Received: 10 December 2023 | Accepted: 4 November 2024

DOI: 10.1111/1365-2656.14226

Journal of Animal Ecology

RE S EA RC H ARTI CLE

I ntra specific Va riation in Evolutio n and Ecology

Reproductive success and offspring survival decline for female elephant seals past prime age

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Funding information
Office of Naval Research; Arnold and Mabel Beckman Foundation; David and Lucile Packard Foundation; Division of Integrative Organismal Systems, Grant/
Award Number: 2052497; National Science Foundation; Sloan Foundation Census of Marine Life

Handling Editor: Marléne Gamelon

Abstract

1. Maternal age can influence reproductive success and offspring fitness, but the timing, magnitude and direction of those impacts are not well understood. Evolutionary theory predicts that selection on fertility senescence is stronger than maternal effect senescence, and therefore, the rate of maternal effect senescence will be faster than fertility senescence.
2. We used a 36- year study of northern elephant seals (Mirounga angustirostris) to investigate reproductive senescence. Our dataset included 103,746 sightings of 1203 known- age female northern elephant seals.
3. We hypothesized that fertility (maternal reproductive success), offspring survival and recruitment into the breeding population, and male offspring production would decline with advanced maternal age. Furthermore, we hypothesized that older females would shorten their moulting haul out to allow for more time spent foraging.
4. We found evidence for both fertility and maternal effect senescence, but no evidence for senescence impacting offspring recruitment or sex ratio. Breeding probability declined from 96.4% (95% CI: 94.8%–97.5%) at 11 years old to 89.7% (81.9%–94.3%) at 19 years old, and the probability of offspring survival declined from 30.3% (23.6%—38.0%) at 11 years old to 9.1% (3.2%—22.9%) at 19 years old.
5. The rates of decline for fertility and maternal effect senescence were not different from each other. However, maternal effect senescence had a substantially greater impact on the number of offspring surviving to age 1 compared to fertility senescence. Compared to a hypothetical non- senescent population, maternal effect senescence resulted in 5.3% fewer surviving pups, whereas fertility senescence resulted in only 0.3% fewer pups produced per year. These results are

1 | INTRODUCTION increase in offspring mortality with increasing maternal age (Moorad & Nussey, 2015). Offspring sex ratios may also change with maternal Reproductive senescence, or a decrease in reproductive output age. The Trivers—Willard hypothesis predicts that mothers with suwith advanced age, is widespread among animals, including 68% of perior body condition will give birth to more males, if male offspring mammals (Lemattre et al., 2020). However, the timing and magnitude require greater parental investment and have greater potential for of senescence across reproductive traits are highly variable, com- reproductive output (Trivers & Willard, 1973). If body condition deplicating our understanding of the evolution and ecology of ageing clines with age, females may give birth to fewer male offspring.

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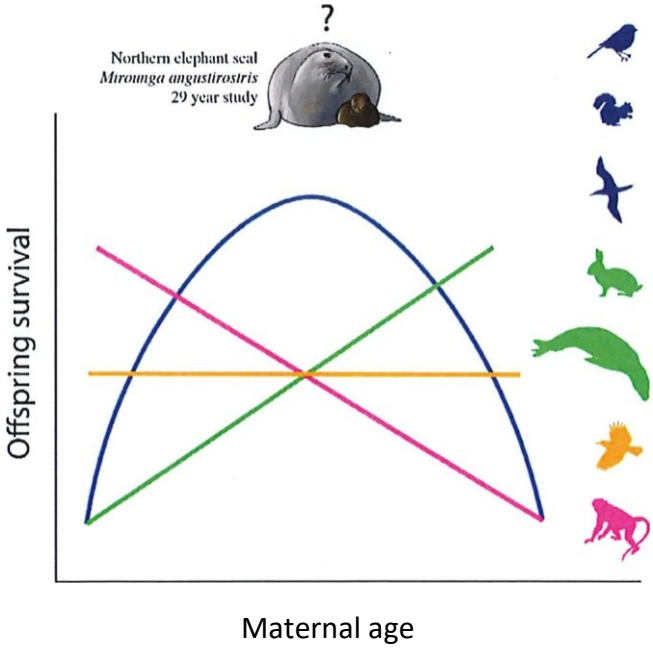
J Anim Ecol. 2025;94:423–435. wileyonlinelibrary.com/journal/jane | 423

consistent with evolutionary theory predicting weaker selection on maternal effect than fertility senescence. Maternal effect senescence may therefore be more influential on population dynamics than fertility senescence in some systems.

KEYWORDS
ageing, life history, marine mammal, maternal effect, phenology, senescence, sex ratio

in wild animals (Lemattre & Gaillard, 2017). In addition to impacting Empirical data demonstrate variable effects of age on reproducfertility, maternal age was shown to affect offspring phenotypes in tive traits (Figure 1). The most common effect appears to be an ini93% of populations across a range of taxa, with a tendency towards tial increase in performance as animals grow and gain experience, negative impacts with advanced age (Ivimey- Cook & Moorad, 2020). followed by a 'prime age' plateau and eventual decline during seThese negative effects, known as maternal effect senescence, nescence (Emlen, 1970). For example, in red squirrels (Tamiasciurus manifest as decreased offspring quality (e.g. body condition, sur- hudsonicus), great tits (Parus major) and blue- footed boobies (Sula Vival or recruitment) with increasing maternal age (Ivimey-Cook & nebouxii), offspring survival and recruitment (defined by the first Moorad, 2020). Although fertility senescence and maternal effect reproductive event) followed the typical ageing pattern: an initial senescence are similar, age- specific selection acts independently increase at young maternal ages, followed by a plateau at prime age on each process, resulting in differing rates of decline (Moorad & and then a decrease at older ages (Bouwhuis et al., 2010; Descamps Nussey, 2015). Evolutionary theory predicts that due to indirect et al., 2008; Torres et al., 2011). However, contrasting patterns have genetic effects, age- dependent selection for maternal effects will also been observed. Instead of a concave relationship, offspring decline faster than for fertility, resulting in a steeper rate of decline survival increased with maternal age in an experimental population for maternal effect senescence than fertility senescence (Moorad & of European rabbits (Oryctolagus cuniculus; Rödel et al., 2009), deNussey, 2015). This occurs because a log- linear increase in mortal- creased in rhesus macaques (Macaca mulatta; Hoffman et al., 2010) ity with increasing maternal age will result in a faster than log- linear and did not change in red- billed choughs (Pyrrhocorax pyrrhocorax;



Great tit
Partts major
49 year study

Red squirrel
Tamiasciurus hudsonicus
16 year study

Blue-footed booby
Sula neb01t.vii
21 year study

European rabbit
Oryctolagus cunicttlus
12 year study

Weddell seal
Lepton.vchotes "'eddellii 17 year study

FIGURE 1 The dominant patterns of maternal effect senescence as measured by offspring survival past the end of maternal care. The most common is a concave-down relationship (in blue) characterized by increasing offspring survival until a peak at prime age, then decreasing survival with advanced maternal age, but there may also be positive relationships, negative relationships or no relationship.

