: conceived and supervised the study
LJE-H, LF, CK, MC-L, KAV-R, and EG-M: collected the data
LJE-H, LF, and AGH: conducted the analysis and wrote the accompanying RMarkdown document (Supplementary File 1)
LJE-H, LF, JK, AGH, and CK: interpreted the results
LJE-H, LF, and CK: wrote the manuscript
All authors helped to revise the manuscript and approved the final version.

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CONFLICT OF INTEREST

We declare no conflict of interest in regards to our submitted work.

DATA ACCESSIBILITY

We provide all computer code and documentation as a html vignette written in Rmarkdown (Supplementary File 1) together with all the raw datasets needed to reproduce our modeling and analyses – these files can be found in this project's Open Science Framework repository (https://doi.org/10.17605/OSF.IO/UCW6J) and GitHub page (https://leberhartphillips.github.io/snowy_plover_eggs/).

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Keywords: *Charadrius nivosus*, female-female competition, mating system, season, reproductive investment, snowy plover

Abstract:

Gamete size variation *between* the sexes is central to the concept of sex roles, however, to what extent gamete size variation *within* sexes relates to sex role variation remains unclear. Comparative and theoretical studies suggest that, when clutch size is invariable, female polygamy leads to a reduction of egg size, whereas increased female-female competition for mates favors early breeding. To understand whether and how breeding phenology, egg size, and mating behavior are related at the individual level, we studied the reproductive histories of 426 snowy plover females collected over 15 years. Egg size but not mating strategy were highly repeatable for individual females. Consistent with theoretical predictions, we found that polyandrous females were the earliest breeders and that early clutches contained smaller eggs than clutches initiated later, however, the latter effect was only moderate. Neither egg size nor mating behavior showed clear signs of an age-related deterioration, on the contrary, prior experience acquired either through age or local recruitment enabled females to nest early. Taken together, these results suggest that gamete size variation is not linked to female mating behavior at the individual level.

Teaser Text:

Comparative avian analyses have linked female polyandry and sex-role reversal to the production of smaller eggs: the notion being that smaller eggs allow polyandrous females to lay multiple sequential clutches quickly. Our research, however, has found that this process is more complex at the individual level. We found that females who started breeding early in the season were more likely to be polyandrous and produce smaller eggs. Experience was also found to give older and local females a competitive advantage over younger and inexperienced females vying for early breeding opportunities. Despite this, we found limited evidence that egg size reduction gives a competitive advantage in the scramble for mates. Instead, seasonal

variations in egg size can be attributed to other factors, such as the survival of early-hatching chicks, resource limitations during egg production, and individual differences. We found that senescence had little impact on egg size or mating behavior. Future research should examine how seasonality, age, and mating behavior impact the reproductive fitness of males, who provide more parental care than females in many sex role reversed systems. By studying these effects in concert, we can gain a deeper understanding of sex roles in natural populations.

INTRODUCTION

Anisogamy is a fundamental prerequisite for the concept of sex roles (e.g., Darwin 1871; Bateman 1948; Wade and Shuster 2002; Schärer et al. 2012; Lehtonen et al. 2016). In species with conventional sex roles, males, the producers of many small gametes, invest into acquiring matings to sire as many offspring as possible, whereas females, the producers of few large gametes, aim to improve the survival prospects of their offspring by obtaining critical resources and providing parental care. However, there are many species where sex roles do not conform to this conventional paradigm (reviewed in Janicke et al., 2016). Moreover, there can also be considerable gamete size variation within the sexes – however, the causes and consequences of this intrasexual variation remains unclear (Bernardo, 1996; Immler et al., 2011). For example, the largest eggs produced by some females are typically at least 50% larger than the smallest eggs produced in the same population (Christians, 2002) and occasionally the largest egg can be more than twice as heavy as the smallest viable egg (Svagelj & Quintana, 2011). Such among-individual variation in egg size may have important consequences for individual fitness and could be linked to different reproductive strategies of females. Egg size is an important life history trait under maternal control that is positively associated with offspring fitness (Smith & Fretwell, 1974; Williams, 1994; Christians, 2002; Krist, 2011). Egg size typically reflects hatchling quality: the amount of nutrients provided to the developing offspring are especially important during early life (Williams, 1994; Krist, 2011). Because resources for maternal investment during oogenesis are typically limited, among- and within-female variation in egg size may signal a trade-off between offspring quality and quantity.

In oviparous organisms, egg size represents a basic measure of maternal 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 (Smith & Fretwell, 1974;

Williams, 1994; Christians, 2002; Krist, 2011). Within species a substantial proportion of the egg size variation can be explained by consistent individual differences between females which are highly repeatable across breeding attempts (Christians, 2002). In some cases, intraspecific variation in egg size is related to among-female variation in reproductive strategies (Slagsvold *et al.*, 1984) and is occasionally linked to discrete demographic classes such as reproductive morphs (Beck *et al.*, 2022; Giraldo-Deck *et al.*, 2022).

Given the strong association between egg size variation and life-history traits or maternal investment it is not surprising that there are strong temporal components related to egg size variation, such as seasonality and senescence. Reproductive output is often age-dependent (Bouwhuis et al., 2009; Dingemanse et al., 2020; Hammers et al., 2012; Jankowiak et al., 2018; Lemaître et al., 2015; Reznick et al., 2004; Riecke et al., 2023; Salguero-Gómez et al., 2016; Zhang et al., 2015) whereby an individual's performance increases over early life to a maximum, followed by senescent decline. Senescence is a consequence of age-dependent trade-offs between energy investments in reproduction at the expense of somatic repair (Kirkwood & Rose, 1991). Decreasing egg and/or clutch size can indicate reproductive senescence that reduces female reproductive performance with older ages (Reid *et al.*, 2003; Beamonte-Barrientos *et al.*, 2010; Dingemanse *et al.*, 2020; Fay *et al.*, 2021). Conversely, polyandry has been associated to female age, with older more experienced females being more likely to be polyandrous than younger females (Oring *et al.*, 1994). Such observations of higher mating rates at older ages suggest that differences in individual quality or experience are related to female mating behavior (Whittingham & Dunn, 2010), which could in turn be linked to among- and within-female variation in egg size.

Another source for temporal variation in egg size is seasonality. Egg size often changes throughout the reproductive season, especially in birds (Dittmann & Hötker, 2001; Skrade & Dinsmore, 2013; Weiser *et al.*, 2018; Kubelka *et al.*, 2020; Verhoeven *et al.*, 2020). At the population level, reproductive performance often declines with season which may coincide with declining egg sizes (Varpe, 2017; Weiser *et al.*, 2018). Several processes may contribute to this trend. First, in environments with limited or seasonally dependent resources, breeding early may provide favorable conditions for raising offspring reducing the amount of parental care required and maximizing offspring survival prospects (Varpe, 2017; Weiser *et al.*, 2018). Consistent with this, offspring that are born early in the season often have higher survival prospects than offspring born late in the season (Festa-Bianchet, 1988; Reznick *et al.*, 2006;

Plard *et al.*, 2015; Cruz-López *et al.*, 2017; Varpe, 2017). Second, only high quality and experienced females may be able to reproduce early in the season because of potential increased physiological stress for early egg-laying females, and/or the increased likelihood of brood failure in environments with high stochasticity, such as low food availability, inclement weather, or frequency-dependent predation risk (Borgmann *et al.*, 2013; Ockendon *et al.*, 2013). Therefore, less experienced or low-quality females may need to postpone their reproduction to a later date when conditions are more benign. Third, alternation between extended breeding and non-breeding periods may contribute to differences in egg and, consequently, offspring quality: when breeding is restricted to a certain period of the year, females can use the preceding non-reproductive period to amass resources for investment into egg or clutch size of their initial breeding attempt (Yohannes *et al.*, 2010). As the breeding season advances, less time is available for successful breeding attempts and as a consequence females may acquire fewer resources for egg production resulting in fewer and or/smaller eggs in late clutches (Wallander & Andersson, 2003).

An underappreciated evolutionary process explaining egg size variation within species is sexual selection acting on females. Although sexual selection is considered to shape predominantly male-male competition, it is increasingly acknowledged that sexual selection also operates on females with strong female-female competition for mates (Clutton-Brock, 2007; Kraaijeveld *et al.*, 2007; Fromonteil *et al.*, 2023). In some species, competition over mating opportunities is stronger in females than in males, leading to a reversal of conventional sex roles (Oring & Lank, 1982; Rosenqvist, 1990; Andersson, 2004; Goymann *et al.*, 2015; Fritzsche *et al.*, 2021). Theoretical models have linked intrasexual competition to variation in gamete size, with more intense competition leading to smaller gametes (Wade & Shuster, 2002; Lehtonen *et al.*, 2016). Notably, this relationship is not restricted to males, as there is some support for female-female competition over mates, the hallmark of social polyandry, resulting in a reduction of egg size. For instance, at the species level, a comparative analysis of birds showed that a lineage's egg size tends to decrease following the evolution of polyandry (Oring & Lank, 1982; Rosenqvist, 1990; Andersson, 2004; Goymann *et al.*, 2015; Fritzsche *et al.*, 2021) – supposedly due to the selective advantages that producing smaller eggs has on minimizing the laying period between matings (Goymann *et al.*, 2015).

Andersson (2004) presented a theoretical quantitative genetics model in which intense female scramble competition (i.e., whereby females jostle for available males to commence breeding)

shapes breeding phenology and egg size variation in females. According to the model, early breeding provides substantial advantages as it allows these females enough time to pursue sequential breeding attempts or to replace a failed first attempt (i.e., "re-nesting"; Morrison *et al.*, 2019). Early breeding should therefore be tightly correlated with female polyandry and, ultimately enhance the fitness of polyandrous females. Laying smaller eggs can provide another competitive edge in female-female competition over males: when clutch sizes are uniform, females that produce small eggs can complete their clutch faster than those that produce larger eggs and hence gain a competitive edge in the competition for mates especially when breeding synchrony is high and additional males are limited. A lower boundary for egg size is provided by reduced offspring viability because smaller eggs have fewer nutrients (Williams, 1994; Blomqvist *et al.*, 1997; Krist, 2011; Giraldo-Deck *et al.*, 2022). However, despite its highly persuasive character, the predictions on breeding phenology, egg size, and their relationship with female mating behavior provided in Andersson's (2004) model remain to be tested empirically at the individual level.

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 and (predominantly) nidifugous young (Lack, 1968; Rahn *et al.*, 1975). Clutch size is highly uniform within shorebird species and rarely exceeds four eggs (Rahn *et al.*, 1975) meaning that egg size represents an adequate proxy for maternal investment. As a clade, shorebirds also exhibit a disproportionately high prevalence of polyandry (Andersson, 2005; Colwell, 2010; Oring, 1986). Here, we investigate breeding phenology, egg size variation, and their relation with female mating strategy in snowy plovers (*Charadrius nivosus*) using a 15-year longitudinal mark-recapture dataset. The snowy plover is a long-lived shorebird (longevity record: 20 years; Colwell et al., 2017) exhibiting flexible sex-specific parental roles with sequential social monogamy and polygamy occurring in the same population (Warriner *et al.*, 1986; Eberhart-Phillips *et al.*, 2017). In parts of the species' range, the breeding season can extend up to six months allowing for multiple nesting attempts following successful fledging of young or replacing failed nests due to depredation or flooding (Eberhart-Phillips, 2019; Plaschke *et al.*, 2019). On average, females have higher polygamy potential and more partners per season than males, who in turn, provide more parental care than females, specifically for boods (Carmona-Isunza *et al.*, 2017; Cruz-López *et al.*, 2017; Eberhart-Phillips *et al.*, 2017). The reason for the higher polygamy potential in females is a surplus of males in the adult breeding population (Stenzel *et al.*, 2011; Carmona-Isunza *et al.*, 2017; Eberhart-Phillips *et al.*, 2017).

Consequently, sequential polyandry, whereby females regularly desert their broods after hatching to start a new breeding attempt with another male, is commonly observed in snowy plovers (Warriner *et al.*, 1986). Female desertion for re-mating declines with season in polyandrous plovers (Amat *et al.*, 1999; Székely *et al.*, 1999; Cruz-López *et al.*, 2017; Kupán *et al.*, 2021) suggesting that female-female competition for mates should be most pronounced early in the season.

To disentangle the relationships between gamete size, breeding phenology, and female mating behavior, we examined the reproductive histories of 426 snowy plover females. First, we investigated the correlates of re-nesting and female polyandry. We hypothesized that early nesting females would have higher probabilities of re-nesting or becoming sequentially polyandrous: early nesting females can rejoin the mating pool faster and therefore have higher potential to secure an additional breeding attempt compared to later nesting females. Secondly, we explored the predictors of clutch initiation date for a given female in a season. We hypothesized that early nesting females would have a competitive advantage over late nesters – either due to a direct body size advantage or an indirect advantage gained through prior experience as a previous breeder or local natal recruit. To evaluate this, we explored how body size, age, and origin (i.e., immigrant or natal recruit) were related to female nesting phenology and the likelihood of re-nesting or polyandry. Third, we examined the pattern of egg size variation in relation to season, age, and female body size. We predicted that early-laying females would produce the smallest eggs compared to later laying females due to the costs associated with intense female-female competition at the start of the season, i.e., the 'race' to breed early and maximize re-nesting or polyandry potential (Andersson, 2004). If reproductive senescence affects egg size variation, we predicted egg size to follow a quadratic relationship with female age. Alternatively, if female polyandry increases with age, we predicted a negative linear relationship of egg size with female age.

