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Authors

Payne, Allison R
Czapanskiy, Max F
Kilpatrick, A Marm
et al.

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

Allison R. Payne[1] | Max F. Czapanskiy[2,3,4] | A. Marm Kilpatrick[1] | Patrick W. Robinson[1] | Cara M. O. Munro[1] | Kelli Ong[1] | Adrien Bastidas[1] | Alegra O. Negrete[1] | Brecken Theders[1] | Bryn Stillwell[1] | Danissa Coffey[1] | Elijah Schweitzer[1] | Elise Baugh[1] | Jasmine Salazar[1] | Keenan Chau-Pech[1] | Mason Rodrigues[1] | Mimi Chavez[1] | Savanna Wright[1] | Sofia Rivas[1] | Joanne Reiter[5] | Daniel P. Costa[1,4] | Roxanne S. Beltran[1]

[1]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California, USA

[2]Department of Ocean Sciences, University of California, Santa Cruz, California, USA

[3]Bren School of Environmental Science and Management, University of California Santa Barbara, Santa Barbara, California, USA

[4]College of Creative Studies, University of California Santa Barbara, Santa Barbara, California, USA

[5]Institute of Marine Sciences, Long Marine Laboratory, University of California Santa Cruz, Santa Cruz, California, USA

Correspondence
Allison R. Payne
Email: allisonpayne01@gmail.com

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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

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

1 | INTRODUCTION

Reproductive senescence, or a decrease in reproductive output with advanced age, is widespread among animals, including 68% of mammals (Lemaître et al., 2020). However, the timing and magnitude of senescence across reproductive traits are highly variable, complicating our understanding of the evolution and ecology of ageing in wild animals (Lemaître & Gaillard, 2017). In addition to impacting fertility, maternal age was shown to affect offspring phenotypes in 93% of populations across a range of taxa, with a tendency towards negative impacts with advanced age (Ivimey-Cook & Moorad, 2020). These negative effects, known as maternal effect senescence, manifest as decreased offspring quality (e.g. body condition, survival or recruitment) with increasing maternal age (Ivimey-Cook & Moorad, 2020). Although fertility senescence and maternal effect senescence are similar, age-specific selection acts independently on each process, resulting in differing rates of decline (Moorad & Nussey, 2015). Evolutionary theory predicts that due to indirect genetic effects, age-dependent selection for maternal effects will decline faster than for fertility, resulting in a steeper rate of decline for maternal effect senescence than fertility senescence (Moorad & Nussey, 2015). This occurs because a log-linear increase in mortality with increasing maternal age will result in a faster than log-linear increase in offspring mortality with increasing maternal age (Moorad & Nussey, 2015). Offspring sex ratios may also change with maternal age. The Trivers–Willard hypothesis predicts that mothers with superior body condition will give birth to more males, if male offspring require greater parental investment and have greater potential for reproductive output (Trivers & Willard, 1973). If body condition declines with age, females may give birth to fewer male offspring.

Empirical data demonstrate variable effects of age on reproductive traits (Figure 1). The most common effect appears to be an initial increase in performance as animals grow and gain experience, followed by a 'prime age' plateau and eventual decline during senescence (Emlen, 1970). For example, in red squirrels (*Tamiasciurus hudsonicus*), great tits (*Parus major*) and blue-footed boobies (*Sula nebouxii*), offspring survival and recruitment (defined by the first reproductive event) followed the typical ageing pattern: an initial increase at young maternal ages, followed by a plateau at prime age and then a decrease at older ages (Bouwhuis et al., 2010; Descamps et al., 2008; Torres et al., 2011). However, contrasting patterns have also been observed. Instead of a concave relationship, offspring survival increased with maternal age in an experimental population of European rabbits (*Oryctolagus cuniculus*; Rödel et al., 2009), decreased in rhesus macaques (*Macaca mulatta*; Hoffman et al., 2010) and did not change in red-billed choughs (*Pyrrhocorax pyrrhocorax*;