Reid et al., 2010). Other species exhibited even more complicated seals (Leptonychotes weddellii) exhibited opposing effects of maternal age on offspring survival (positive effect) and senescence patterns. Wandering albatrosses (Diomedea exulans) exhibit recruitment (negative effect; Hadley et al., 2007). Quantifying patterns paternal, but not maternal, effect senescence (Fay et al., 2016) and Weddellof

reproductive and maternal effect senescence in additional wild populations is therefore critical for testing and refining evolutionary theories of ageing.

In this study, we used nearly four decades of data on northern elephant seals to assess fertility senescence and maternal effect senescence, including offspring survival after maternal allocation and

offspring recruitment. A six- decade mark- recapture programme at Aio Nuevo Reserve, California, has provided high- resolution demographic data across generations by tracking individuals from birth across their up to 20- year lifespans (Le Boeuf et al., 2019). Elephant seals are capital breeders (Jönsson, 1997; Stephens et al., 2009), spending most of their time on foraging trips at sea to accumulate sufficient fat stores for reproduction (Le Boeuf et al., 2000). Female elephant seals come to land for two key lifehistory events: the —1- month breeding haul- out in winter to give birth, nurse pups and breed (Condit et al., 2022), and the —1- month moulting haul out in spring to undergo a catastrophic moult (Beltran et al., 2024). In between the haul out periods, elephant seals undertake two foraging migrations, with the post- breeding and post- moulting migrations lasting approximately 75 and 220 days, respectively (Robinson et al., 2012). Females allocate substantial resources to producing a single pup each year, and reproductive success is tightly linked to mass gain during the postmoult foraging trip (Beltran et al., 2023). Maternal care is limited to a 26.8day (95% Cl: 23.5—30.1) nursing period (Costa et al., 1986; Reiter et al., 1981).

Although fertility and maternal effect senescence have not been investigated previously in elephant seals, other age- dependent processes have been studied. Adult female survival begins to decrease (i.e. actuarial senescence) around 16 years old (Condit et al., 2014). Offspring quality, in terms of both survival and size, increases with maternal age until roughly 9 years old (Le Boeuf et al., 2019). However, the effects of advanced maternal age on offspring survival have not been investigated. Finally, previous research testing the Trivers—Willard hypothesis in northern elephant seals did not find any shift in

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to examine how maternal age impacts fertility and ma

sex ratio with age, but focused on development until prime age, rather than a decline after prime age (Le

Boeuf et al., 1989).

1988), so we hypothesized that the additional time for foraging would come at the expense of the moulting haul out.

2 | METHODS

2.1 | Field methods

The Aöo Nuevo, California population of northern elephant seals has been marked and observed for several decades (Le Boeuf et al., 2019). Seals are tagged with alphanumeric flipper tags at the time of weaning (approximately 1 month old), allowing for a demographic database of known- age individuals. We made daily attempts to observe tagged individuals during the breeding and moulting seasons, approximately January through June of each year from 1987 to 2023. Daily observations allow for a relatively precise estimate of the timing of life-history events, including the day of arrival and departure for breeding and moulting seasons (Beltran et al., 2024). Seals are typically present for the breeding season regardless of breeding status (Le Boeuf & Reiter, 1988). Because elephant seals must give birth on land, unobserved seals must either give birth at another colony, give birth at Aäo Nuevo without being seen, or skip breeding that year. Dispersal to other colonies can occur, but it is rare (<1%) for adult females after they have recruited (Condit et al., 2023; Zeno et al., 2008). For animals breeding at Afio Nuevo, daily observation effort makes breeding a highly detectable behaviour. It is therefore likely that unobserved seals are non- breeders. We further discuss the implications of this for our estimates of senescence in the 'Observation Frequency' sections of the methods and results.

When observing a tagged breeding female, we collected information about her pup status (present or absent) and pup sex (male or female). Pup sex was determined in the field by visual inspection based on the presence or absence of a penile opening (Reiter et al., 1978). When possible, we used hair- bleach to mark pup

to find pups and attach permanent unique flipper tags to measure future

fur with a temporary unique identifier to link pups to their mothers in our database. After weaning, this identifier allowed us

maternal effect senescence in elephant seals. We analysed maternal age and breeding probability, offspring survival and reproduction, offspring sex and phenology. We hypothesized that northern elephant seals would have decreased breeding probability beyond prime age (HI, fertility senescence) and that offspring born to mothers past prime age would have decreased first- year survival and recruitment into the breeding population (H2, maternal effect senescence). We predicted that older mothers would give birth to more male offspring until prime age, after which mothers should produce fewer male offspring (H3, sex ratio). Finally, we hypothesized that older mothers would shorten the duration of the moulting haul out to maximize the amount of time spent on the post- breeding foraging trip (H4, phenology). If older seals need more time to accumulate the energy requirements for both maintenance and reproduction, then a greater portion of the annual cycle would need to be devoted to regaining those fat stores. The breeding haul out is highly synchronous (Le Boeuf & Reiter, survival and reproduction. This analysis includes adult female seals observed on four or more days during the breeding season (December 1—March 15). The threshold number of days was chosen to minimize errors in tag identification and the presence or absence of offspring. Seals were considered breeders in a given year if they were observed with a pup at least once that year; otherwise, they were considered

non- breeders. We were then able to quantify life- history timing, reproductive success, offspring first- year survival and recruitment and offspring sex ratios for 1203 knownage female northern elephant seals, with 103,746 sightings (4404 seal- year combinations; Figure 2). All research procedures were conducted under the National Marine Fisheries Service (NMFS) marine mammal permit numbers 786-1463, 87-143, 14636, 19108 and 23188 and authorized by the University of California, Santa Cruz Institutional Animal Care and Use Committee, the California State Park system and the University of California Natural Reserve System.