MATERIALS AND METHODS

Data collection

We studied the reproductive effort and breeding schedules of snowy plovers at Bahía de Ceuta – an important breeding site located on the coast of Sinaloa, western Mexico (23º54'N, 106º57'W). Details on the study site and population are provided elsewhere (e.g., Cruz-López et al., 2017; Eberhart-Phillips et al., 2020). In brief, we annually monitored breeding birds from mid-April until early July and collected mark-recapture data following the methods described

in Székely et al. (2011) . We searched for nests using telescopes and mobile hides to minimize disturbance. Upon finding a nest, we measured the length and width of each egg to the nearest tenth of a mm to determine their size (Figs. S1a, b). Using these egg dimensions, we calculated egg volume (Fig. S1c) following (Hoyt, 1979) as:

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

where K is 0.486, a volume-index constant for snowy plovers determined by (Székely *et al.*, 1994) through the use of an egg volumeter (Hanson, 1954). The modal clutch size of snowy plovers is three (86.2%) and is the maximum number of eggs we have observed in this population (Eberhart-Phillips *et al.*, 2020a). We regularly checked incomplete nests until the clutch was complete and assigned the age of these nests according to the date of the last egg laid (Plaschke *et al.*, 2019). If the clutch was complete upon discovery and had not been incubated longer than 10 days (92.5%; N = 778 nests), we determined its lay date by floating the egg and estimating the stage of embryonic development. For successful clutches that had been incubated for more than 10 days (5.4%, N = 45 nests), we back-calculated the laying date based on the hatching date assuming an incubation period of 25 days (Plaschke *et al.*, 2019). In the rare case that the nest did not hatch (2.1%, N = 18 nests) and we discovered it after day 10 of incubation, we assumed that the nest was 17 days old upon discovery (i.e., the midpoint between the minimum age of 11 days and the 25-day incubation period).

We identified previously marked nesting adults based on their unique colour ring combination. We captured unmarked adults on their nests during incubation using funnel traps (Hall & Cavitt, 2012) and assigned a unique colour ring combination for subsequent recognition. In the rare circumstance when we were unable to identify parents before hatching, we attempted to capture parents while they tended the chicks. As snowy plovers only show a small degree of sexual dimorphism, we determined the sex of all captured plovers in the field through a combination of plumage characteristics (Argüelles-Tico *et al.*, 2015), time of capture (i.e. females typically incubate during the day and males during the night; Vincze *et al.*, 2017), and other behavioral cues (e.g., sex-specific brood care; Kupán et al., 2021). For a subset of adults (57.5%), we confirmed sex molecularly from DNA extracted from blood samples by 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.*, 2009b; dos Remedios *et al.*, 2010).

222 We visited known active nests every four or five days to determine the status of the nest (e.g.,
223 active, depredated, etc.) until the 20th day after egg laying and thereafter daily until the eggs
224 hatched or failed. We weighed the chicks shortly after hatching (879 [84.7%] within 24 hours
225 after hatching, 159 [15.3%] during the second day after hatching) and marked them with an
226 alphanumeric metal and a single color ring for subsequent identification in the chance that these
227 individuals would be recruited into the breeding population as adults in future years.

228 For the years 2006 to 2016 all longitudinal data collected has been compiled as part of the
229 *CeutaOPEN* project – an open-access database for individual-based field studies in
230 evolutionary ecology and conservation biology (Eberhart-Phillips *et al.*, 2020a). We accessed
231 these data directly from the open source repository (Eberhart-Phillips *et al.*, 2020b) and
232 supplemented them with data from four additional field seasons: 2017–2020. Please refer to
233 our RMarkdown vignette that connects to *CeutaOPEN* and reproduces all analytical methods
234 and results presented below (Supplementary File 1). All of our field activities were performed
235 and permitted in accordance with the approved ethical guidelines outlined by SEMARNAT
236 (Secretariat of Environment and Natural Resources, Mexico).

237 *Statistical Analyses*
238 To evaluate the relationship between female breeding behavior, nesting phenology, and egg
239 size, our investigation implemented three step-wise analyses that: 1) established the factors
240 related to a female's potential to have multiple breeding attempts either through polyandry or
241 re-nesting, 2) identified the key female traits linked to lay date, and 3) dissected the elements
242 explaining within- and among-female variation in egg volume investment. A central trait of
243 interest in these three analyses was female age, as we needed to acknowledge age-dependent
244 variation in the repeated measures of individuals over the 15-year period of data collection. We
245 first present our statistical methods for estimating the age of females that entered the population
246 as adults, then we describe our models for investigating the interplay between female breeding
247 behavior, nesting phenology, and egg size.

248 *Statistical estimation of age for females first encountered as adults*—To estimate the ages of
249 unknown individuals in our marked population, we conducted a capture-mark-recapture
250 analysis using the 'Bayesian Survival Trajectory Analysis' (BaSTA) package in R (v1.9.4,
251 Colchero et al., 2012), which uses a Bayesian hierarchical framework to fit parametric survival
252 functions of the marked population while accounting for imperfect detection (see

Supplementary Text A for details). In short, the capture histories of unknown-age individuals (89.9%, N = 383) are cast against the survival function of the known-age population (10.1%, N = 43) to produce posterior age estimates. To acknowledge uncertainty in the BaSTA age estimate of an unknown age individual: we ran bootstrap simulations for each of the following models 1000 times, with every iteration randomly drawing a birth year estimate for unknown aged individuals from their posterior distributions provided by BaSTA. For each simulation, we evaluated the influence of birth year uncertainty by examining the effect size distribution of the 1000 bootstraps in relation to the 95% confidence interval for effect sizes of the original model that used the median birth year estimate from BaSTA. Lastly, we considered a time-since marking capture-mark-recapture model and determined that the recapture probability of our dataset was not biased by individual heterogeneity in post-marking processes (see Supplementary Text B for details).

A key methodological issue for studying age related processes in wild populations is that stochastic extrinsic mortality reduces the frequency of individuals in older age classes, hence making it challenging to disentangle between- vs. within-individual age-dependent variation – a phenomenon known as "selective disappearance" (van de Pol & Verhulst, 2006a; Nussey *et al.*, 2008). Investigations using longitudinal data to test for age-related processes are particularly suitable for this task, as they can control for the confounding effects of selective disappearance through repeated measures of individuals as they age (van de Pol & Verhulst, 2006a; Nussey *et al.*, 2008; Dingemanse *et al.*, 2020). We controlled for selective appearance and disappearance of females differing in the trait of interest by fitting 'first observed age' and 'last observed age' as fixed effects – a method that estimates between-individual age effects introduced by selective disappearance and appearance (Dingemanse et al., 2020; van de Pol & Verhulst, 2006a, 2006b). We also modelled within-individual age effects by fitting linear and quadratic forms of a within-group deviation score for age (henceforth 'age-deviance'), calculated for individual i at age j as: $age_{ij} - [first\ observed\ age]_i$ (van de Pol & Verhulst, 2006a; Snijders & Bosker, 2011) – essentially describing the number of years since the bird's arrival to the population. To ensure that intercepts of our age-dependent 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 at age 0, which is an empirically meaningless estimate. Moreover, we followed common statistical approaches to investigate age-related processes in birds (e.g., Bouwhuis et al., 2009, 2010; Dingemanse et al., 2020; Graham et al., 2019; Herborn et al., 2016; Schroeder et al., 2012) by

286 fitting a quadratic function of age to model age-specific trends. Lastly, in all models tarsus
287 length was included as a fixed effect proxy of female structural size, and was averaged over an
288 individual's lifetime of repeated measurements, i.e., our *a priori* expectation was that tarsus
289 length is static throughout adult life and that any variation in this trait was due to measurement
290 error.

291 *Modelling seasonal variation in polyandry potential ("Polyandry model")*—Our sample for
292 studying seasonal polyandry dynamics included 426 females for which the identity of their
293 mates had been verified through observation. We defined observed polyandry as a binomial
294 variable that scored an individual as being monogamous or polyandrous each year based on
295 our observations of them having one or multiple breeding partners, respectively (see Fig. S2
296 for an example of the sampling distribution). Overall, we observed 92 cases of polyandry from
297 76 females over the 15-year period (annual average incidence of observed polyandry: 11.8%,
298 range: 0–25.6%). To assess the relationship between the likelihood of polyandry and lay date,
299 age, and female structural size, we fitted a binomial linear mixed effects model that tested the
300 likelihood of polyandry predicted by the fixed effects of first lay date, age-deviance (see
301 above), first observed age, and tarsus length. We included individual ID and year as random
302 effects.

303 *Modelling seasonal variation in re-nesting potential ("Re-nesting model")*—Our sample for
304 studying seasonal re-nesting dynamics included 177 females for which the fate of their first
305 nest of the season had been verified as a failure. We defined re-nesting as a binomial variable
306 that scored an individual as being a re-nester or a single-nester each year based on our
307 observations of them attempting to re-nest after the loss of their first clutch or not, respectively.
308 Overall, we observed 64 cases of re-nesting from 55 females over the 15-year period following
309 a failed attempt (annual average incidence of observed re-nesting: 27%, range: 0–58.3%). To
310 evaluate re-nesting dynamics, we fitted a binomial linear mixed effects model that tested the
311 likelihood of re-nesting predicted by the fixed effects of first lay date, age-deviance, first
312 observed age, and tarsus length. We included individual ID and year as random effects.

313 *Modelling individual variation in lay date ("Lay date model")*— We modeled the effect of age
314 on a female's first lay date using a univariate mixed-effect structure that included age-deviance,
315 age-deviance-squared, first observed age, and last observed age as fixed covariates, and
316 individual and year as random intercepts. Furthermore, we included average tarsus length was

317 as a fixed covariate in addition to recruitment status as a two-level fixed effect that described
318 whether a breeding female hatched locally ("local recruit") or was first encountered as an adult
319 of unknown origin ("immigrant"). Our sample for studying lay date dynamics used the same
320 nest-level sample as the polyandry model above, however, as we were interested in how the
321 recruitment status of an individual influenced breeding phenology, we excluded data from 2006
322 as this was the first year when we began individual marking of all birds in the population. This
323 subset resulted in 568 nests from 376 females. We visualized the distribution of lay dates to
324 confirm normality and to assess the population-level variance in breeding schedule – an
325 indication of inter-female breeding asynchrony and the intensity of competition for mates
326 (Andersson, 2004).

327 *Modelling individual variation in egg volume ("Egg volume model")*—Our sample for
328 studying egg volume dynamics included 2392 eggs from 841 nests belonging to 426 females.
329 56 (13.1%) females had three or more years of repeated measures (Fig. S2), 83 (19.5%) had
330 two years of repeated measures, and 286 (67.4%) were measured in a single year. Furthermore,
331 43 (10.1%) individuals in our sample were marked as hatchlings but later recruited as breeding
332 adults in subsequent years ("known age"), with the remaining 383 (89.9%) individuals being
333 initially marked as adults ("unknown age"). We modelled within-individual age effects on egg
334 volume by fitting a univariate mixed-effect model that included linear and quadratic forms of
335 age-deviance, and assessed between-individual age effects by additionally incorporating first
336 observed age and last observed age as fixed covariates. Female tarsus length was also included
337 as a covariate to control for female body size, and we incorporated a quadratic function of lay
338 date to assess seasonal variation in egg volume as several shorebird studies report seasonal
339 increases (Skrade & Dinsmore, 2013; Kwon *et al.*, 2018) or decreases in egg volume (Dittmann
340 & Hötker, 2001; Skrade & Dinsmore, 2013; Kwon *et al.*, 2018; Kubelka *et al.*, 2020;
341 Verhoeven *et al.*, 2020). To disentangle within- from between-individual effects of lay date on
342 egg size, we used the same logic as with age above: first lay dates of all individuals each year
343 represented the between-individual seasonal effect, whereas the deviation in first lay dates of
344 an individual relative across all successive breeding attempts for a given season represented
345 the within-individual seasonal effect. We included random intercepts for nest, individual ID,
346 and year, and assumed a Gaussian error distribution for egg volume.

347 *Evaluating effect sizes and uncertainty*—We used packages "lme4" (Bates *et al.*, 2015), "rptR"
348 (Stoffel *et al.*, 2017) and "partR2" (Stoffel *et al.*, 2020) in the R version "Bunny-Wunnies Freak

Out" (R Core Team, 2020) to conduct our statistical modelling and assessed homoscedasticity by visually examining residuals (see Fig. S3). For each of the four mixed-effect models described above, we evaluated the uncertainty in our parameter estimates by simulating 1000 parametric bootstraps via the "partR2::partR2" function (Stoffel *et al.*, 2020). Likewise, we derived nest-, individual-, and year-level repeatabilities (i.e., intra-class correlations) by simulating 1000 parametric bootstraps of the four mixed-effect models using "rptR::rpt". We report fixed effects as standardized regression coefficients (i.e., beta weights) and repeatability as the 'adjusted repeatability' – interpreted as the repeatability of a given hierarchical group after controlling for fixed effects (Nakagawa & Schielzeth, 2010).

RESULTS

Sample summary

The modal clutch size of the 841 clutches was 3 eggs (724 nests, 86.1%; 2-eggs: 103 nests, 12.3%, 1-egg: 14 nests, 1.6%). Average egg length was 3.09 cm (0.10 cm SD, range: 2.72–3.49 cm, Fig. S1a) and width was 2.24 cm (0.05 cm SD, range: 2.02–2.40 cm, Fig. S1b), which translated into an average egg volume of 7.59 cm^3 (0.46 cm^3 SD, range: 6.00–8.98 cm^3). The average egg volume of a clutch strongly predicted the average hatch weight of the subsequent brood (β [95% CIs]: 0.63 [0.55–0.70]; $R^2_{marginal} = 0.370$ [0.310–0.436]; Figs. S1c and S4, Table S1, see Supplementary Text D for methods). Based on BaSTA's estimated birth year, 185 of the 383 unknown-age females in our sample were first observed nesting at age 1 (48.3%), 120 at age two (31.3%), 72 at age three (18.8%), five at age 4 (1.3%), and one at age 5 (0.3%). Of the 43 locally hatched females in our sample, 29 first nested at age one (67.4%), six were first observed nesting at age two (14.0%), two at age 3 (4.7%), three at age 4 (7.0%), three at ages 5, 7, and 8, respectively (7.0%). Female tarsus size was not related to their annual apparent survival (see Supplementary Text C for details). The average local tenure of all females in the sample was 1.57 years (2.15 SD) with an average age span of 3.12 years (2.03 SD, median: 3, range: 1–14 years) and an average of 1.56 years of observed ages per female (1.04 SD, median: 1, range: 1–8 age-specific observations). Females in our sample were typically observed nesting every consecutive year since their first observation, however, some individuals skipped years (Fig. S2, average yearly interval between nesting attempts = 1.07, 0.27 SD). On average, made 1.43 (0.56 SD) nesting attempts per season (median = 1, range 1 to 3). The lifetime number of chicks produced by females in years when they were polyandrous, was 2.18 (1.83–2.53 95% CI) chicks more than in years when were monogamous (Fig. S9; N = 14 years, 426 females, 841 nests).