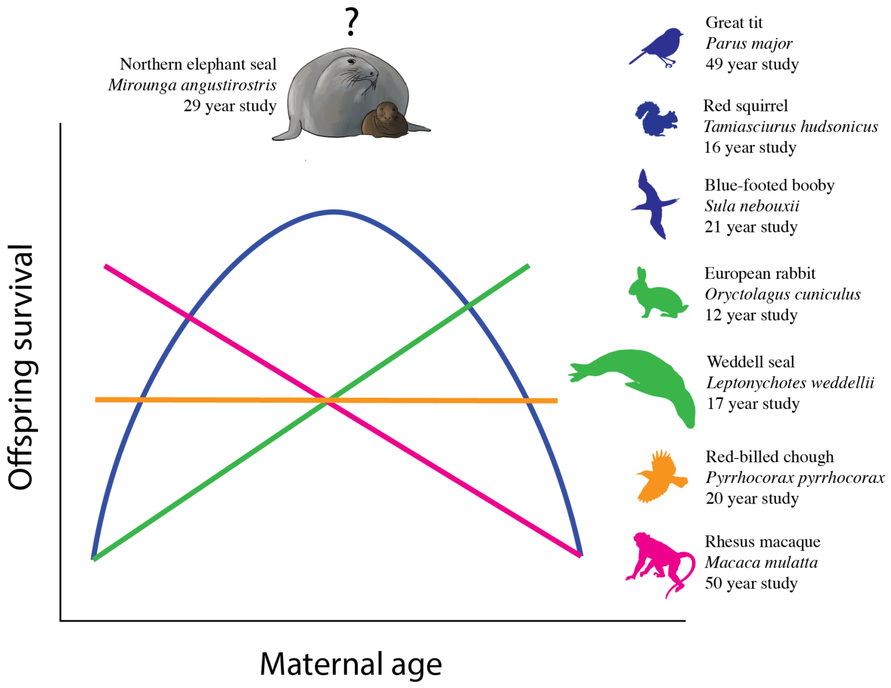

FIGURE 1 The dominant patterns of maternal effect senescence as measured by offspring survival past the end of maternal care. The most common is a concave-down relationship (in blue) characterized by increasing offspring survival until a peak at prime age, then decreasing survival with advanced maternal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

Reid et al., 2010). Other species exhibited even more complicated senescence patterns. Wandering albatrosses (*Diomedea exulans*) exhibit paternal, but not maternal, effect senescence (Fay et al., 2016) and Weddell seals (*Leptonychotes weddellii*) exhibited opposing effects of maternal age on offspring survival (positive effect) and recruitment (negative effect; Hadley et al., 2007). Quantifying patterns of 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 Año 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 life-history 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 post-moult foraging trip (Beltran et al., 2023). Maternal care is limited to a 26.8-day (95% CI: 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 sex ratio with age, but focused on development until prime age, rather than a decline after prime age (Le Boeuf et al., 1989).

Our objective was to examine how maternal age impacts fertility and 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 (H1, 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, 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 Año 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 Año 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 Año 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 fur with a temporary unique identifier to link pups to their mothers in our database. After weaning, this identifier allowed us to find pups and attach permanent unique flipper tags to measure future 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 known-age 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 | 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 lme4 R package, version 1.1–32 (Bates et al., 2015). Data and code are available on Dryad (https://doi.org/10.5061/dryad.pg4f4qrx1).

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 = −4). 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 (H1, fertility senescence). Comparisons of model sensitivity to threshold age for all hypotheses can be found in the supplemental material (Figure S1, 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 S1), 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.