2.2 I Statistical analyses

We estimated the effect of age on three reproductive parameters and two phenological parameters using generalized linear mixed effects models (GLMMs). We fit models with the Ime4 R package, version 1.1—32 (Bates et al., 2015). Data and code are available on Dryad (https://doi. org/10. 5061/ dryad. pg4f4 qrxl).

We used threshold piecewise (segmented) regression models to quantify the effects of senescence, where the coefficients for age are allowed to vary before and after a threshold age that represents the onset of senescence. The onset of actuarial senescence in northern elephant seals (i.e. a decline in annual survival) occurs after age 16 (Condit et al., 2014). However, weaning success appears to peak earlier, around age 12 (fig. 4 in Le Boeuf et al., 2019), suggesting that fertility senescence may precede actuarial senescence. We include in our models a binary Senescent variable encoding whether seals were post- senescent (i.e. seals 11 years old and older) or not (i.e. seals younger than 11 years old), allowing the coefficient for age to change post- senescence. We transformed age by subtracting the threshold, 11 years (e.g. treated a 7- year- old seal as age This formulation treats the intercept as the expected value at the threshold and ensures no discontinuity with respect to age (Berman et al., 2009; Tompkins & Anderson, 2019). We present results using a threshold onset of senescence of 11 years old for all hypotheses because this threshold was the best fit for the hypothesis for which we had the most data (HI, fertility senescence). Comparisons of model sensitivity to threshold age for all hypotheses can be found in the supplemental material (Figure Sl, Table S4). We used Akaike information criterion (AIC; Akaike, 1973) to confirm that a threshold model outperformed a linear or quadratic model (Tables S2 and S3). All adult seals included in these analyses were at least 4 years old (when the majority of elephant seals begin to breed, Reiter & Le Boeuf, 1991). We do not include 3 year olds (of which —36% breed, Reiter & Le Boeuf, 1991) because our intention was to study intermittent breeding rather than the first reproductive event.

2.2.1 | Fertility senescence

To test for fertility senescence (Table Sl), we fit a GLMM to breeding status (binomial distribution, logit link) as a function of age interacting with the senescent binary variable, with year and individual as random effects (n = 4404 seal- year observations of 1203 individuals). We only included seal- years where the seal was observed during the breeding season.

2.2.2 | Maternal effect senescence

We tested for maternal effect senescence using two measures of offspring success: survival and recruitment. While juveniles do not always return to the colony in the year after birth, we calculated that 95% of juveniles that survive to age 1 are seen within 7 years of their birth. Offspring first- year survival for both male and female pups was therefore determined by whether the seal was observed again within 7 years of birth. Offspring recruitment was determined by whether female offspring successfully produced their own offspring; male reproductive success is not tracked in this population. Although offspring survival and recruitment are correlated because recruitment is contingent upon survival, we included both because offspring survival includes a larger sample size but offspring recruitment is a more biologically relevant measure of offspring success.

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We fit GLMMs to offspring survival and recruitment (binomial distribution, logit link) as a function of maternal age interacting with the 'senescent' binary variable (Table Sl). The offspring survival model included both year and individual as random effects. The offspring recruitment model included only year as a random effect because the random effect variance for individual was estimated to be O (and the results were identical with or without it). This is likely due to the smaller sample size compared to offspring survival because male offspring were excluded from the recruitment analysis. Because 95% of pups that survived were observed within 7 years, we included offspring born before 2016, 7years prior to the end of the study period. This yielded sample sizes of 618 male and female individuals for the survival model and 421 female individuals for the recruitment model. Our observations may underestimate offspring survival because they do not include juveniles that permanently emigrated to other breeding colonies or temporarily emigrated and died. However, it is unlikely that offspring emigration varies with maternal age, and therefore our inferences about senescence should not be influenced by juvenile emigration.

2.2.3 | Offspring sex ratio

We tested whether offspring sex ratios were affected by senescence (n = 1786 offspring from 796 mothers). We fit a GLMM to offspring sex ratio (binomial distribution, logit link) as a function of maternal age interacting with the senescent binary variable, with year and individual as random effects (Table Sl).

2.2.4 | Annual cycle phenology

We tested whether annual cycles, specifically the duration of the breeding and moulting haul out phases, were affected by senescence for all seals (including both breeders and non- breeders; Table Sl). We used data from 2011 and later (n = 387 individuals and 1122 individual- years), when additional sampling effort was made to determine life history phenology reproduction and offspring survival remained constant after age 11. The observed pup production (in the age- structured population) can be described by Equation 1.

$$F_1 = \frac{\sum_{a=4}^{20}}{20} \quad \text{bana} \quad \text{ia=ana} \qquad (1)$$

where Fl is fertility in the age- structured population described by pup production per mother per year, a is age, b is estimated breeding percentage and n is the number of mothers in that age class. In the hypothetical non- senescing population (h), pup production does not decrease after age 11 (Equation 2).

$$F_2 = \frac{\text{ill bana +>20 blin} \quad a=4 \quad a=12 \quad a}{20} \qquad (2)$$