Seasonal variation in polyandry and re-nesting potential

A female's probability of being polyandrous in a given season was strongly dependent on the date she laid her first nest, with early breeders being more likely to be polyandrous than late breeders (β [95% CIs]: -2.10 [-2.77, -1.69]; $R^2_{marginal}$ = 0.33 [0.23, 0.45]; Figs. 2a and S5, Table S2). Likewise, a female's likelihood of re-nesting following a failed attempt decreased with advancing first lay date (β: -1.79 [-5.79, -1.31]; $R^2_{marginal}$ = 0.40 [0.27, 0.6]; Figs. 2e and S6, Table S3). We found no effect of female tarsus length on the likelihood of being polyandrous (β: 0.22 [-0.05, 0.54]; $R^2_{marginal}$ = 0.001 [0, 0.18]; Fig. S5, Table S2) or re-nesting (β: -0.09 [-0.47, 0.29]; $R^2_{marginal}$ = 0.001 [0, 0.43]; Fig. S6, Table S3). We found a clear effect of age at first breeding on the likelihood of re-nesting, with females that initiated local breeding at an older age being the most likely to re-nest (β: 0.41 [0.06, 1.7]; $R^2_{marginal}$ = 0.03 [0, 0.44]; Fig. S6, Table S3). This was the same for polyandry, albeit the effect was weaker (β: 0.21 [-0.07, 0.48]; $R^2_{marginal}$ = 0.001 [0, 0.19]; Fig. S5, Table S2). We found no evidence that polyandry or re-nesting potential was related to age since first breeding (i.e., age-deviance; Figs. S5 and S6). The lay date distribution of polyandrous females was bimodal, with peaks in the first and second nests occurring 11.1 days before and 29.1 days after the unimodal seasonal peak for monogamous females (Fig. 2b). Similarly, the lay date distribution of re-nesting females was also bimodal, with peaks in the first and replacement clutches occurring 9.7 days before and 28.4 days after the unimodal seasonal peak for single nesters (Fig. 2d). Females had low repeatability among years in polyandry (adjusted individual cross-year repeatability, r [95% CIs] = 0.01 [0, 0.15]; Fig. S5, Table S2) and re-nesting (r = 0.03 [0, 0.14]; Fig. S6, Table S3). When pooled together to assess multi-clutching behavior (i.e., the probability of simply laying two nests or one regardless of the outcome of the first nest or the identity of the second male), females had higher repeatability than when polyandry or re-nesting were assessed separately (r = 0.35 [0, 0.86]; Fig. S10, Table S7).

Individual variation in lay date

Females showed moderate repeatability in their first lay date among years (r = 0.19 [0.06, 0.32] 95%CI; Fig. 1, Table S4). We found strong support for the effect of origin on first lay date: females that locally hatched and later recruited into the breeding population initiated nests 7.80 days earlier (95% CI: [5.09, 10.50]) on average compared to conspecifics whose origin was unknown (Figs. 1 and 3b). The next strongest fixed effect was within-individual age: young females laid later nests compared to older females with lay date advancing by ~2.17 days per

year until age six (95% CI: [1.41, 2.93]; Fig. 3a), after which the uncertainty in the trend became unwieldly in the oldest age classes of our sample (Fig. 3a). Notably, female size did not affect lay date (Fig. 1 and S7a), nor did between-individual effects of first or last age at breeding (Fig. 1).

Individual variation in egg volume

Overall, our model accounted for 71.2% ([68.2, 74.3] 95%CIs) of variation in egg volume, with fixed effects explaining 7.9% ([5.1, 12.3] 95%CIs) of this variation (Table S5). Females were highly repeatable in their egg volumes between clutches: $r = 0.47$ ([0.41, 0.53] 95%CIs; Fig. 1, Table S5). Furthermore, eggs within the same clutch were moderately repeatable in volume ($r = 0.18$ [0.14, 0.22]; Fig. 1, Table S5). The strongest fixed effect explaining egg volume variation was the structural size of the mother (β_{tarsus} [95% CI]: 0.23 [0.15, 0.29]; semi-partial R^2 of female tarsus = 0.05 [0.02, 0.09]; Figs. 1 and S3b, Table S5): larger females laid larger eggs than smaller females (model predicted difference: 0.58 cm^3 [0.34, 0.81] 95%CI). The second strongest effect was the between-individual quadratic season function (Fig. 2c): eggs were smallest at the start of the season (model prediction: 7.18 cm^3 [6.98, 7.37] 95%CI) and largest shortly after the middle of the season (model prediction: 7.68 cm^3 [7.60, 7.76] 95%CI). Average egg volume also increased between sequential clutches within individuals but with smaller magnitude than the population-level trend (β_{within} [95%CI]: 0.10 [0.06, 0.14], predicted increase of 0.21 cm^3 [0.04, 0.38]). Senescence in egg volume was not supported (β_{age} [95% CIs]: 0.00 [-0.06, 0.6], β_{age^2}: -0.05 [-0.09, -0.01]; semi-partial R^2 of senescence function = 0.003 [0, 0.05]; Fig. 1, Table S5). Furthermore, we found no support for selective (dis)appearance of individuals according to egg volume, as the 95% CIs for first and last observed ages of reproduction overlapped zero (Fig. 1, Table S5).

To further acknowledge uncertainty in the age-estimates provided by BaSTA, we re-analyzed the egg volume model using only known-aged females. Notably, this strengthened the effect sizes of 'mother tarsus length' and the within-individual age effects (i.e., 'linear age' and 'quadratic age'). For example, the 'mother tarsus length' effect (β_{tarsus}) increased to 0.33 [0.09, 0.51 95% CI], the 'linear age' effect (β_{age}) increased to -0.05 [-0.21, 0.11], and the 'quadratic age' effect (β_{age^2}) increased to -0.10 [-0.24, 0.05] (Table S6). However, given that the sample size of the known-aged female data set was greatly reduced, this analysis is arguably underpowered: the 95% confidence intervals bounding the effect sizes increased and, in many cases, overlapped zero. Furthermore, the bootstrap simulations incorporating the individual

446 birth-year posteriors estimated from BaSTA confirmed the results of all age-dependent models
447 (Fig. S8).

448 DISCUSSION

449 Increased competition for mating opportunities in species with conventional sex roles is
450 typically seen as a consequence of anisogamy where the production of many small gametes
451 allows polygamous males to maximize their reproductive potential (Darwin, 1871; Bateman,
452 1948; Wade & Shuster, 2002; Schärer *et al.*, 2012; Lehtonen *et al.*, 2016). Applying this
453 paradigm to females, an increasing competition over mates should therefore be associated with
454 the evolution of smaller eggs. Andersson (2004) developed a theoretical quantitative genetic
455 model of female sexual selection by scramble competition over males in an attempt to explain
456 reduced egg size in polyandrous species. Andersson's (2004) model predicted that scramble
457 competition for males should lead to egg size reduction and early breeding in sequentially
458 polyandrous females of species with largely invariable clutch sizes. We tested the predictions
459 of Andersson's (2004) model empirically at the individual level: examining the links between
460 breeding phenology, individual mating strategies, and egg size variation in a population of
461 snowy plovers that contains monogamous and polyandrous females (Cruz-López *et al.*, 2017;
462 Eberhart-Phillips *et al.*, 2017; Kupán *et al.*, 2021). Consistent with Andersson's (2004)
463 predictions, we found that female polyandry was associated with early breeding and that early
464 clutches typically contained smaller eggs than clutches laid later in the season – both between
465 and within individual females. In our population, early breeding females whose nesting
466 attempts were successful invariably deserted the brood shortly after hatching (Cruz-López *et*
467 *al.*, 2017; Kupán *et al.*, 2021) and the resulting collinearity between mating behavior and first
468 lay date prevented us from explicitly testing whether mating behavior was directly related to
469 egg size.

470 Although the statistical associations between breeding phenology, egg size and female mating
471 behavior are intriguing, we note that their impact on the egg size variation observed in this
472 population is rather limited. First, despite snowy plovers' unusual mating system with
473 sequential polyandry, monogamy, and occasionally polygyny occurring in the same population
474 (Warriner *et al.*, 1986; Eberhart-Phillips *et al.*, 2017), the egg size variation we report is not
475 more pronounced than in other birds: the proportional difference between the largest and
476 smallest egg in our population was approximately 50%, which is of very similar magnitude to
477 the intraspecific range observed within other bird populations (Christians, 2002). Other

constraints may provide limitations on egg size variation in snowy plovers. Waders produce relatively large eggs that provide vital reserves for their precocial young and the moderate egg size variation observed in snowy plovers could indicate that females are unable to reduce egg size further without jeopardizing chick viability. Second, we note that structural size of females had a stronger effect on egg size variation than breeding phenology. This is consistent with other studies (Christians, 2002; Giraldo-Deck *et al.*, 2022) showing that larger females produce larger eggs than smaller females. Third, we found that, as demonstrated in other studies (e.g., Christians, 2002), female identity explained the largest part of the variation in egg size and repeatability of egg size in females was very high. The high repeatability suggests that egg size may have considerable genetic variation, although it has been suggested that many loci with small effects seem to encode this life history trait (Santure *et al.*, 2013).

In contrast to egg size, female mating behavior showed a very low individual repeatability across years. The observed low individual consistency is most likely related to the high stochastic nature of nest survival where the main sources of clutch/brood failure in our population are flooding, predation, and chick mortality through starvation (Cruz-López *et al.*, 2017). Early breeding females whose nests failed, typically stayed together with their mate for rapid renesting. These females may have intended to become polygamous but since their replacement clutch hatched later in the season when conditions for chicks or remating are less favorable, they switched to a monogamous strategy that involves longer brood care. Snowy plover females can adjust their brood care efforts flexibly according to the value and needs of the young (Kupán *et al.*, 2021). Female care and re-mating efforts are inversely related to each other and show strong seasonality. Early in the breeding season when survival prospects for the chicks and re-mating opportunities are high, and their mate can successfully rear the chicks alone, females typically desert their broods right after hatching of the chicks to quickly start a new breeding attempt with another male (Székely *et al.*, 1999; Cruz-López *et al.*, 2017; Kupán *et al.*, 2021). Females whose chicks hatch later in the season, typically remain with the brood and provide care jointly with their mate. However, desertion during brood care is tightly associated with chick mortality (Kupán *et al.*, 2021). When survival prospects of their offspring are deteriorating and chicks die despite the joint care, initially caring females desert their broods and presumably remate elsewhere where environmental conditions are better. Such high plasticity in female care and mating strategies allows females to flexibly respond to nest and chick survival, and is an important ecological modulator of breeding behavior in snowy plovers.

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 throughout the breeding season (Kwon et al., 2018, n.b., the presented effect size is small). However, many investigations of seasonal egg size dynamics did not disentangle whether the observed changes were due to within- or between-individual effects. A study that included 15 arctic shorebirds suggested that indeed between-individual variation may account for more of the seasonal variation in egg size than within-individual variation (Weiser *et al.*, 2018). In our population, early season nesters produced smaller eggs on average than females initiating nests at a later date. These seasonal changes were driven by within individual changes: females generally increased egg volume between consecutive nesting attempts (albeit the effect size was small), suggesting that maternal investment during early breeding attempts is impaired by physiological limitations. Mutually non-exclusive constraints may include low food availability (Steigerwald *et al.*, 2015), and carry-over costs associated with intense competition (Duckworth, 2006) or migratory status (Crossin *et al.*, 2010). In contrast, delayed breeders can take advantage of a slower pace to gather more resources and maximize investment prior to clutch initiation – whilst having only enough time for a single breeding attempt. Although we did not collect any direct empirical data on temporal changes in food availability during our study (e.g., with pit-fall traps), the invertebrate prey communities of salina ecosystems (i.e., like that of our study population) are well documented to have dynamic emergence and quiescent phenologies (Britton & Johnson, 1987), providing important ecological context and support of our notion that resource availability for egg-laying female snowy plovers is highly. The observed decrease of egg size in clutches produced at the end of season is consistent with such constraints for breeding females as females are in a rush to complete their clutches and finish incubation before the onset of catastrophic floods caused by increased precipitation and tide height at the end of the breeding season (Plaschke *et al.*, 2019).

Despite being long-lived – the oldest documented female in our sample was at least 13 years old (longevity record: 20 years; Colwell et al., 2017) – and investing substantially in reproduction year-after-year, we found no evidence of age-dependent trade-offs in egg size or polyandry potential. Contrary to our predictions derived from senescence theory, older females initiated nests earlier in the season compared to their younger conspecifics – indicating age-

543 dependent competitive ability that may initially increase the polygamy potential of females
544 (Oring *et al.*, 1994). Age-dependent variation in lay date followed a non-linear pattern: lay date
545 advanced with each year of age until a peak at age six, after which the age-lay date trajectory
546 was unclear because of limited sampling in older age classes. In snowy plovers, occasionally
547 females re-mate with or retain their last mate in the following season (Halimubieke *et al.*,
548 2019), presumably to skip the time consuming mate search and start breeding early – a process
549 that could also explain the age-dependent advance in lay date we observed. Furthermore,
550 locally recruited females (i.e., hatched locally) bred earlier than immigrant females indicating
551 a role for prior experience giving competitive advantage for breeders in our population.