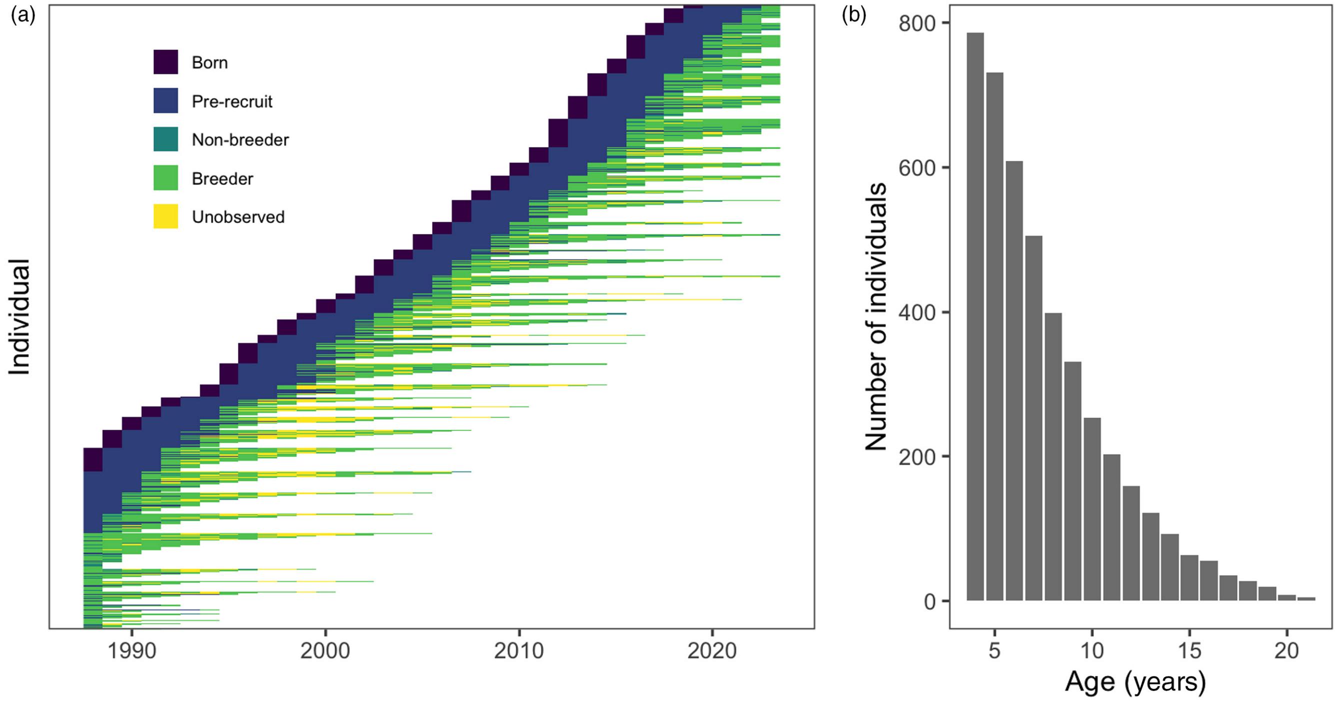

FIGURE 2 (a) Several hundred elephant seals from each cohort are tagged during their birth year (purple) and observations take place for the rest of their lives so that breeding status (greens and blues) and observation status (yellow) can be assigned and compared to age. Raw longitudinal data for 1203 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.

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.

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 S1). 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 0 (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, 7 years 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 S1).

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 S1). 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 throughout the entire annual cycle. We only included animals that were 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 reproduction and offspring survival remained constant after age 11. The observed pup production (in the age-structured population) can be described by Equation 1.

$$F_1 = \frac{\sum_{a=4}^{20} b_a n_a}{\sum_{a=4}^{20} n_a} \tag{1}$$

where F_1 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 (F_2), pup production does not decrease after age 11 (Equation 2).

$$F_2 = \frac{\sum_{a=4}^{11} b_a n_a + \sum_{a=12}^{20} b_{11} n_a}{\sum_{a=4}^{20} n_a} \tag{2}$$

Similarly, to account for the influence of maternal effects in the observed (M_1) and hypothetical (M_2) populations, we add a term s to estimate the observed (Equation 3) and hypothetical (Equation 4) quantity of pups that survive to age 1.

$$M_1 = \frac{\sum_{a=4}^{20} b_a n_a s_a}{\sum_{a=4}^{20} n_a} \tag{3}$$

$$M_2 = \frac{\sum_{a=4}^{11} b_a n_a s_a + \sum_{a=12}^{20} b_{11} n_a s_{11}}{\sum_{a=4}^{20} n_a} \tag{4}$$

We calculated the proportional difference between F_1 and F_2 to estimate the impact of fertility senescence on the number of births. Similarly, we used the proportional difference between M_1 and M_2 to estimate the impact of maternal effect senescence on offspring survival.