Ya=ana

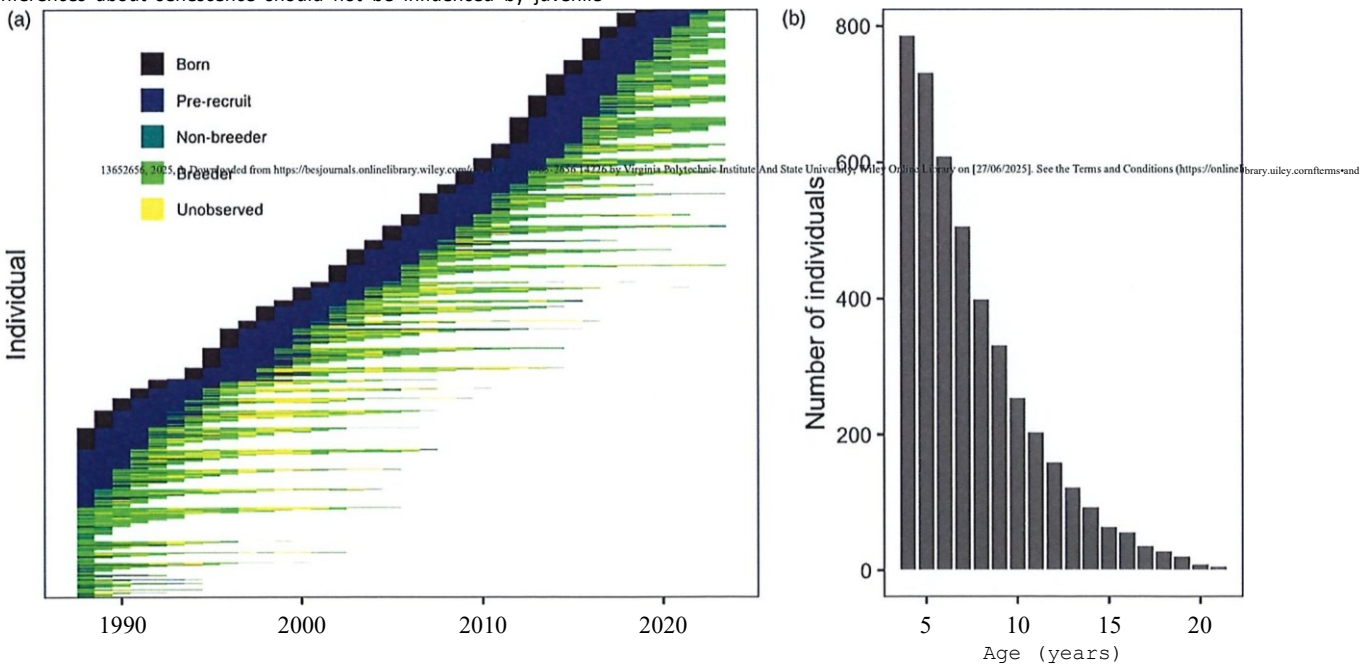


FIGURE 2 (a) Several hundred elephant seals from each cohort are tagged during their birth year (purple) and observations take place for the rest of their lives so that breeding status (greens and blues) and observation status (yellow) can be assigned and compared to age.
Raw longitudinal data for 1203 known- age female elephant seals and their observations from birth, to recruitment, to presumed death. (b) Histogram of the number of seals in each age class in the dataset across all cohorts.

Similarly, to account for the influence of maternal effects in the observed (Ml) and hypothetical (M2) populations, we add a term s to estimate the observed (Equation 3) and hypothetical (Equation 4) quantity of pups that survive to age 1.

throughout the

entire annual cycle. We only included animals that were

ia20=4banaSa

$$M_1 = \frac{}{\sum_{n=4}^{20} n_a} \quad (3)$$

seen during the moult haul out for at least 7 days, the minimum amount of time needed to undergo the visible moult (Beltran et al., 2024). We fit a GLMM to the duration of a haul out in days (gamma distribution, log link) as a function of age interacting with the senescent binary variable and the type of haul out (breeding vs moulting), using year and individual as random effects. We only included animals that had observations for each of the four parameters necessary to determine haul out durations in a given year (January—December): arrival for breeding, departure after breeding, arrival for moulting and departure after moulting.

2.3 | Population dynamics

We compared the observed population to a hypothetical non-senescent population to determine the effects of senescence on overall pup production at the colony. In the hypothetical population, we assumed that

2.4 I Potential confounding factors and an alternative age measure

Confounding factors other than senescence—including selective appearance and disappearance and biases in observation frequency—can lead to the illusion of a decline in performance with age. For any hypotheses where we found a significant relationship, we performed post hoc analyses to assess whether these confounding factors could explain the relationships instead of senescence. We also examined an alternate measure for age, years to death, which is a proxy for biological age (Levine, 2013).

2.4.1 | Selective appearance and disappearance

We compared our base models with models that included a term for age of first reproduction (i.e. selective appearance), a model that included a term for longevity (i.e. selective disappearance) and a model containing both (combined selective appearance and disappearance; van de POI & Verhulst,
2006).

2.4.2 | Observation frequency

Not all seals were detected in all years. A non- detection year during the seal's lifespan (i.e. an unobserved year between age four and the last observed year) could represent a missed animal at Affo Nuevo or

Ella—4 a a a + 20-12 20 blinaS11 b n s

$$M_2 = \frac{}{\text{ia=ana}}20 \quad (4)$$

impact of maternal effect senescence on offspring survival.

We calculated the proportional difference between Fl and h to estimate the impact of fertility senescence on the number of births. Similarly, we used the proportional difference between Ml and M2 to estimate the

temporary emigration. In either case, the animal may or may not have reproduced that year. Because of this uncertainty, we may underestimate fertility senescence if observations decline with age or overestimate fertility senescence if observations increase with age. We assessed this potential bias by testing whether the probability of detection was related to age and whether that effect could generate the appearance of senescence in a nonsenescent population (i.e. if observations increase with age). For this analysis, we excluded the last year of observation for each animal, because animals were necessarily observed in that year. For all years between age 4 and the year prior to the last observation, we determined whether each animal was observed. We used AIC weights to select between a linear model (GLMM with binomial response, logit link estimating the probability of an animal being observed as a function of age, with year and individual as random effects) and a threshold model (GLMM with binomial response, logit link estimating the probability of an animal being observed as a function of age interacting with the senescent binary variable, with year and individual as random effects).

2.4.3 | Biological versus chronological age

3 | RESULTS

3.1 | Fertility senescence

The proportion of seals that successfully produced a pup increased up to the threshold age of 11 years old (i.e. for younger seals) and decreased for seals older than the threshold (Figure 3, Table S5; results were similar for threshold ages 9—13; Figure SIA, Table S4), with the latter providing evidence for fertility senescence. The fitted model suggested that breeding probability declined from 96.4% (95% Cl: 94.8%—97.5%) at 11 years old to 89.7% (81.9%—94.3%) at 19 years old. Breeding probability also varied substantially among years (Figure 3, Table S3). In the best reproductive year (2001), breeding probability declined from 98.6% (11 years old) to 95.9% (19 years old). In the worst reproductive year (2018), it declined from 88.7% (11 years old) to 71.9% (19 years old).