552 Egg size did not change clearly with female age. Several studies of oviparous organisms have
553 observed age-dependent variation in egg size, with some studies finding a positive relationship
554 (Cooch *et al.*, 1992; Flint & Sedinger, 1992; Robertson *et al.*, 1994; Warner *et al.*, 2016;
555 Verhoeven *et al.*, 2020) and others observing a negative relationship (Reid, 1988; Potti, 1993;
556 Ito, 1997). Recent longitudinal studies of wild avian systems showed a quadratic relationship
557 with a prominent increase in egg size in early life, followed by a peak and then a late-life
558 decline (Bouwhuis *et al.*, 2009; Jankowiak *et al.*, 2018). In captive avian systems, the early life
559 increase in egg size is also observed, but not the late-life decline likely due to ad libitum food
560 (Woodard & Abplanalp, 1971). A quadratic age relationship provided the best fit for a possible
561 relationship between egg size and age in our study, but the effect was not statistically clear.
562 This finding did not change when we repeated the analysis including only the 45 females of
563 known age (10% of the original sample). We acknowledge that our relatively small sample of
564 known-age individuals presents a limitation to our study – we cannot exclude a moderate effect
565 of senescence on egg size. Nevertheless, one potential explanation for the lack of a clear
566 senescence trend observed in egg size is that there is little room for further reduction because
567 of viability constraints for the chicks. In shorebirds, chicks are not fed by the parents but rather
568 must forage for themselves immediately after hatching and larger chicks that hatch from larger
569 eggs typically survive better than smaller chicks (Blomqvist *et al.*, 1997; Giraldo-Deck *et al.*,
570 2022). The extra nutrients provided by a large egg may be crucial for the chick survival during
571 the first few days of life when foraging efficiency is reduced as chicks still learn how to catch
572 prey (Ricklefs, 1968). Consequently, additional reductions of egg size may not be feasible as
573 the knock-on effects for chick survival are too costly (Williams, 1994; Starck & Ricklefs,
574 1998), therefore limiting a females' potential to save resources by reducing egg volume. The

chick viability constraints may also provide an explanation why the variation in egg size at the population level is relatively low.

Conclusions

Past species-level studies have linked polyandry and sex-role reversal to reduced female gamete size (Slotow, 1996; Andersson, 2004), as smaller eggs would permit females to produce several clutches in rapid succession (Liker *et al.*, 2001). In our individual-level investigation we found that early nesting females were more likely to be polyandrous and produced clutches containing smaller eggs than females that started their first breeding attempt later in the season. Starting to breed early in the season is an important pre-determinant of female polygamy. Prior experience can provide both older and local females a competitive advantage over younger and naïve conspecifics scrambling for early breeding opportunities that are at the heart of the polyandrous mating strategy (Andersson, 2004). However, evidence supporting an adaptive egg-size adjustment to obtain a competitive advantage in the scramble competition for mates was weak. Rather we found that the potential for egg size reduction is limited in snowy plovers and the observed seasonal variation in egg size can also be explained by other constraints that include a survival advantage for early hatching chicks, resource constraints during the egg-producing phase and, most importantly, between individual differences. Senescence did not seem to have a major impact on egg size variation nor on the mating behavior of females. Future research of polyandrous systems should also examine the impact of seasonality, age, and mating behavior on the reproductive fitness of males, as males provide a larger share of parental care than females and therefore should have a more direct impact on the survival prospects of the young. Examining the effects of season- and age-dependent trade-offs on individual fitness and variation in mating tactics will enable a deeper understanding about selective advantages and constraints of diverse and plastic sex roles in natural populations.

DATA ACCESSIBILITY

We provide all computer code and documentation as a html vignette written in Rmarkdown (click here: File S1) together with all 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/UCW6J

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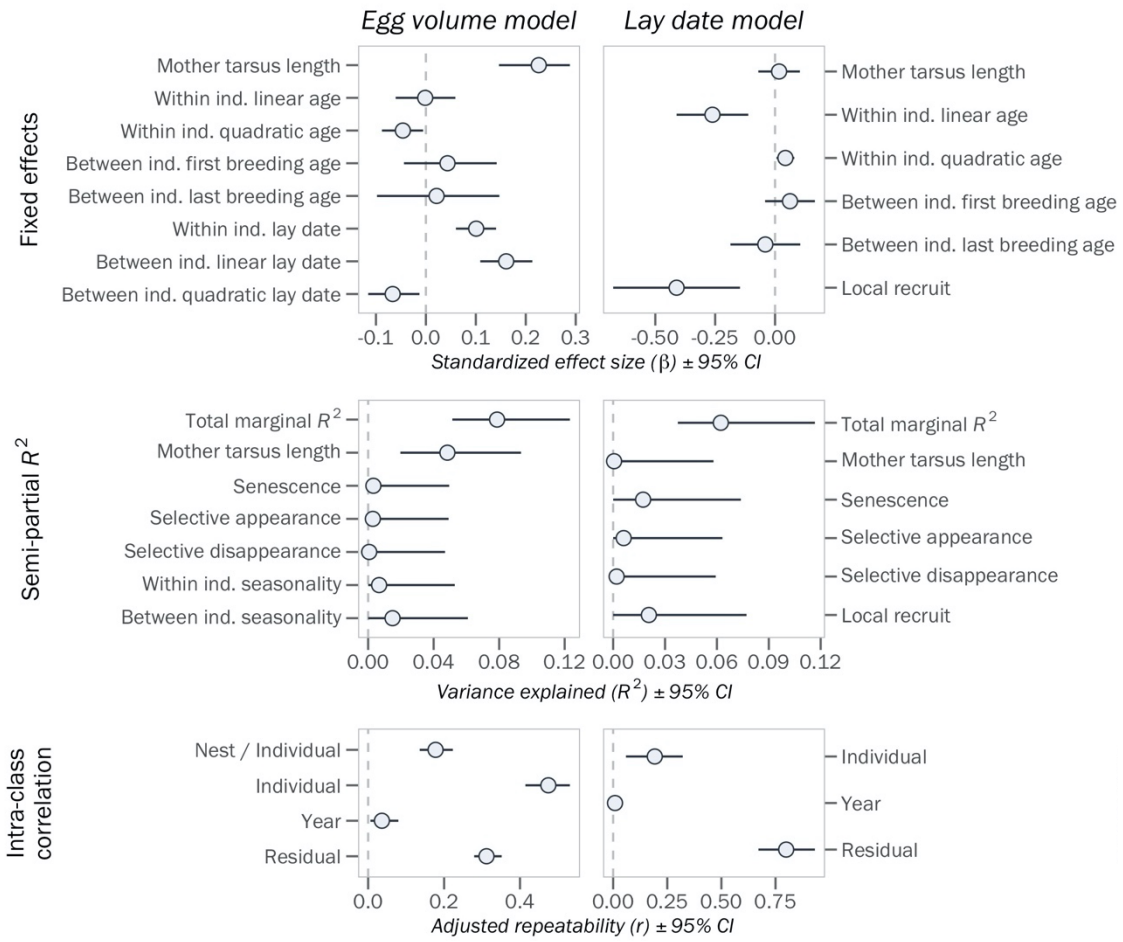
935 **FIGURES**



936 **Figure 1.** Sources of egg volume (left) and lay date (right) variation. Top row: standardized
937 effect sizes (± 95% CI) of fixed effects. Middle row: variance explained by fixed effects (note:
938 the term 'Senescence' describes the collective variation explained by the linear and quadratic
939 within-individual age effects in the top row; the term 'Selective appearance' and 'Selective
940 disappearance' describe the variation explained by the between individual first- and last-
941 breeding age fixed effects of the top row, respectively; the term 'Within ind. seasonality'
942 describes the variation explained by the within individual lay date effect in the top row, and
943 the term 'Between ind. seasonality' describes the collective variation explained by the linear
944 and quadratic lay date effects in the top row). Bottom row: adjusted repeatabilities (± 95% CI)
945 of random effects.

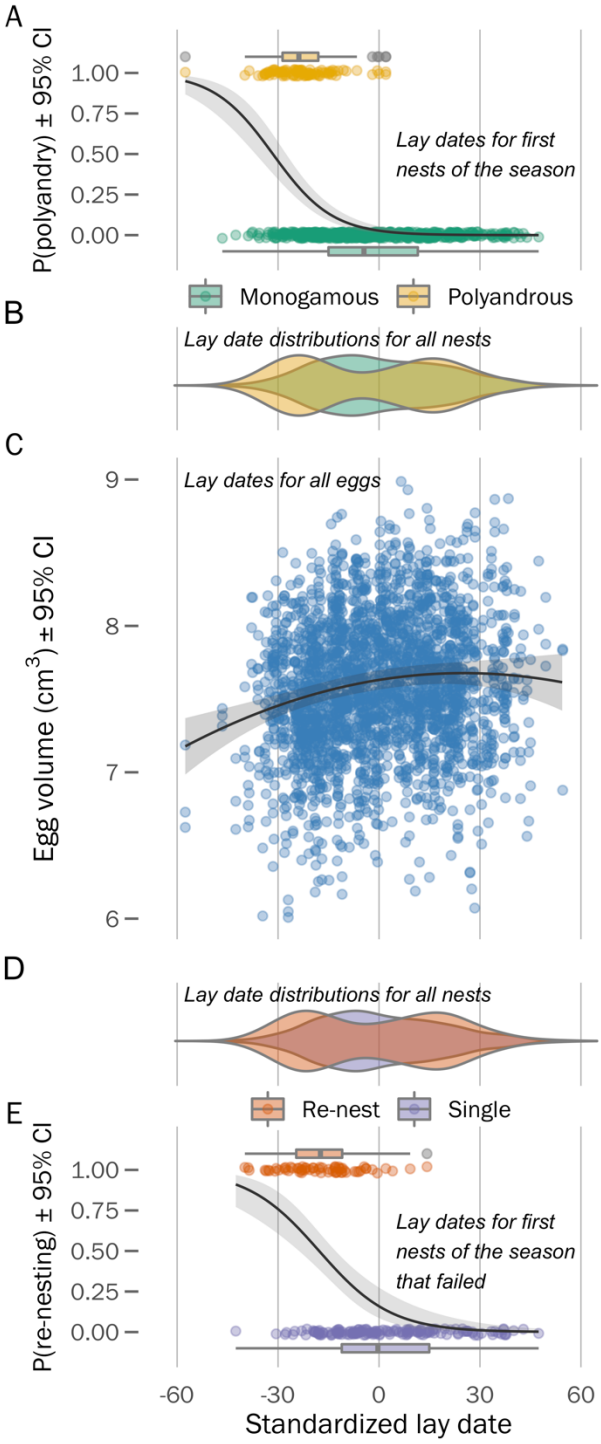


Figure 2. Phenology of mating behaviors, re-nesting, egg laying, and egg size in 426 female snowy plovers breeding at Bahía de Ceuta. A) Relationship between polyandry potential and lay date of a female's first nest of the season. Each datum is the lay date of an individual's first nest and their observed local mating behavior of each year. B) Lay date distributions of all nests for females that were polyandrous (yellow; 92 nests from 76 females) or monogamous (green; 573 nests from 403 females). C) Seasonal variation in egg volume – trend shows the between-individual polynomial function of the model prediction. Each datum is an egg's

volume (cm^3) and lay date. D) Lay date distributions of all nests for females that laid replacement clutches (orange; 64 nests from 127 females) or did not re-nest (purple; 146 nests from 134 females) following failure of their first nest. E) Relationship between re-nesting potential and lay date of a female's first nest of the season. As with panel (A), each datum is the lay date of an individual's first nest and their observed local re-nesting activity of each year. Late date is standardized for each year across all panels.

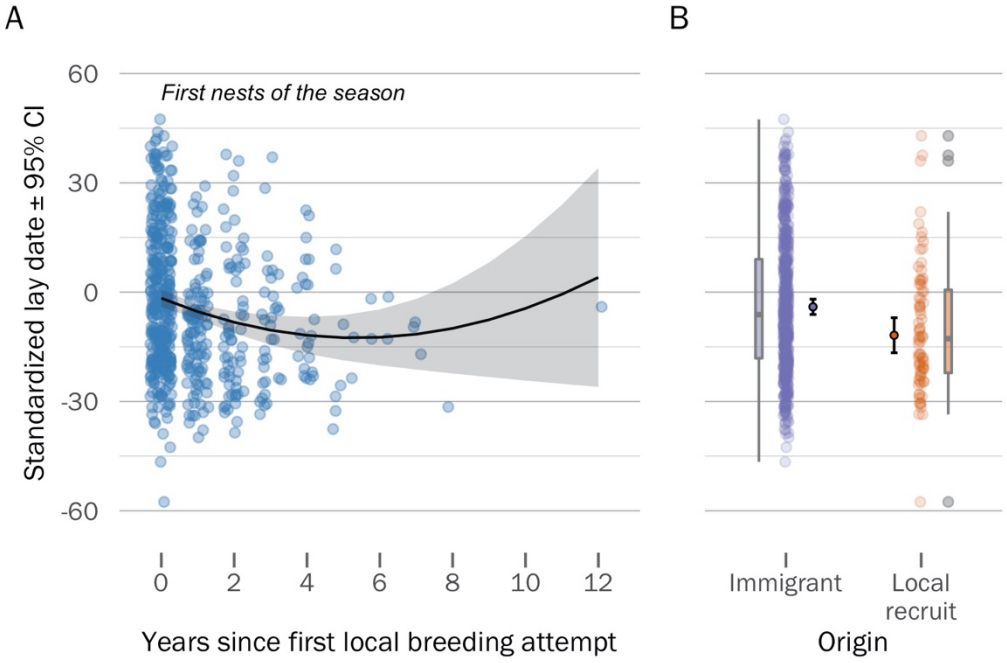


Figure 3. Age- and origin-dependent breeding phenology of female snowy plovers. A) Within-individual variation in age-specific nest initiation date – as females gained more experience in the local population, they started nesting earlier, however this trend reversed at older ages (albeit with high uncertainty). Each datum represents an individual's 'age-deviance' (i.e., a within-group centred measure of the number of years since the individual's first observed local breeding attempt, see *Methods* for more details) and the lay date of its first nest each year. B) Origin-specific variation in nest initiation date – females that hatched locally and recruited into the breeding population (orange) tended to nest earlier than birds originating from elsewhere (purple). Inner-most distributions show the model estimates and 95% CI, outer-most box plots show the inter-quartile ranges of the raw data (point-cloud).

SUPPLEMENTARY TABLES

Table S1. Relationship between the average egg volume of a clutch and the average chick weight at hatching. See Supplementary Text D for methods.

Chick hatch weight	Mean estimate	95% confidence interval
Fixed effects β (standardized)		
Average egg volume of clutch	0.60	[0.55, 0.66]
Partitioned R^2		
Total Marginal R^2	0.37	[0.3, 0.43]
Total Conditional R^2	0.47	[0.38, 0.56]
Random effects σ^2		
Mother identity	0.01	[0, 0.02]
Year	0.01	[0, 0.02]
Residual	0.09	[0.08, 0.11]
Adjusted repeatability r		
Mother identity	0.05	[0, 0.12]
Year	0.05	[0.01, 0.11]
Residual	0.90	[0.81, 0.98]
Sample sizes n		
Year	14	
Individuals	425	
Observations (i.e., Nests)	840	

Table S2. Relationship between the lay date of an individual's first nest and their likelihood of polyandry each year. Fixed effect size of 'first nest lay date' is the standardized estimate on the logit scale.