2.4 | 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 Pol & 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 Año Nuevo or 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 non-senescent 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

The chronological age (years since birth) of an individual may not reflect 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 = −7 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.

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 S1A, Table S4), with the latter providing evidence for fertility senescence. The fitted model suggested that 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. 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% CI: 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 S1B; Table S4).

3.3 | Offspring sex ratio

The sex ratio of offspring tended towards more males above the 11-year-old age threshold (Figure 5, Table S8), but the trend was

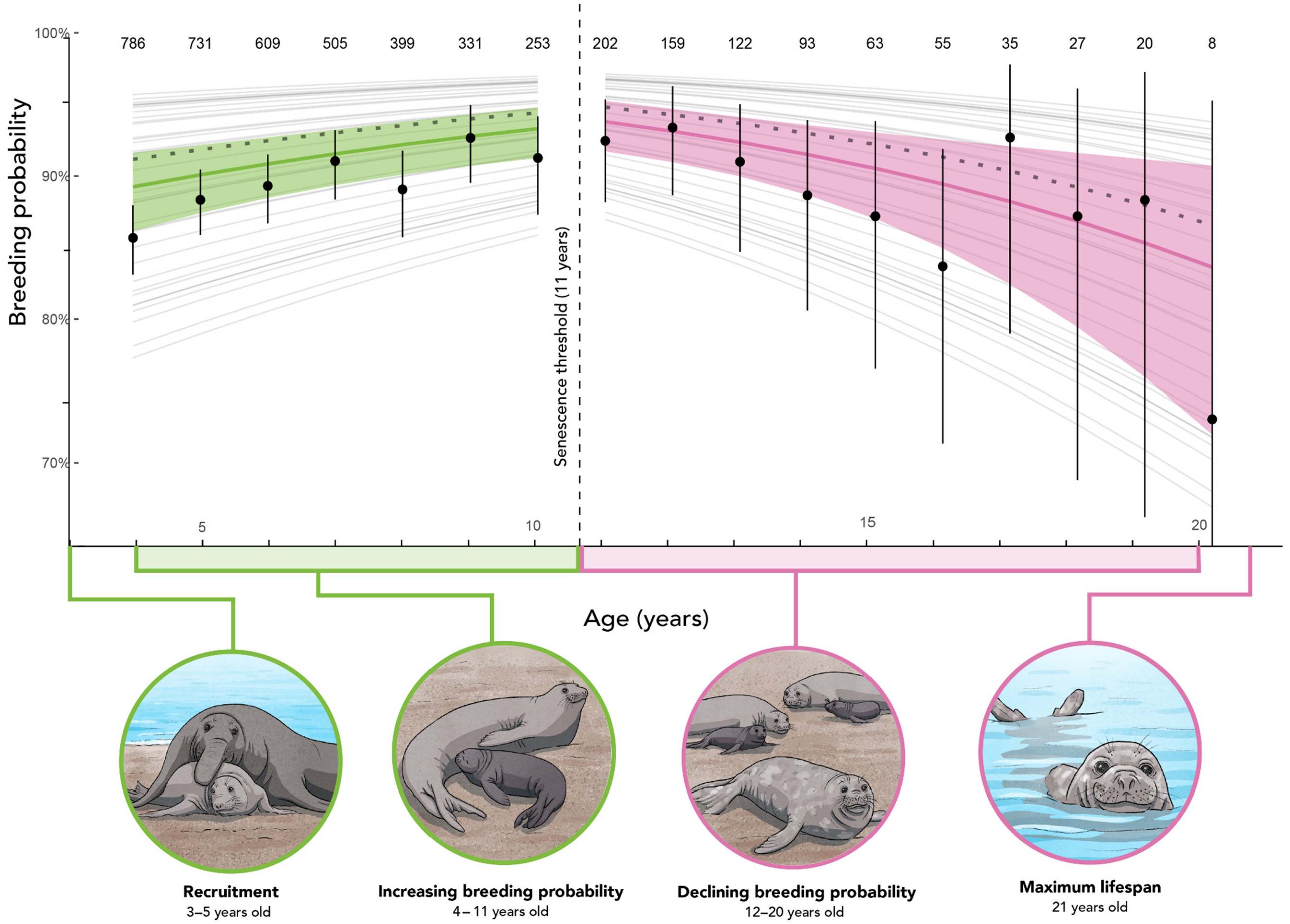

FIGURE 3 Breeding probability for adult female elephant seals increased up to age 11, and decreased after age 11, with the latter providing evidence for fertility senescence. Black points and error bars show the mean and 95% CI of breeding rates. Sample sizes for each age class are included above the 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 Figure S1 and Table S4. Illustrations by Alex Boersma.

in the opposite direction of our predictions and not significant ($p = 0.757$, Figure S1D, 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 S1), 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% CI: 24.6–26.6) days for 4-year-old animals and 27.5 (26.4–28.6) days for 10-year-old animals. The moulting haul out was 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 (F_1) and 94.5% for the hypothetical non-senescing population (F_2). The rate of offspring survival to year 1 was 23.6% for the observed population (M_1) and 24.9% for the hypothetical population (M_2). Fertility senescence therefore resulted in 0.3% fewer pups produced per year, while maternal effect senescence resulted in 5.3% fewer pups surviving overall.