3.2 | Maternal effect senescence

Offspring survival decreased with maternal ages at and above 11 years old (Figure 4a, Table S6), but the decline with age on offspring recruitment did not reach statistical significance (p = 0.160, Figure 4b, Table S5), indicating mixed evidence of maternal effect senescence.

The fitted model suggested that pup survival declined from 30.3% (95% Cl: 23.5%—38.1%) when mothers were 11 years old to 9.1% (3.3%—22.9%) for 19- year- old mothers. Offspring survival also varied substantially between years. In the best offspring survival year (2016), offspring survival declined from 49.7% to 18.6% for mothers 11 and 19 years old. In the worst survival year (1994), it declined from 19.0% to 5.1% for mothers 11 and 19 years old. This decline in survival for older mothers was statistically significant for age thresholds of 11 and older (Figure SIB; Table S4).

3.3 | Offspring sex ratio

The chronological age (years since birth) of an individual may not reflect The sex ratio of offspring tended towards more males above the their biological age because ageing rates vary within populations (Levine, 2013; Martin & Festa- Bianchet, 2011). Years- to- death, a proxy for biological age, may be a better predictor for senescence patterns than chronological age (Levine, 2013). We repeated our analysis for the fertility senescence hypothesis using biological age, setting the breakpoint for senescence at biological age years (i.e. 7 years prior to final observation), based on visual inspection of the raw data for the peak in reproduction. This required us to limit our sample to animals with known longevity (last observation in 2020 or earlier), which reduced our sample size to n = 3167 seal- year observations of 934 individual animals. We also fit the model for threshold biological ages between —10 and —3 years to assess whether our results were sensitive to the choice of breakpoint. Finally, we re- fit the chronological fertility senescence model using the known-longevity dataset and compared chronological versus biological age models using AIC.

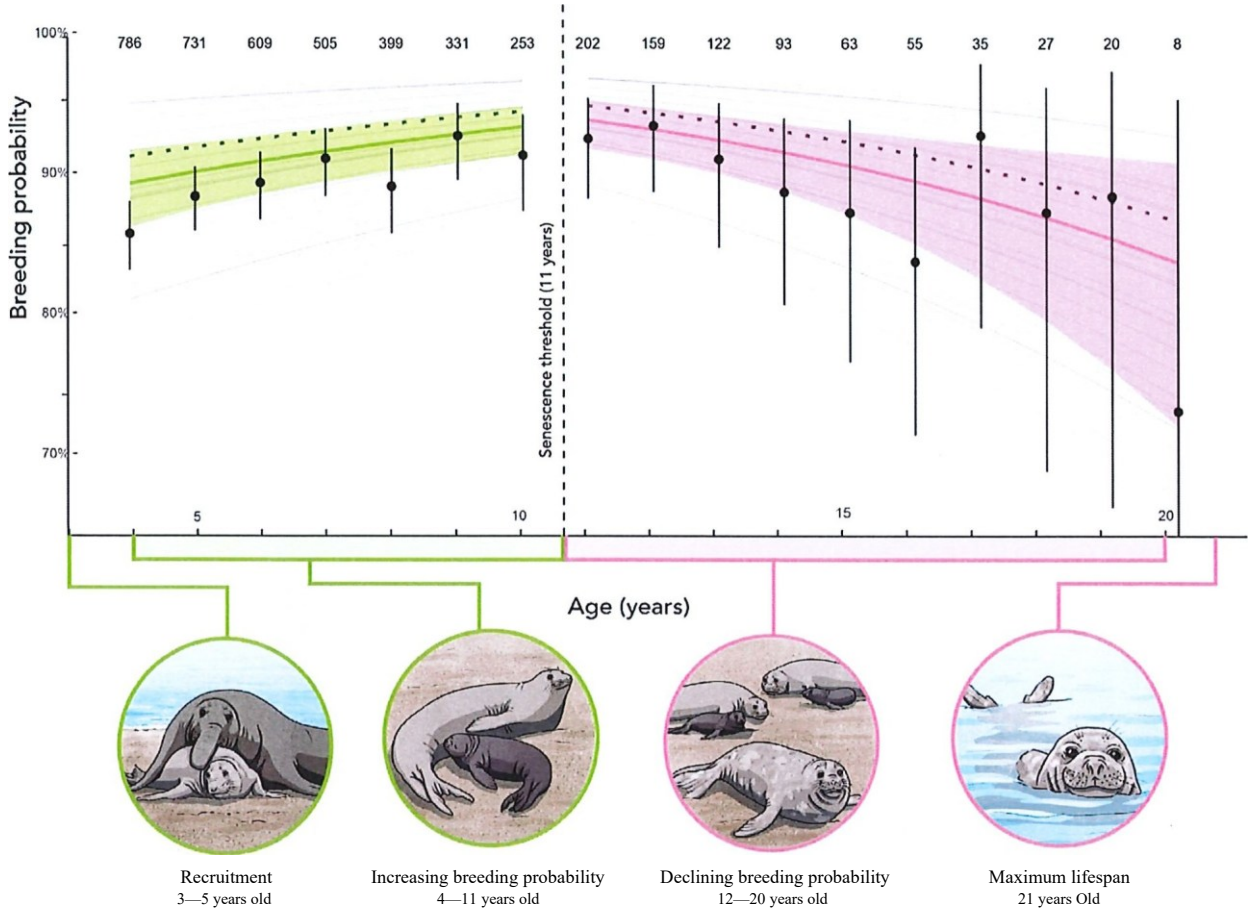


FIGURE 3 Breeding probability for adult female elephant seals increased up to age 11, and decreased after age 11, with the latter providing evidence for fertility senescence. Black points and error bars show the mean and 95% Cl of breeding rates. Sample sizes for each age class are included above the points. Thin grey lines show the mean response for each year of the study (i.e. including the random effect of year). The thick solid lines and shaded areas show the mean response and 95% confidence interval of the fitted model, weighted by the number of seals observed in each year. The unweighted fitted model is shown by the dotted grey line. We show the weighted model because of the large impact of the random effect of year and different number of seals among years. For analyses of other threshold ages, see

11- year- old age threshold (Figure 5, Table S8), but the trend was Slfor 4- year- old animals and 27.5 (26.4—28.6) days for IO- year- old animals. and Table S4

The moultinghaul out was in the opposite direction of our predictions and not significant (p = 0.757, Figure SID, Table S4). In our analysis of the model sensitivity to the senescent threshold, we found that at some thresholds, this effect became significant; however, the coefficients were very close to zero (Figure SI), suggesting that the relationship is relatively weak.