Polyandry probability	Mean estimate	95% confidence interval
Fixed effects β (logit standardized)		
First nest lay date	−2.10	[-2.77, -1.69]
Age since first breeding	−0.01	[-0.29, 0.25]
First breeding age	0.21	[-0.07, 0.48]
Mother tarsus length	0.22	[-0.05, 0.54]
Partitioned R^2		
Total Marginal R^2	0.34	[0.24, 0.45]
First nest lay date	0.33	[0.23, 0.45]
Age since first breeding	0.00	[0, 0.18]
First breeding age	0.00	[0, 0.19]
Mother tarsus length	0.00	[0, 0.18]
Total Conditional R^2	0.36	[0.25, 0.52]
Random effects σ^2		
Individual	0.08	[0, 1.55]
Year	0.11	[0, 0.39]
Adjusted repeatability r		
Individual	0.01	[0, 0.15]
Year	0.01	[0, 0.05]
Sample sizes n		
Years	14	
Individuals	426	
Observations (i.e., Nests)	665	

Table S3. Relationship between the lay date of an individual's first nest and their likelihood of re-nesting following breeding failure in a given year. Fixed effect size of 'first nest lay date' is the standardized estimate on the logit scale.

Re-nesting probability	Mean estimate	95% confidence interval
Fixed effects β (logit standardized)		
First nest lay date	−1.79	[-5.79, -1.31]
Age since first breeding	0.20	[-0.19, 0.73]
First breeding age	0.41	[0.06, 1.7]
Mother tarsus length	−0.09	[-0.47, 0.29]
Partitioned R^2		
Total Marginal R^2	0.42	[0.29, 0.61]
First nest lay date	0.40	[0.27, 0.6]
Age since first breeding	0.01	[0, 0.43]
First breeding age	0.03	[0, 0.44]
Mother tarsus length	0.00	[0, 0.43]
Total Conditional R^2	0.44	[0.3, 0.96]
Random effects σ^2		
Individual	0.15	[0, 1153.43]
Year	0.00	[0, 2.8]
Adjusted repeatability r		
Individual	0.03	[0, 14.04]
Year	0.00	[0, 0.21]
Sample sizes n		
Years	13	
Individuals	177	
Observations (i.e., Nests)	209	

Table S4. Sources of lay date variation. Note: within the *Partitioned* R^2 sub-table the term 'Senescence' describes the collective variation explained by the linear and quadratic within-individual age effects in the top sub-table, the term 'Selective appearance' and 'Selective disappearance' describe the variation explained by the between individual first- and last-breeding age fixed effects of the top sub-table, respectively.

Lay date of first nest	Mean estimate	95% confidence interval
Fixed effects β (standardized)		
Mother tarsus length	0.02	[-0.07, 0.1]
Local recruit	−0.41	[-0.68, -0.15]
Within ind. linear age	−0.26	[-0.41, -0.11]
Within ind. quadratic age	0.04	[0.01, 0.08]
Between ind. first breeding age	0.06	[-0.04, 0.17]
Between ind. last breeding age	−0.04	[-0.19, 0.11]
Partitioned R^2		
Total Marginal R^2	0.06	[0.04, 0.12]
Total Conditional R^2	0.23	[0.13, 0.38]
Mother tarsus length	0.00	[0, 0.06]
Local recruit	0.02	[0, 0.08]
Senescence	0.02	[0, 0.07]
Selective appearance	0.01	[0, 0.06]
Selective disappearance	0.00	[0, 0.06]
Random effects σ^2		
Individual	60.69	[18.94, 117.67]
Year	2.00	[0, 12.89]
Residual	283.38	[229.95, 326.82]
Adjusted repeatability r		
Individual	0.19	[0.06, 0.32]
Year	0.01	[0, 0.03]
Residual	0.80	[0.67, 0.93]
Sample sizes n		
Years	13	
Individuals	376	
Observations (i.e., Nests)	568	

Table S5. (*displayed on next page*) Sources of egg size variation. Note: within the *Partitioned* R^2 sub-table the term 'Senescence' describes the collective variation explained by the linear and quadratic within-individual age effects in the top sub-table, the term 'Selective appearance' and 'Selective disappearance' describe the variation explained by the between individual first- and last-breeding age fixed effects of the top sub-table, respectively; the term 'Within ind. seasonality' describes the variation explained by the within individual lay date effect in the top sub-table, and the term 'Between ind. seasonality' describes the collective variation explained by the linear and quadratic lay date effects in the top sub-table.

991 **Table S5. (*caption on previous page*)**

Egg volume	Mean estimate	95% confidence interval
Fixed effects β (standardized)		
Mother tarsus length	0.23	[0.15, 0.29]
Within ind. linear age	–0.00	[-0.06, 0.06]
Within ind. quadratic age	–0.05	[-0.09, -0.01]
Between ind. first breeding age	0.04	[-0.04, 0.14]
Between ind. last breeding age	0.02	[-0.1, 0.15]
Within ind. lay date	0.10	[0.06, 0.14]
Between ind. linear lay date	0.16	[0.11, 0.21]
Between ind. quadratic lay date	–0.07	[-0.12, -0.01]
Partitioned R^2		
Total Marginal R^2	0.08	[0.05, 0.12]
Total Conditional R^2	0.71	[0.68, 0.74]
Mother tarsus length	0.05	[0.02, 0.09]
Senescence	0.00	[0, 0.05]
Selective appearance	0.00	[0, 0.05]
Selective disappearance	0.00	[0, 0.05]
Between ind. seasonality	0.01	[0, 0.06]
Within ind. seasonality	0.01	[0, 0.05]
Random effects σ^2		
Nest / Individual	0.04	[0.03, 0.04]
Individual	0.10	[0.08, 0.12]
Year	0.01	[0, 0.02]
Residual	0.06	[0.06, 0.07]
Adjusted repeatability r		
Nest / Individual	0.18	[0.14, 0.22]
Individual	0.47	[0.41, 0.53]
Year	0.04	[0.01, 0.08]
Residual	0.31	[0.28, 0.35]
Sample sizes n		
Years	14	
Individuals	426	
Nests	841	
Observations (i.e., Eggs)	2392	

Table S6. Sources of egg volume variation when using only known-aged females. See caption of Table S1 for definitions of table terms.

Egg volume (known-age analysis)	Mean estimate	95% confidence interval
Fixed effects β (standardized)		
Mother tarsus length	0.33	[0.09, 0.51]
Within ind. linear age	−0.05	[-0.21, 0.11]
Within ind. quadratic age	−0.10	[-0.24, 0.05]
Between ind. first breeding age	0.05	[-0.32, 0.38]
Between ind. last breeding age	−0.03	[-0.41, 0.36]
Within ind. lay date	0.09	[-0.03, 0.22]
Between ind. linear lay date	0.14	[-0.02, 0.3]
Between ind. quadratic lay date	−0.17	[-0.34, 0]
Partitioned R^2		
Total Marginal R^2	0.13	[0.06, 0.32]
Total Conditional R^2	0.74	[0.67, 0.83]
Mother tarsus length	0.09	[0.02, 0.29]
Senescence	0.01	[0, 0.23]
Selective appearance	0.00	[0, 0.22]
Selective disappearance	0.00	[0, 0.22]
Between ind. seasonality	0.04	[0, 0.25]
Within ind. seasonality	0.01	[0, 0.22]
Random effects σ^2		
Nest / Individual	0.05	[0.03, 0.08]
Individual	0.07	[0.03, 0.14]
Residual	0.05	[0.04, 0.06]
Adjusted repeatability r		
Nest / Individual	0.29	[0.17, 0.46]
Individual	0.41	[0.19, 0.58]
Residual	0.30	[0.21, 0.41]
Sample sizes n		
Years	14	
Individuals	43	
Nests	112	
Observations (i.e., Eggs)	319	

Table S7. Relationship between the lay date of an individual's first nest and their likelihood of re-nesting or being polyandrous (i.e., "multi-clutching") in a given year. Fixed effect size of 'first nest lay date' is the standardized estimate on the logit scale.

multiclutching probability	Mean estimate	95% confidence interval
Fixed effects β (logit standardized)		
First nest lay date	−1.83	[-2.3, -1.52]
Age since first breeding	−0.04	[-0.26, 0.19]
First breeding age	0.11	[-0.12, 0.33]
Female tarsus length	−0.03	[-0.25, 0.19]
Partitioned R^2		
Total Marginal R^2	0.37	[0.28, 0.47]
First nest lay date	0.37	[0.28, 0.46]
Age since first breeding	0.00	[0, 0.17]
First breeding age	0.00	[0, 0.17]
Female tarsus length	0.00	[0, 0.17]
Total Conditional R^2	0.40	[0.3, 0.51]
Random effects σ^2		
Individual	0.35	[0, 0.86]
Year	0.40	[0, 0.69]
Adjusted repeatability r		
Individual	0.02	[0, 0.12]
Year	0.03	[0, 0.08]
Sample sizes n		
Years	14	
Individuals	426	
Observations (i.e., Nests)	665	

SUPPLEMENTARY FIGURES

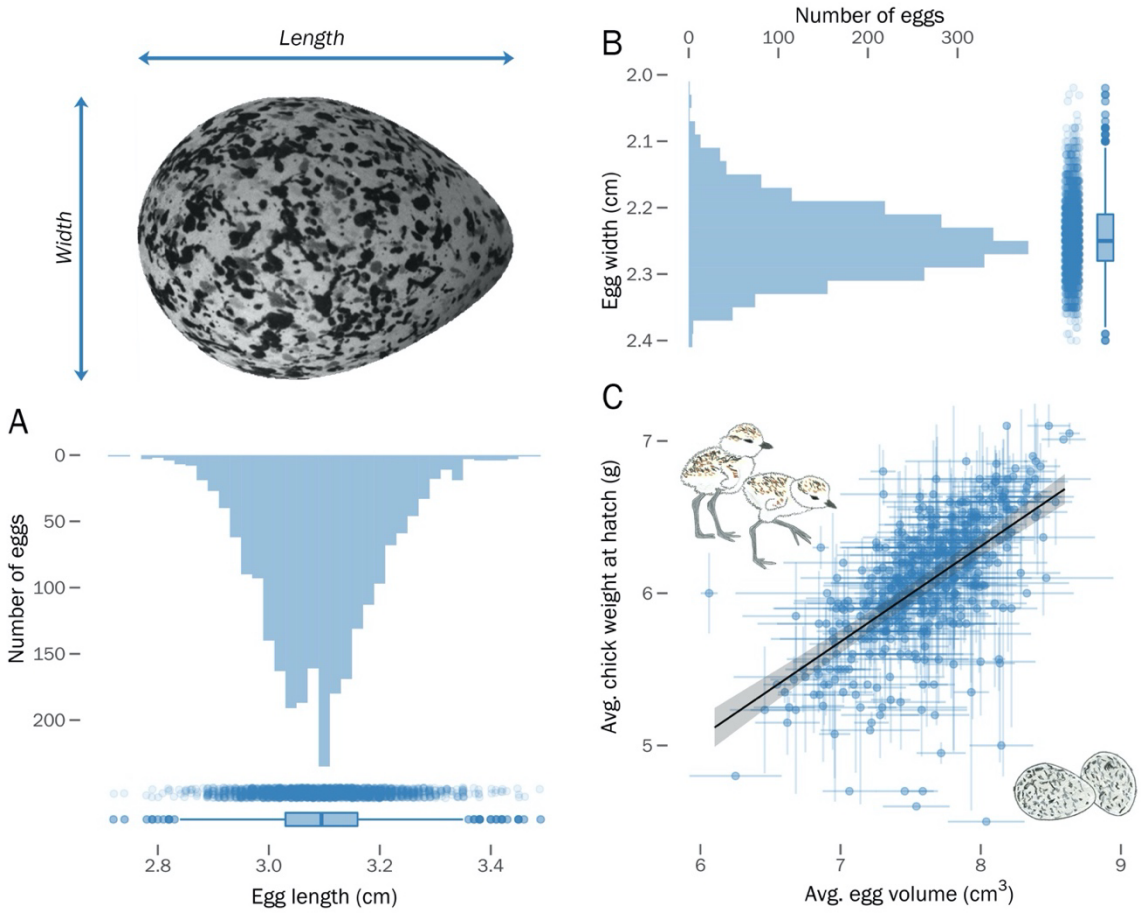


Figure S1. Egg size variation for snowy plovers breeding in Bahía de Ceuta, Mexico between 2006 and 2020. Egg volume was estimated using an allometric equation combining length (A) and width (B) measurements collected in the field (see *Methods*). C) Average egg volume of a clutch was highly correlated with the clutch's average chick weight at hatch (β [95% CIs]: 0.628 [0.552–0.704]; $R^2_{marginal} = 0.370$ [0.310–0.436]). Ribbon shows the 95% CI of the model prediction, vertical and horizontal error bars visualize within clutch variation in egg volume and chick hatch weight (1 SD); see Supplementary Text D for modelling methods.