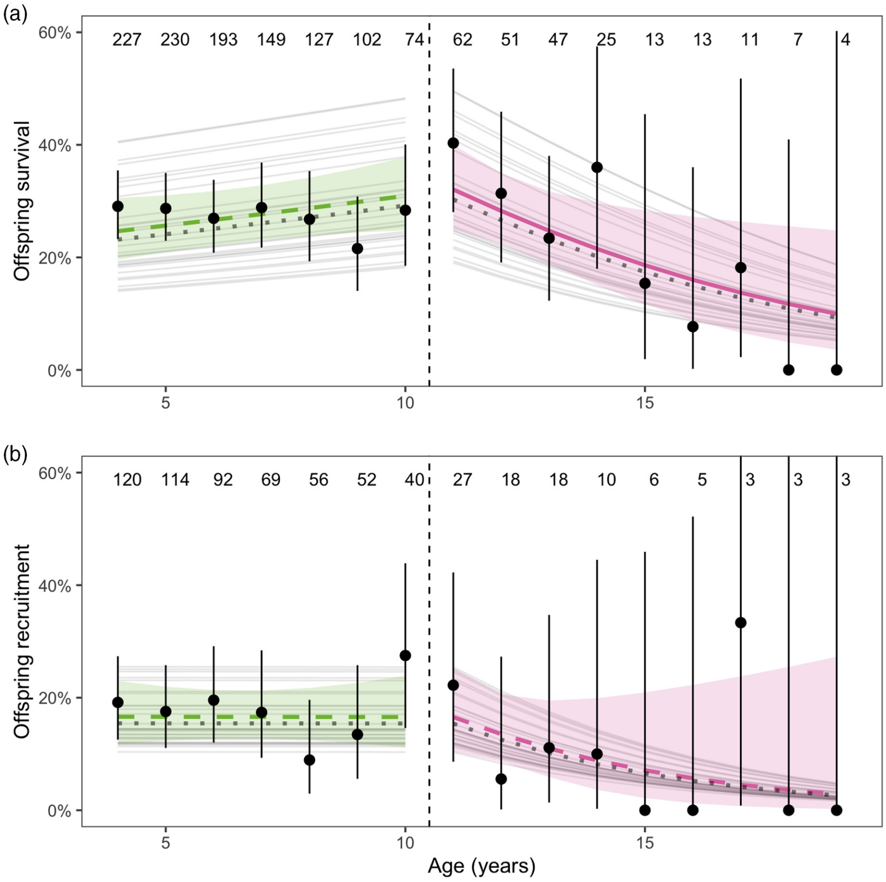

FIGURE 4 Elephant seal offspring survival (a) but not recruitment (b) decreased significantly with maternal age above the threshold age of 11 years. Both male and female offspring were included in the survival analysis, but only female offspring were included for recruitment. This caused some values of recruitment to be higher than survival at the same maternal age. Black points and error bars show means and 95% CI of survival or recruitment for each maternal age. 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 and solid lines show the weighted mean response and 95% CI, 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 S1 and Table S4.

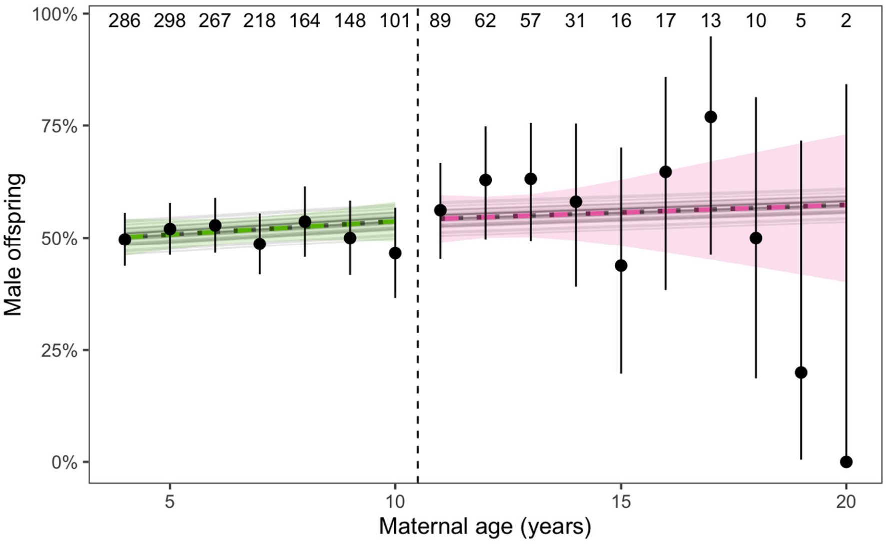

FIGURE 5 There was no significant trend in offspring sex ratio above or below the age threshold for senescence. Black points and error bars show the mean and 95% CI. Sample sizes for each age class are included above the points. Thin grey lines show the mean response for each year of the study (i.e. including the random effect of year). Thick dashed lines show the weighted mean response and 95% CI; neither trend was significant (Table S6). The unweighted fitted model is indicated by a dotted grey line. For analyses of other threshold ages, see Figure S1 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 (H1) or offspring survival (H2a). The coefficient for the interaction between 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 S10).

3.6.2 | 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% CI:

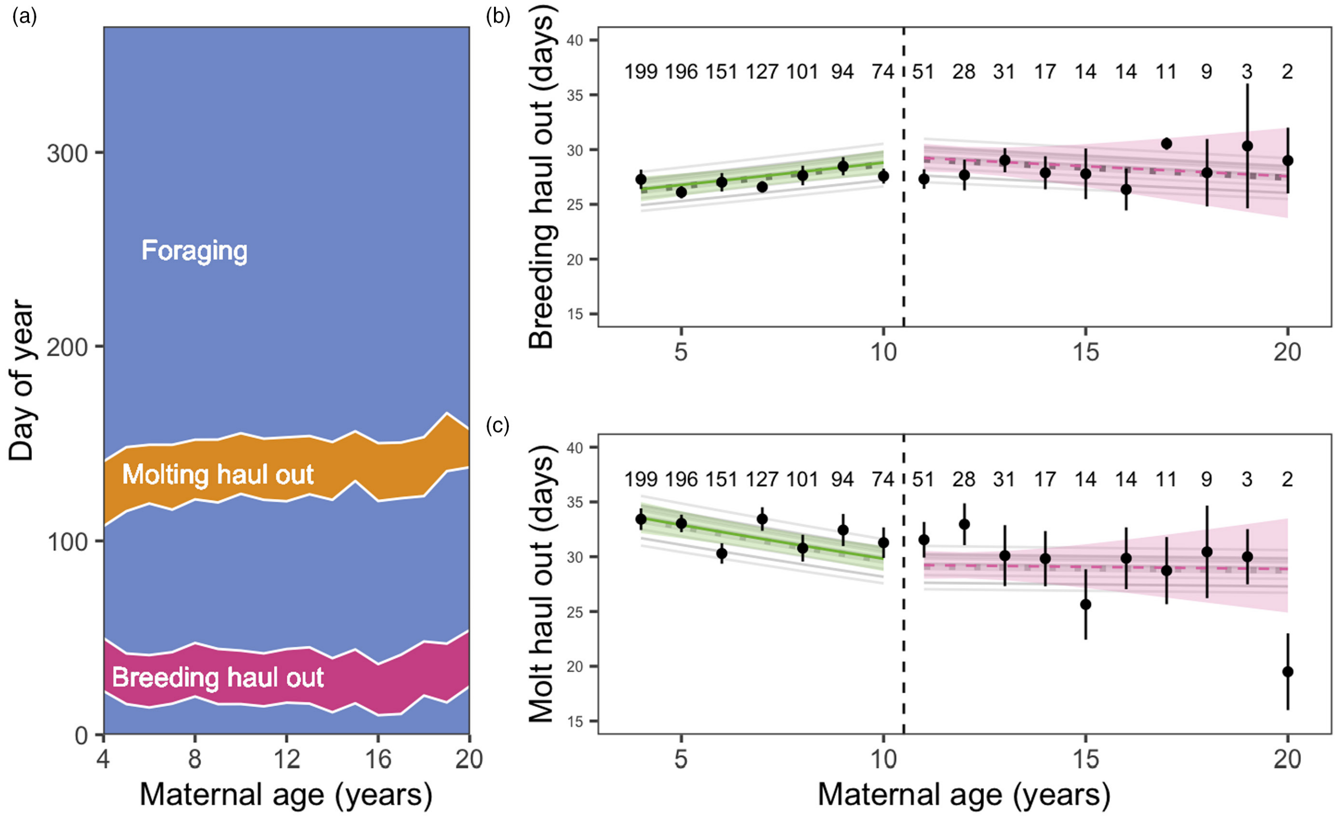

FIGURE 6 Neither moulting nor breeding haul out duration varied with age for older seals. (a) Raw data plotting the observed annual time allocation averaged over all $n = 387$ individuals. (b and c) Points and error bars represent the mean and CI for haul out durations. Sample sizes for each age class 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 S1, 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 (ΔAIC = 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 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 (ΔAIC = 4.13; AIC weight for chronological age 0.89, for biological age 0.11; Table S11). 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 Weddell seals identified either an asymptotic relationship of reproductive output with age (Le Boeuf et al., 2019) or a declining relationship from the age of first reproduction (i.e. no 'prime age' plateau; Hadley et al., 2007). Our results, contrary to these studies, suggest that elephant seals follow a more typical reproductive senescence trajectory. Differences in sample sizes (Hadley et al., 2007) or statistical methods (Le Boeuf et al., 2019) may have contributed to the differences between studies.