3.4 | Annual cycle phenology

Neither the breeding nor moulting haul out durations changed detectably above 11 years of age. However, the breeding haul out duration increased and the moult haul out duration decreased below 11 years of age (Figure 6, Table S9). Overall, the breeding haul out was 25.6 (95% Cl: 24.6—26.6) days
32.2 (30.9—35.5) days for 4- year- old animals and 28.4 (27.3—29.6) days for 10- year- old animals.

3.5 | Population dynamics

Compared to a hypothetical non- senescing population, a population experiencing fertility and maternal effect senescence had fewer pups survive their first year, with maternal effect senescence resulting in a greater decrease than fertility senescence. The breeding probability was 94.2% for the observed population (h) and 94.5% for the hypothetical nonsenescing population (h). The rate of offspring survival to year I was 23.6% for the observed population (Ml) and 24.9% for the hypothetical population (M2). Fertility senescence therefore resulted in 0.3% fewer pups produced per year, while maternal effect senescence resulted in 5.3% fewer pups surviving overall.

(a)

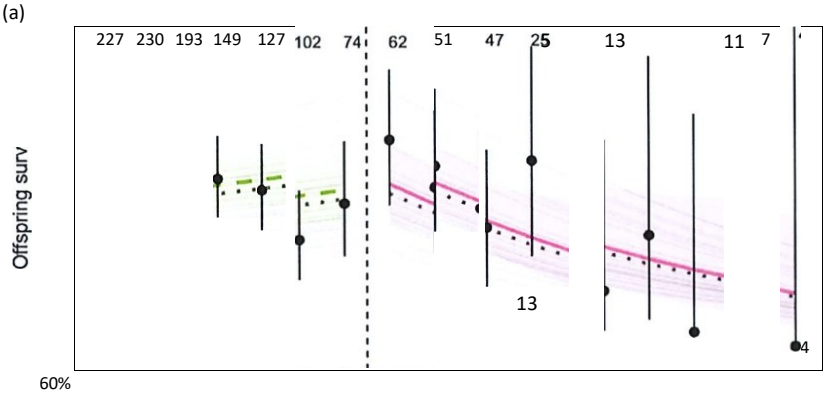
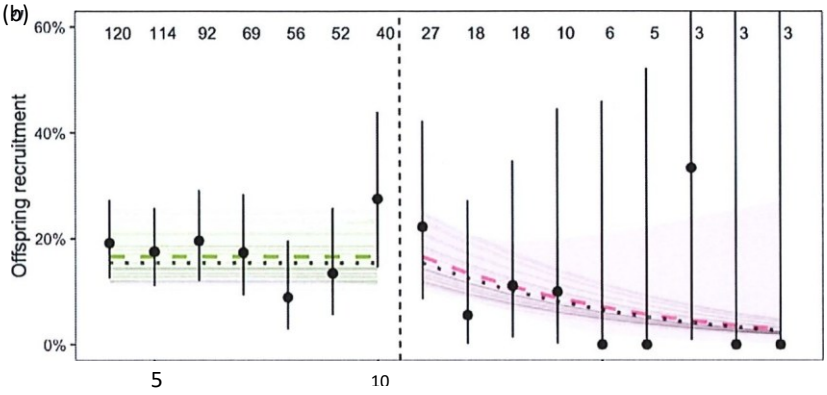


FIGURE 4 Elephant seal offspring survival (a) but not recruitment (b) decreased significantly with maternal age above the threshold age of 11 years. Both male and female offspring were

.> 40%included in the survival analysis, but only female offspring were included for recruitment. This caused some values of recruitment to be higher than survival at the same maternal age. Black points and error bars 20% show means and 95% Cl of survival or recruitment for each maternal age. Sample sizes for each age class are included above the 0%points. Thin grey lines show the mean response

(b)



5 10 15 for each year of the study (i.e. including the random effect of year). Thick dashed and solid lines show the weighted mean response and 95% Cl, with solid lines indicating significant trends. The unweighted fitted model is indicated by a dotted grey line. We show the weighted model because of the large impact of the random effect of year and different number of seals among years. For analyses of other threshold ages, see Figure Sl and Table