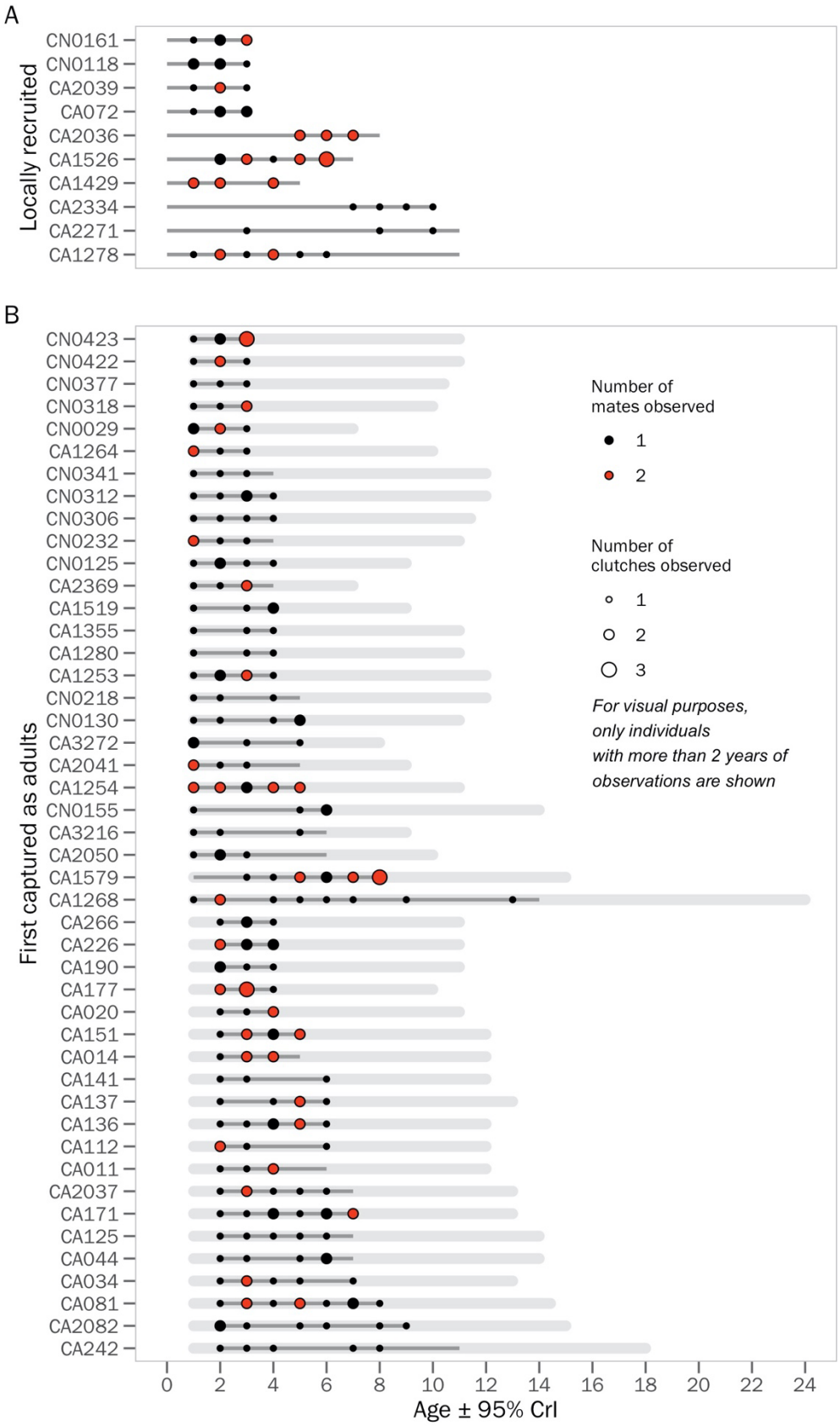


Figure S2. Mating strategy and clutch number of female snowy plovers according to age. Each row shows an individual female in the population for which we have at least three years of

observations (note that our analysis also includes females with one or two years of observation, but given space constraints only individuals with a minimum of three years are plotted in this graph). 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% CrI 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 based on BaSTA's birth year posterior). 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. Note also that the age at first encounter of all known-aged individuals is 0).

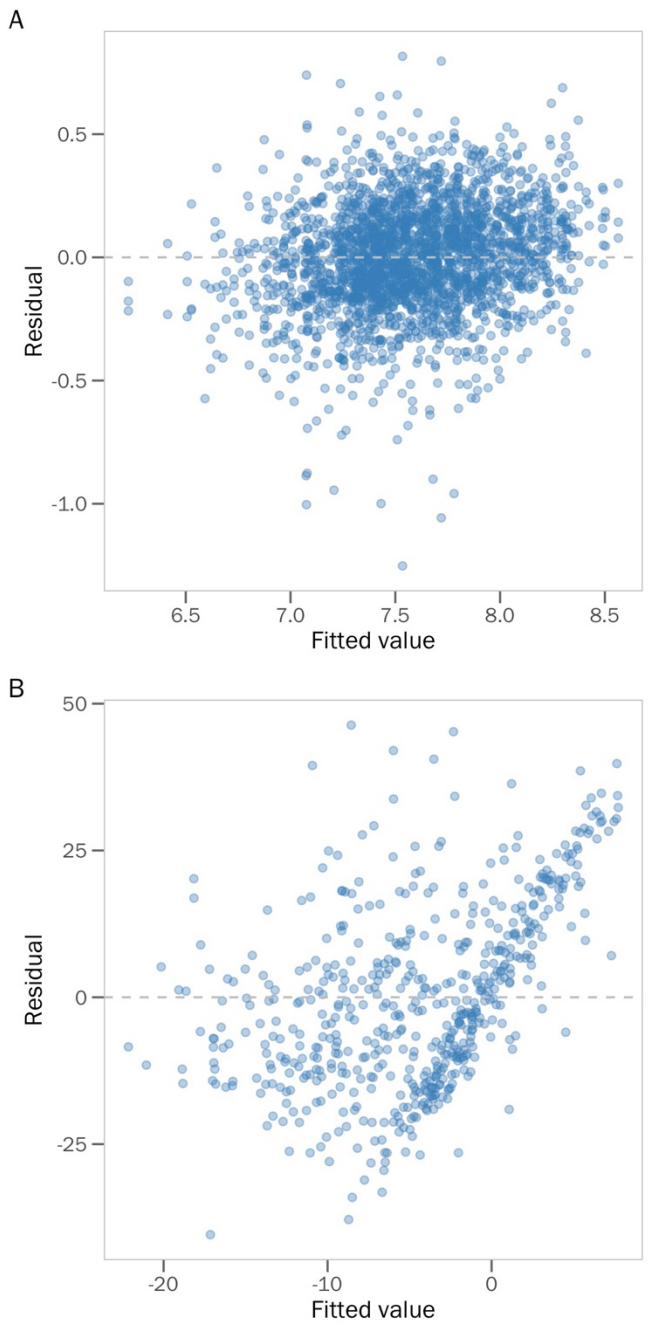
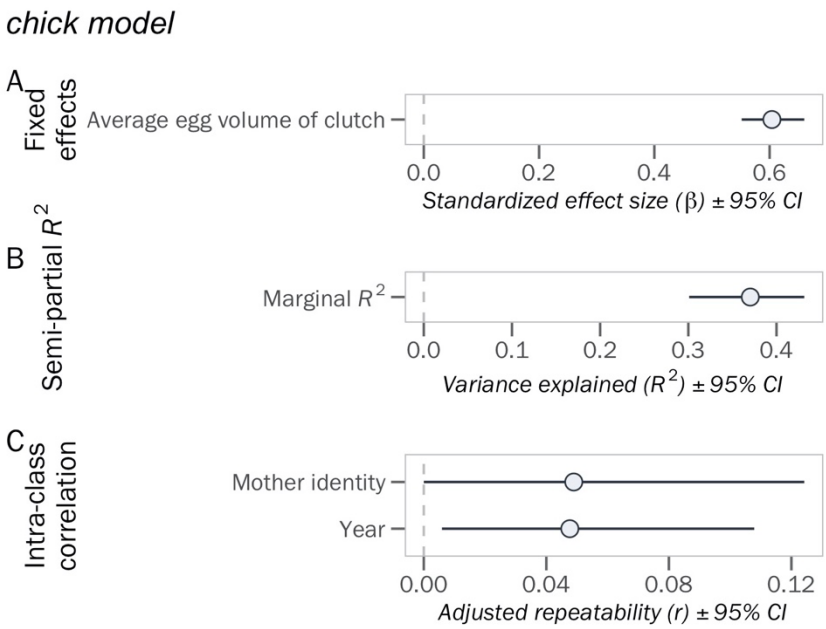
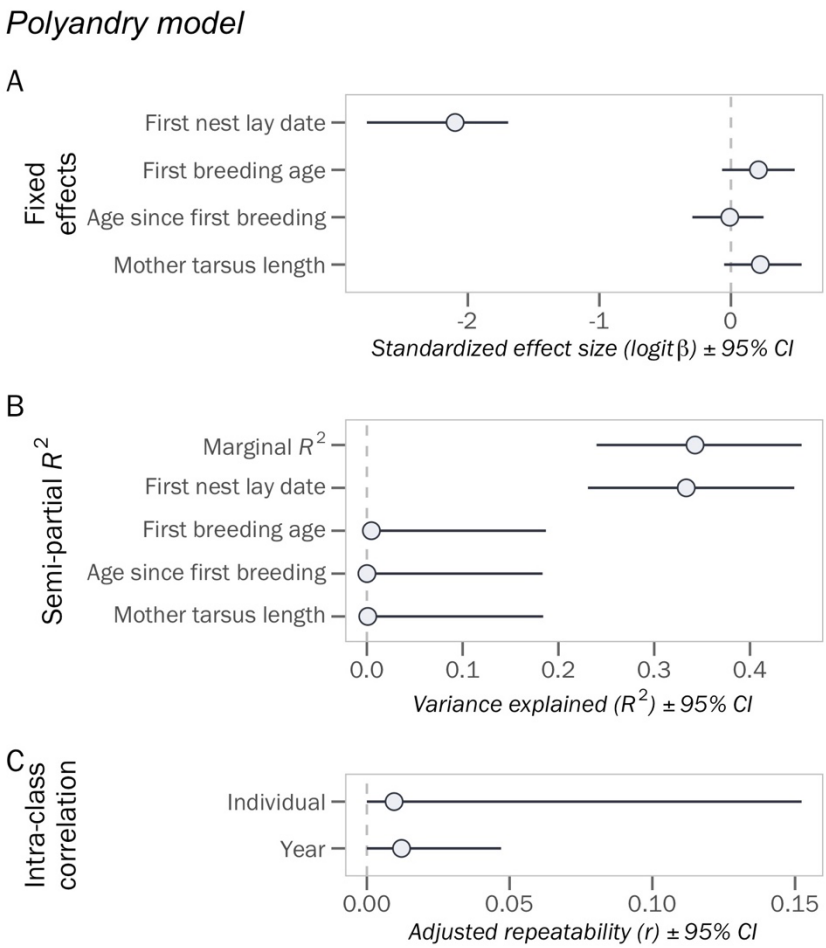


Figure S3. Homoscedastic spread of residuals from the A) 'egg volume' and B) 'lay date' models.



1023 **Figure S4.** Sources of variation in the average hatch weight of chicks.



1024 **Figure S5.** Sources of variation in a female's probability of being polyandrous each year.

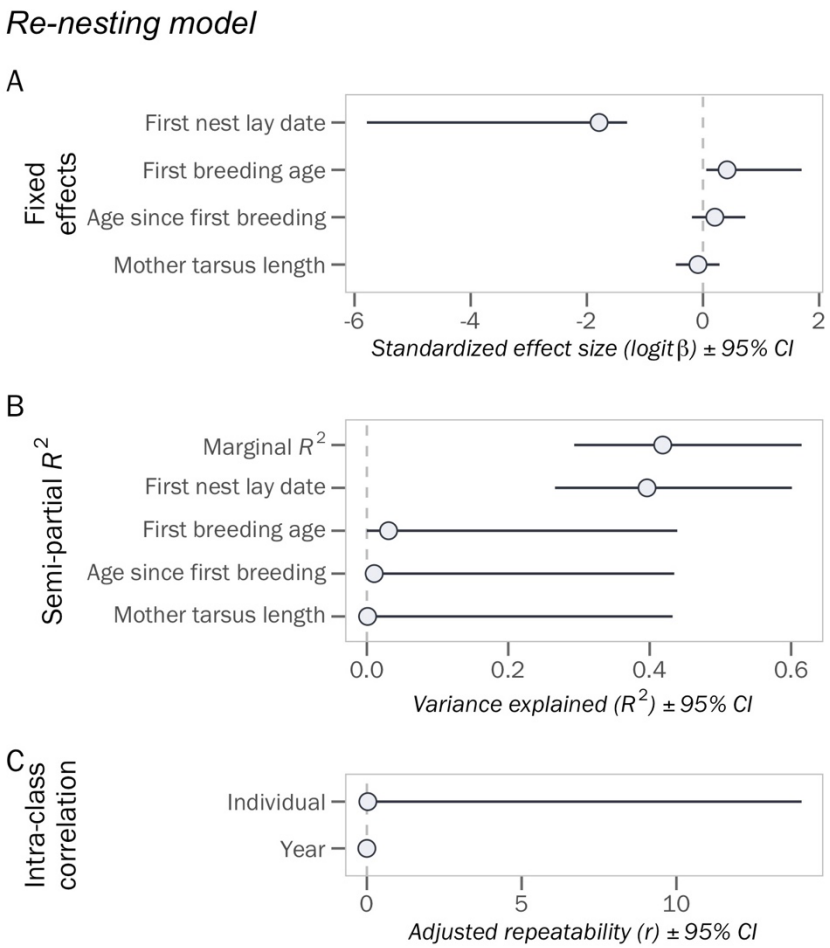


Figure S6. Sources of variation in a female's probability of re-nesting after a failed attempt each year.

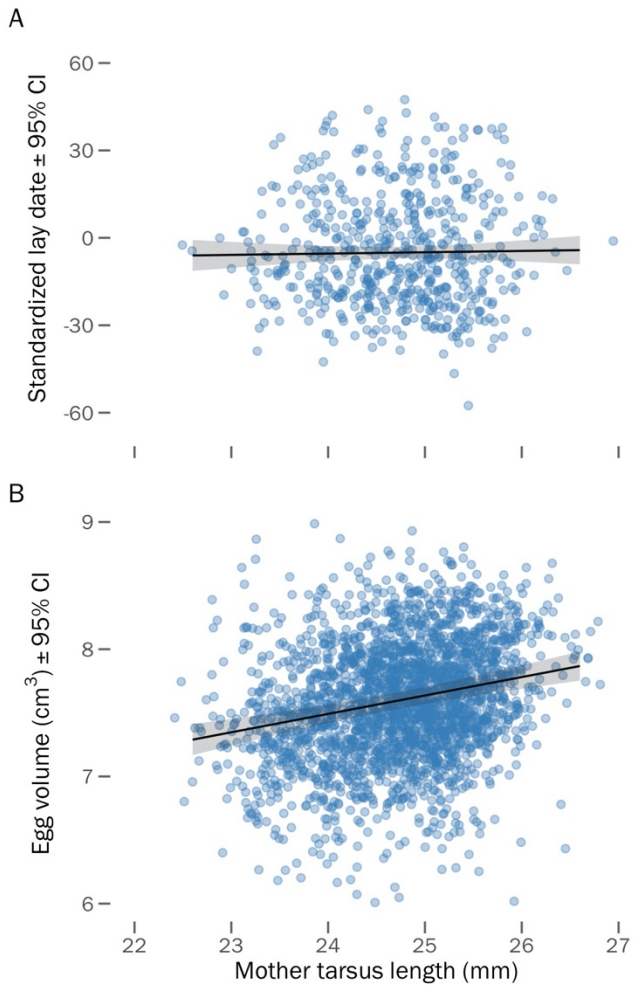


Figure S7. Relationship between a female's structural size (i.e., her tarsus length) and A) the lay date of her first nest of the season, and B) the volume of her eggs.