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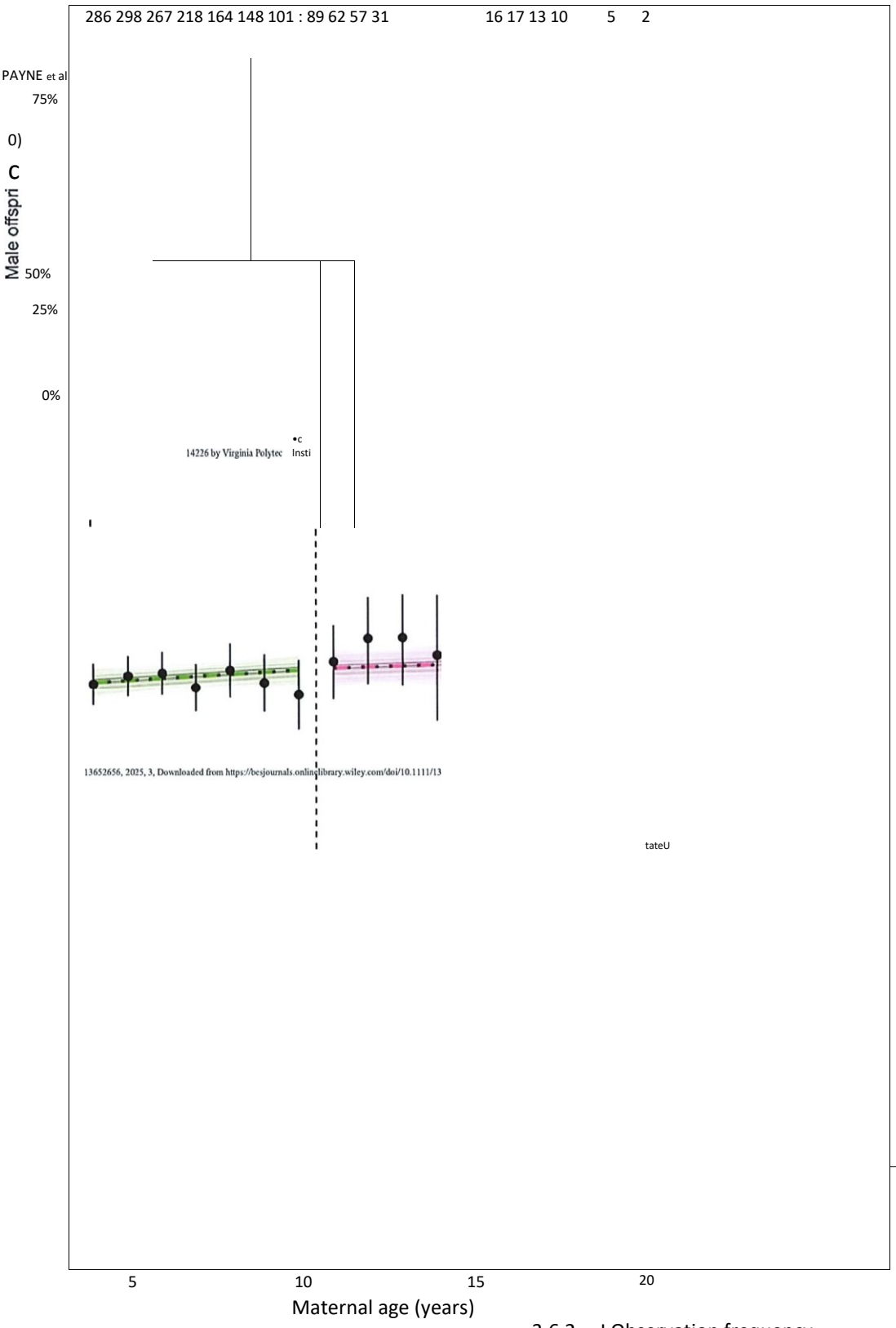
Age (years)

100% FIGURE There was trend in



5 no significant offspring sex ratio above or below the age threshold for senescence. Black points and error bars show the mean and 95% Cl. Sample sizes for each age class are included above the points. Thin grey lines show the mean response for each year of the study (i.e. including the random effect of year). Thick dashed lines show the weighted mean response and 95% Cl; neither trend was significant (Table S6). The unweighted fitted model is indicated by a dotted grey line. For

and Table S4.

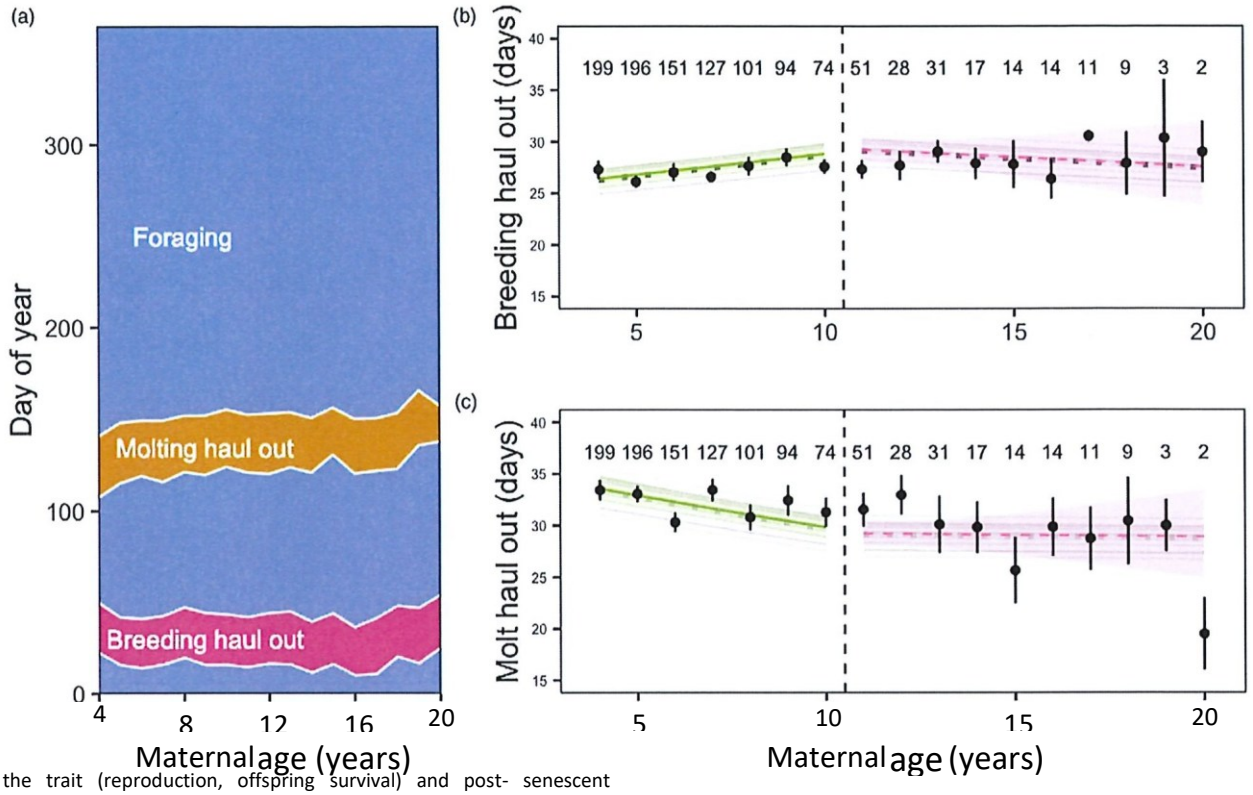
3.6 | Potential confounding factors

3.6.1 | Selective appearance and disappearance

There was no evidence for selective appearance or disappearance influencing the patterns we observed in fertility senescence (HI) or offspring survival (H2a). The coefficient for the interaction between

3.6.2 I Observation frequency

We found that the probability that an animal was detected in a given year decreased with age throughout their lifespan (Figure S3). Detection probability was predicted to be 70.1% (95% Cl:



the trait (reproduction, offspring survival) and post- senescent maternal age was still negative for the models when including terms for selective appearance, selective disappearance and both (Figure S2; Table SIC)).