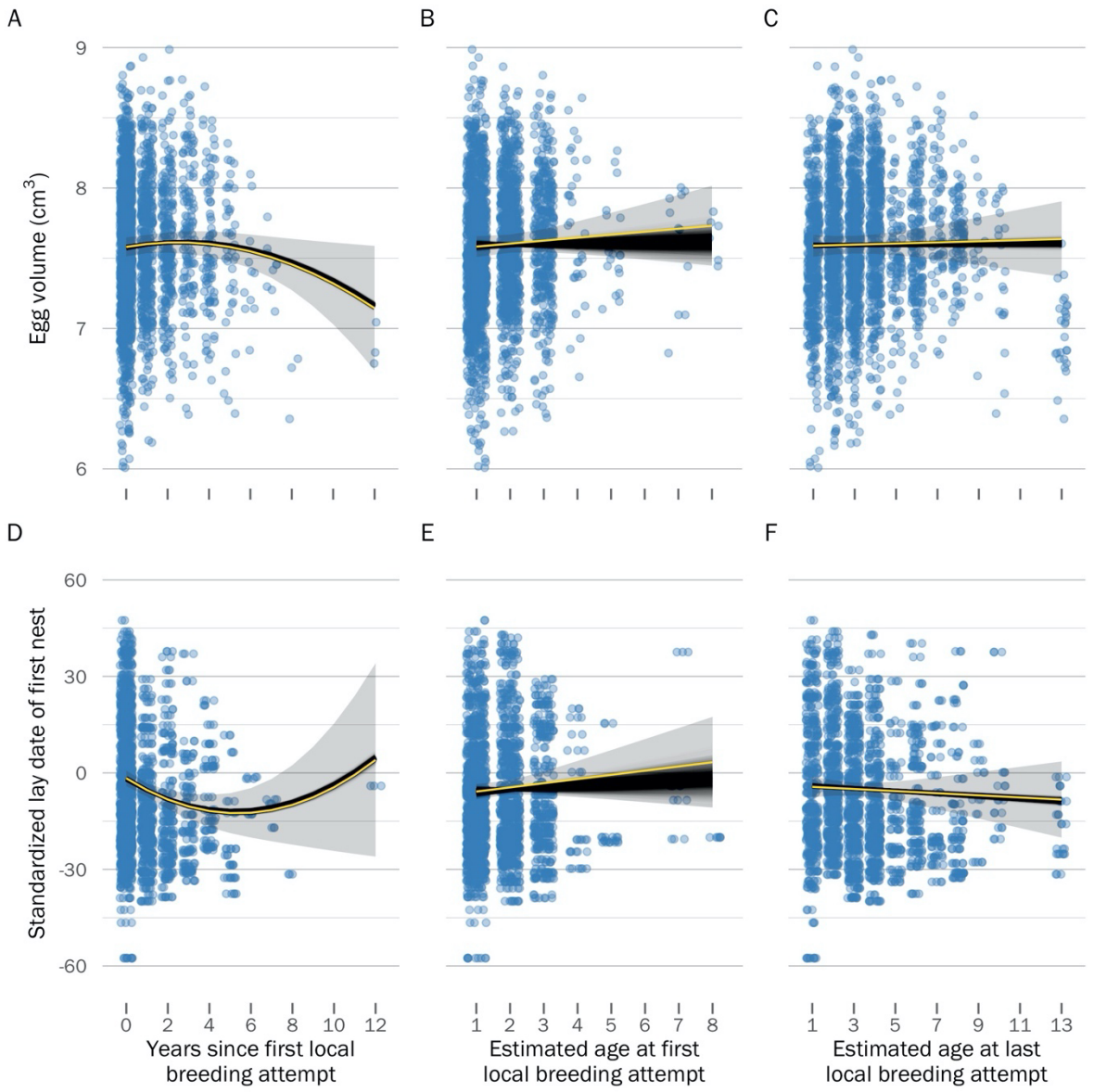
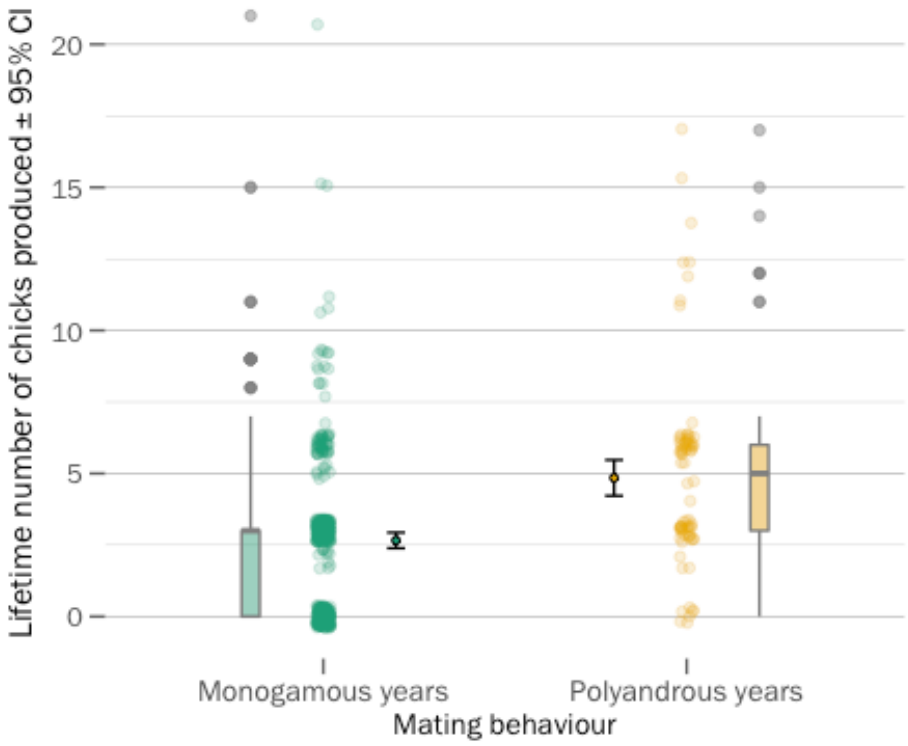


Figure S8. Visualization of the effect of uncertainty in the age estimate provided by BaSTA on age-dependent trends in egg volume (top row) and lay date (bottom row) dynamics. Black trends show the model predictions for the 1000 bootstraps of the BaSTA age estimate posteriors (see *Methods*). Panels A and D show the within-individual trends of the 'age-deviation' score – as expected, these measures are not impacted by uncertainty in the BaSTA age estimate because they are centred for each individual (i.e., the absolute age is irrelevant). Panels B and E show the between-individual trend of the 'age at first breeding' (i.e., selective appearance), and panels C and F show the between-individual trend of the 'age at last breeding' (i.e., selective disappearance). Yellow trends and grey ribbons visualize the 95% CI of the model predictions when using the median age estimate provided by BaSTA (i.e., the effect sizes of the 'egg volume' and 'lay date' models shown in Fig. 1).



1041 **Figure S9.** The lifetime number of chicks produced by females in years when they were
1042 polyandrous was 2.18 (1.83–2.53 95% CI) chicks more than in years when were monogamous
1043 (Fig. S9; N = 14 years, 426 females, 841 nests).

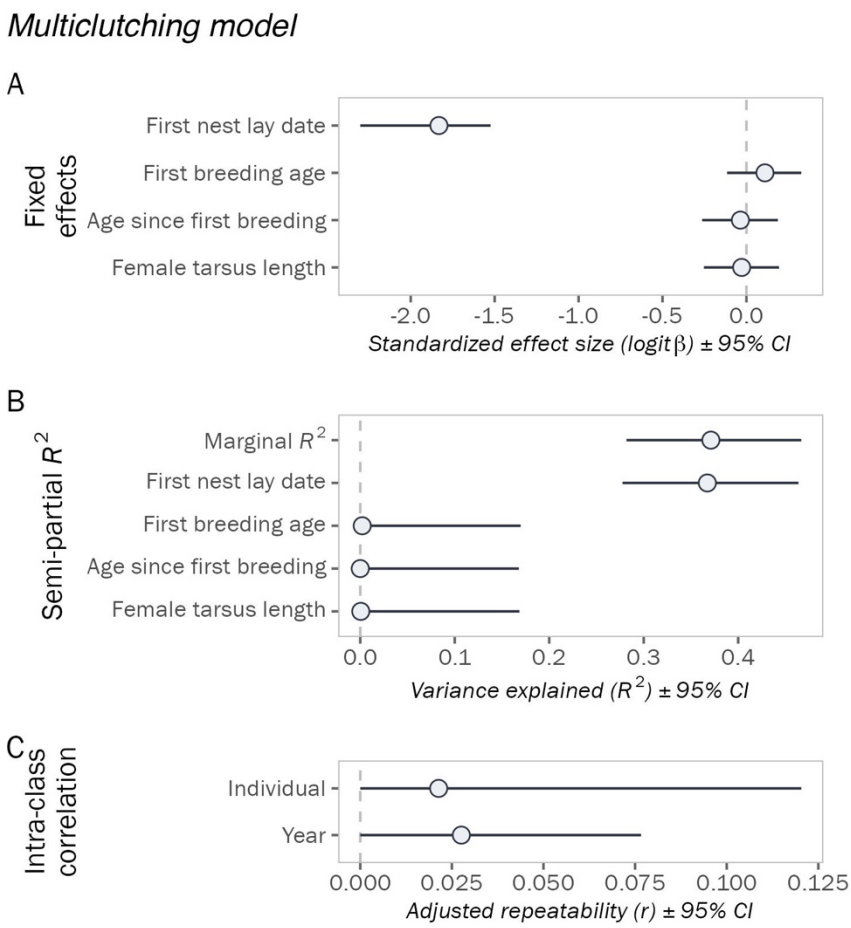


Figure S10. Sources of variation in a female's probability of re-nesting or being polyandrous (i.e., "multi-clutching") in a given year.

SUPPLEMENTARY TEXTS

Supplementary Text A

Age estimation of individuals with unknown origin—Investigating age-dependent processes in the wild is challenging, as analyses often involve a mix of individuals of known or unknown age (Colchero *et al.*, 2012) – with the former being 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. Furthermore, BaSTA derives estimates of birth year of left-truncated individuals from the population mean of the projected survival function. As snowy plovers show sex differences in survival (Eberhart-Phillips *et al.*, 2017; 2018), we used female-specific survival functions for this study. 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 their first breeding season, i.e., we constrained first-year survival probability to 1.

In total, our capture-mark-recapture data comprised records of 450 uniquely marked females, of which 45 hatched locally and subsequently recruited into the adult population as known-age individuals (Fig. S2a), and the remaining 405 females were adults of unknown age and origin. We monitored the presence or absence of marked individuals by recapturing or observing them in the field in all study years except for 2014, amounting to a total of 916 post-birth annual detections of the 450 females in our sample (median annual detections per adult = 2; mean = 2.04, 1.45 SD). We discarded annual detections if a bird was only encountered once via a resighting of a color combination, as single-observations are known to influence capture-mark-recapture analyses (Tucker et al. 2019). A logistic bathtub-shaped mortality model had the best fit to our data – revealing that female mortality rate increased until age 5 years, after which it became constant (Fig. S2b; see Appendix S1 for detailed methods). Using this model, we extracted the birth year estimate posteriors for each unknown-age individual in the capture-mark-recapture sample. Note that three individuals (one first encountered as an adult [CA1579] and two locally hatched recruits [CA2036 and CA1526]; Fig. S3) 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 capture-mark-recapture data for 2006–2020.

To explain how mortality risk is associated with age, we compared four commonly used survival functions: exponential, Gompertz, logistic, and Weibull models. The exponential function keeps survival constant across age (Cox & Oakes, 1984), whereas the other functions allow for age-dependent variation in survival: the Gompertz model is an exponential function in which age-specific mortality is scaled by baseline mortality (Gompertz, 1812; Pletcher, 1999) and the Weibull model is a power function which assumes that baseline and age-specific mortality rates are independent (Pinder *et al.*, 1978). In addition to the stand-alone versions of these functions, we considered two alternative forms of the Gompertz, logistic, and Weibull functions – "Makeham" and "bathtub" shapes. The Makeham shape constrains the survival function to converge to a constant, rather than zero, as age increases (Pletcher, 1999), whereas the bathtub shape enables concavity in the function, such that mortality could decrease at early ages, but increase later in life (Siler, 1979).

We used four parallel simulations to run the Markov chain Monte Carlo (MCMC) optimization procedure in BaSTA with 800,000 iterations, a 100,000 burn-in period, and a thinning interval of 2000 to minimize serial autocorrelation in the chain (see Fig. S2 for simulation diagnostics). We ranked the survival models according to their deviance information criterion (*DIC*) and determined that the logistic model with a bathtub shape fitted our data best (i.e., lowest *DIC*, (Spiegelhalter *et al.*, 2002); Table S1). This logistic model revealed that female mortality rate increased until age 5 years, after which it became constant (Fig. 1b). Using the top model, we extracted the point estimate and 95% credible interval birth year for each individual in the capture-mark-recapture sample.

Literature Cited:

Colchero, F., Jones, O.R. & Rebke, M. (2012) BaSTA: An R package for Bayesian estimation of age-specific survival from incomplete mark-recapture/recovery data with covariates. *Methods in Ecology and Evolution*, **3**, 466–470.

Cox, D.R. & Oakes, D. (1984) *Analysis of Survival Data*. Chapman and Hall, London.