FIGURE 6 Neither moulting nor breeding haul out duration varied with age for older seals. (a) Raw data plotting the observed annual time allocation averaged over all n = 387 individuals. (b and c) Points and error bars represent the mean and CI for haul out durations. Sample sizes for each age class are included above the points. Thin grey lines show the mean response for each year of the study (i.e. including the random effect of year). Thick solid and dashed lines represent the mean response and 95% CI of the fitted model, weighted by the number of seals observed per year, with solid lines indicating significant trends. The unweighted fitted model is indicated by a dotted grey line. Results were categorically similar across a range of threshold ages
(Figure SI, Table S4).

61.7%-77.3%) at age 11 and 59.9% (95% CI: 44.4%-73.7%) at age 19. A linear model outperformed the threshold model (AAIC = 1.52; AIC weight for linear model 0.622, for threshold model 0.38).

3.6.3 | Biological versus chronological age

Biological and chronological age yielded qualitatively similar results for fertility senescence. The coefficient of age for mothers older than —7

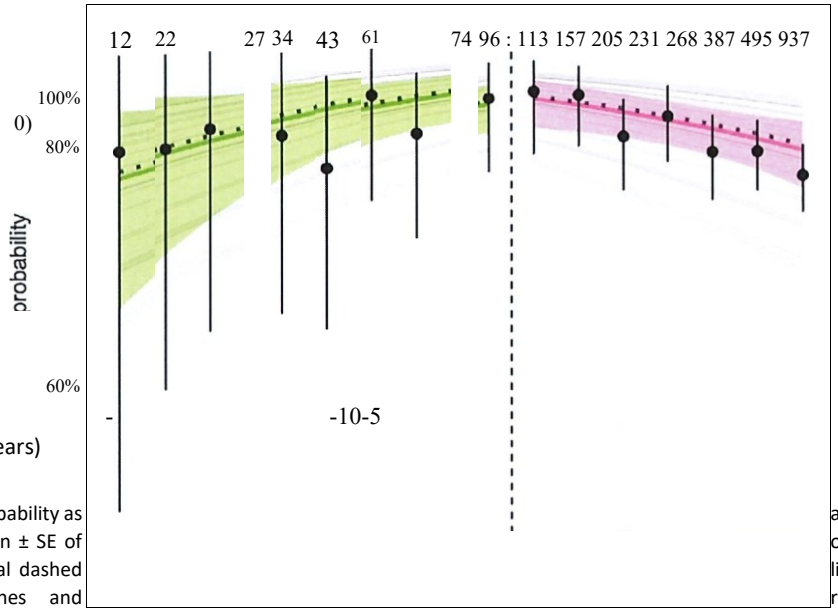


FIG URE 7 Breeding probability as a function of biological age. Points and error bars are the mean ± SE of observed breeding proportions within age classes. The vertical dashed line indicates the threshold for senescence. Solid lines and ribbons are the mean and 95% CI of the population- level breeding probability, estimated by a GLMM with random effects for individual and year. The dotted lines represent the mean of yearly breeding probabilities, weighted by the number of seals observed each year, which match the observed data more closely than the unweighted population- level probabilities. Biological age O was excluded from the model because our sample excluded animals that never bred, which would artificially inflate the breeding probability at that age by limiting the biological age = O those who bred once.

years biological age (i.e. within 7 years of death) was negative. The model using chronological age (years since birth) was a better fit to the data than biological age (years before death) in predicting breeding probability (AAIC= 4.13; AIC weight for chronological age 0.89, for biological age 0.11; Table Sll). Breeding probability declined with age above a 7 age threshold (Figure 7).

4 | DISCUSSION

Our results provide evidence for fertility and maternal effect senescence in elephant seals because seals older than prime age reproduced less frequently and their offspring exhibited reduced survival.

Senescence, rather than selective disappearance or other mechanisms, best explained the observed patterns. We found a decrease in observation frequency throughout a seal's life, indicating that breeding probability and therefore fertility senescence may be underestimated by our methods. Previous studies on age- dependent reproduction in elephant seals and asymptotic relationship of reproductive

Hardenberg et al., 2004). We did not have direct measurements of biological age (e.g. via epigenetic analysis of DNA methylation), so we tested whether years before death (a proxy for biological age) was a decline in offspring survival had a larger effect. If this population did not undergo reproductive senescence (i.e. if fertility rates and offspring survival were constant beyond age 11), then the average annual reproductive output per mother would be 0.945 pups born, of which 0.249 pups would survive to age 1. Due to senescence, reproductive output declines to 0.942 pups born (0.3% fewer) and 0.236 pups surviving to age 1 (5.3% fewer). Thus, even though only 4% of females survive long enough to experience reproductive senescence, in a population that is currently growing relatively slowly (1= 1.038, Lowry et al., 2014), maternal effect senescence likely plays an important role in population dynamics. Additionally, our methods may underestimate rates of fertility senescence due to declining observation frequency with increasing maternal age, which may in turn lead to underestimates of the contribution of fertility senescence to population dynamics.

predation, which is likely a key source of mortality (Kienle et al., 2022), is mostly stochastic and not influenced by seal traits, then the years before death proxy for biological age would conflate many biologically young and old animals that died due to predation. We found that chronological age better explained the observed patterns, suggesting that extrinsic mortality is playing an important role.

Based on the theory of adaptive sex ratios (Trivers & Willard, 1973; Williams et al., 1997), we hypothesized that prime age females would give birth to more male offspring and senescent females would give birth to more female offspring. However, we did not find any evidence for variation in offspring sex ratio with maternal age. Earlier work on elephant seals found no effect of maternal age on offspring sex ratio up to prime age; our results confirm this trend holds through fertility senescence (Le Boeuf et al., 1989). This null result may be due to similar allocation in weaning male and female offspring (Kretzmann et al., 1993). Although adult elephant seals are highly sexually size dimorphic (the mass of adult males is three times the

better predictor of senescence than years since birth (i.e. chronological age; Martin & FestaBianchet, 2011). As a proxy for biological age, years before death should be