Eberhart-Phillips, L.J., Küpper, C., Carmona-Isunza, M.C., Vincze, O., Zefania, S., Cruz-López, M., *et al.* (2018) Demographic causes of adult sex ratio variation and their consequences for parental cooperation. *Nature Communications*, **9**, 1–8.

Eberhart-Phillips, L.J., Küpper, C., Miller, T.E.X., Cruz-López, M., Maher, K.H., Remedios, dos, N., *et al.* (2017) Sex-specific early survival drives adult sex ratio bias in snowy plovers and impacts mating system and population growth. *Proceedings of the National Academy of Sciences of the United States of America*, **114**, e5474–e5481.

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Pinder, J.E., Wiener, J.G. & Smith, M.H. (1978) The Weibull distribution: a new method of summarizing survivorship data. *Ecology*, **59**, 175–179.

Pletcher, S. (1999) Model fitting and hypothesis testing for age-specific mortality data. *Journal of Evolutionary Biology*, **12**, 430–439.

Siler, W. (1979) A Competing-Risk Model for Animal Mortality. *Ecology*, **60**, 750–757.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Van Der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **64**, 583–639.

Tucker, A.M., McGowan, C.P., Robinson, R.A., Clark, J.A., Lyons, J.E., DeRose-Wilson, A., Du Feu, R., Austin, G.E., Atkinson, P.W. & Clark, N.A., Effects of individual misidentification on estimates of survival in long-term mark–resight studies, *The Condor*, **1211**, duy017

Table S-A1. Hierarchical capture-mark-recapture models used to describe mortality patterns of snowy plovers at Bahía de Ceuta, Mexico, between 2006 and 2020. *k:* number of modelled parameters; Δ*DIC:* difference in deviance information criterion (*DIC*) between a given model and the top model. *DIC* value of top model was 5279.1.

Mortality function	Shape	*k*	Δ*DIC*
Logistic	Bathtub	7	0.00
Logistic	Simple	4	90.91
Logistic	Makeham	5	97.01
Weibull	Bathtub	6	139.36
Weibull	Simple	3	211.98
Weibull	Makeham	4	226.01
Gompertz	Bathtub	6	328.12
Gompertz	Simple	3	401.06
Gompertz	Make	4	445.12
Exponential	Simple	2	679.94

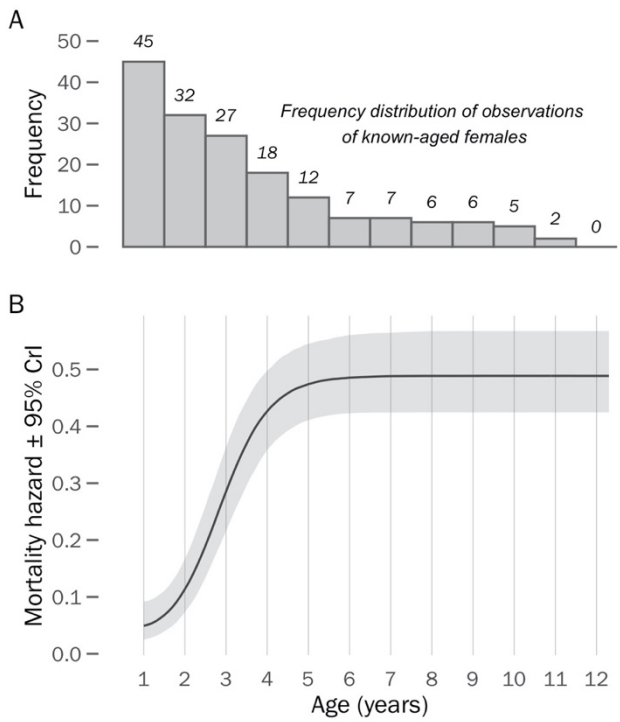

Figure S-A1. Logistic-bathtub mortality function for snowy plover females: a) frequency distribution of age-specific observations of 45 known-aged females and b) age-dependent mortality hazard.

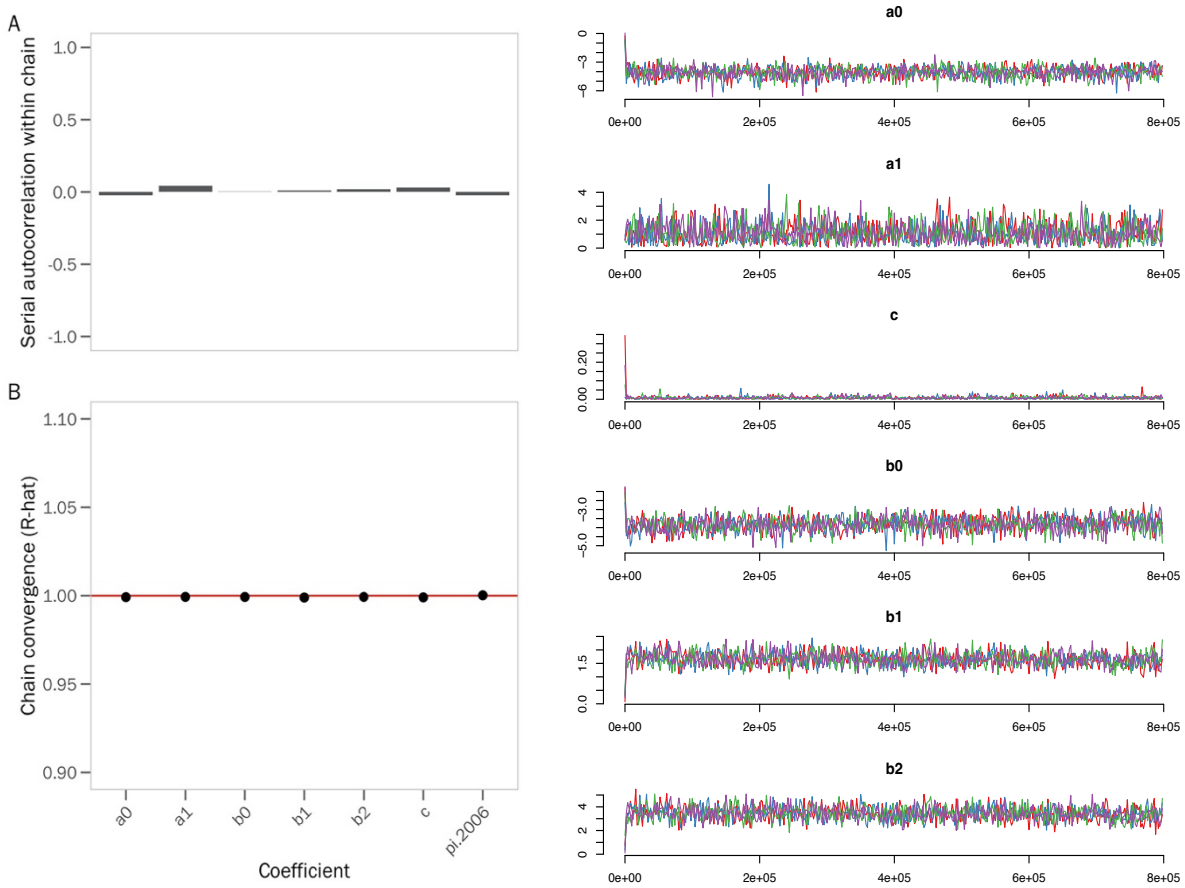

Figure S-A2. Bayesian model diagnostics of the Logistic bathtub shaped survival model. a) Serial autocorrelation of iterations within chains, b) chain convergence (*R-hat*) of model, and c) trace plots of chain dynamics.

Supplementary Text B

Considering the effect of individual heterogeneity in post-marking processes on mark-recapture models of survival

Time-since-marking models control for losses to mortality or permanent emigration that occur during the interval after the first capture occasion (Pradel *et al.* 1997). To code a time-since-marking variable into the design matrix of the mark-recapture model, a time-varying covariate needs to be added that distinguishes the first occasion from all subsequent occasions. Unfortunately, time-varying covariates are unable to be implemented in the latest version of BaSTA, so we evaluated a time-since-marking Cormack–Jolly–Seber (CJS) model with the R package "RMark" (Laake 2013) and demographic parameters were estimated via maximum likelihood implemented in program MARK (White & Burnham 1999). We limited this analysis to unknown-aged individuals (i.e., only included individuals that were first captured as adults) because the first-year survival probability for individuals first marked as juveniles is 100% in our dataset because our dataset is limited to adults that have breeding information.

First, we evaluated the best model capturing variation in recapture probability while keeping apparent survival constant. In addition to the time-since-marking model, we tested an intercept only model, and a factorial time (i.e., year) model. This revealed that the factorial time model was far superior to the other models tested based on AICc statistics (Table S-B1). Furthermore, a comparison between the time-since-marking model and the intercept-only model shows that the DeltaAICc scores differ by <2 units – providing additional support that the time-since-marking model does not improve model fit. We interpret this as encouraging evidence that our inference about recapture probability is not hindered by individual heterogeneity in post-marking processes.

Second, we evaluated the if there was evidence of transience in our mark-recapture dataset that could bias our ability to appropriately estimate survival probability. In RMark we tested a time-since-marking survival model that incorporated annual variation in encounter probability structure shown above (i.e., Phi(~tsm)p(~time), Table S-B1). The results of this analysis revealed no difference in the survival probability of unknown-aged adults transitioning from their first or between subsequent capture occasions (Figure S-B1). Importantly, the estimated survival probability of the first occasion is actually larger than that of subsequent occasions (confidence intervals aside), indicating that there is little evidence that transient adults are biasing our mark-recapture analyses.

Table S-B1. AIC comparisons for three CJS models evaluating sources of variation in encounter probability. A time-since-marking model did not improve model fit over an intercept-only model, suggesting that our inference about recapture probability based on the BaSTA analyses (i.e., Supplementary Text A) are not hindered by individual heterogeneity in post-marking processes**.**

model	MARK model	npar	DeltaAICc	weight
Year	Phi(~1)p(~time)	15	0.00	1.00
constant	Phi(~1)p(~1)	2	35.39	0.00
time-since-marking	Phi(~1)p(~tsm)	3	36.86	0.00

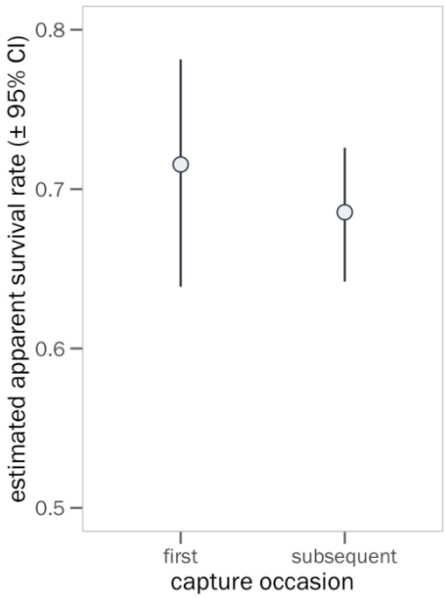

Figure S-B1. Results of a time-since-marking survival model that incorporated annual variation in encounter probability revealed no evidence that transient adults are biasing our mark-recapture-based inference.

Literature cited:

JL Laake *RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01* (NOAA, Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, 2013).

Pradel, R., Hines, J.E., Lebreton, J.D. and Nichols, J.D., 1997. Capture-recapture survival models taking account of transients. *Biometrics*, pp.60-72.

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Supplementary Text C

Considering the effect of body size on female survival

To evaluate if individual quality predicts survival, we included tarsus length as a covariate in the RMark mark-recapture model (as described in Supplementary Text B above, individual covariates are not able to be incorporated into the latest version of BaSTA). Our analysis showed that there was no effect of tarsus length on survival probability (Figure S-C1). An intercept-only model had > 2 DeltaAICc units than the tarsus model (Table S-C1) and the graphical relationship between tarsus and survival unconvincing (Figure S-C1).

Table S-C1. AIC comparisons of two CJS models evaluating the effect of female tarsus length on apparent survival, while acknowledging annual variation in encounter probability.

MARK model	npar	DeltaAICc	weight
Phi(~1)p(~time)	15	0.00	0.74
Phi(~tarsi)p(~time)	16	2.06	0.26

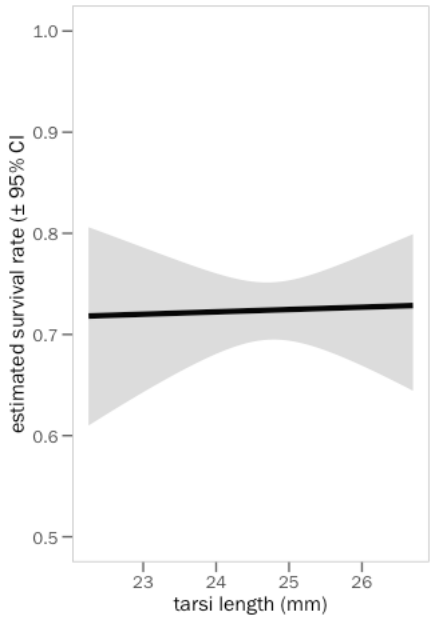

Figure S-C1. Model predictions for a relationship between apparent survival and female tarsus length reveal no relationship, while controlling for imperfect detection and annual variation in encounter probability.

Supplementary Text D

In theory, the selective benefits of larger eggs is that the subsequent hatchlings will be larger and have higher survival owing to more intrinsic reserves provided by the mother (Blomqvist *et al.*, 1997). To link egg size variation to potential fitness consequences of subsequent offspring we evaluated the predicted positive relationship between egg volume and chick weight using the egg dataset described above but reduced observations to the nest level and filtered to only include nests that had chicks measured within one day of hatching, resulting in 456 nests from 276 females. As it was unclear which chick came from which egg, each datum represented the nest-level average of chick weights and egg volumes. We included random intercepts for mother identity and year, and assumed a Gaussian error distribution of egg volume.

Literature Cited:

Blomqvist, D., Johansson, O.C. & Götmark, F. (1997) Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia*, **110**, 18–24.

SUPPLEMENTARY FILES

Supplementary File 1. Commented RMarkdown vignette detailing the analytical steps needed to reproduce all our models and results. Click here to view on your internet browser: https://raw.githack.com/leberhartphillips/snowy_plover_eggs/main/Rmd/Supplementary_File_1/Supplementary_File_1.html