Although we found declines in both breeding probability and offspring survival with age above 11 years old, it is important to note that very few seals survive to experience reproductive senescence. Eighteen per cent of female seals tagged at weaning survive to sexual maturity (age 3), and only 22% of those seals (4% overall) survive to the senescence threshold age of 11. However, previous research has shown that these few older seals can have outsized impacts on pup production in the population (Le Boeuf et al., 2019). We found that the decline in reproduction after prime

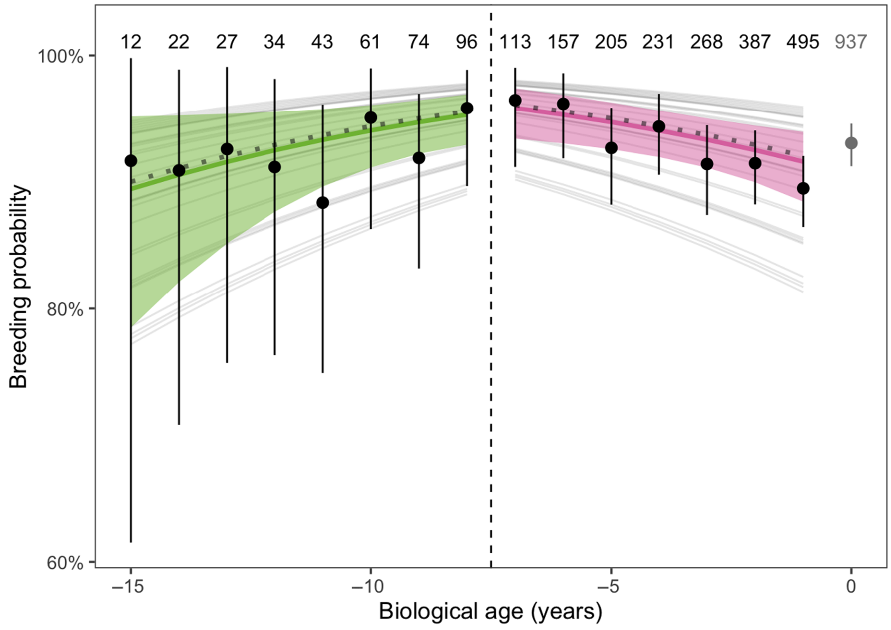

FIGURE 7 Breeding probability as a function of biological age. Points and error bars are the mean ± SE of observed breeding proportions within age classes. The vertical dashed line indicates the threshold for senescence. Solid lines and ribbons are the mean and 95% CI of the population-level breeding 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 0 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 = 0 animals to those who bred once.

age had a small impact on the total number of pups produced, but the 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 ($\lambda = 1.038$, 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.

It has been suggested that senescence should depend more on biological age (years before death) than chronological age (years since birth) because animals physically deteriorate at different rates (Levine, 2013; von 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 better predictor of senescence than *years since birth* (i.e. chronological age; Martin & Festa-Bianchet, 2011). As a proxy for biological age, *years before death* should be a better predictor of senescence than chronological age if most mortality is age-related (e.g. if muscular senescence leads to reduced foraging performance or predator escape over time, Hindle et al., 2009). However, if 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 mass of adult females; Beltran et al., 2022; Haley et al., 1994), male offspring are on average only 7%–8% heavier than females at the time of weaning (Le Boeuf et al., 2019). This difference in maternal allocation may be too small to be substantially influenced by maternal age. If elephant seals do adaptively modify offspring sex ratios, environmental conditions appear to be more influential than maternal age (Kretzmann et al., 1993; Lee & Sydeman, 2009).

Declining foraging efficiency with age is one mechanism for reproductive senescence (Lecomte et al., 2010). If older seals need additional foraging time to meet energy demands for maintenance and reproduction, then a greater portion of their annual cycle would need to be allocated to foraging trips. Since the breeding haul out is highly synchronous (Beltran et al., 2022), we hypothesized that older seals would reallocate time from the moulting haul out to foraging. However, the moulting haul out duration did not significantly change among females 11 years old and older. If seals skip breeding more often as they age, but are not altering their annual cycle, that suggests that the haul out durations are already as short as is physiologically possible. Skipped breeding may therefore become increasingly necessary with advanced age to reset seals' annual cycles.

5 | CONCLUSIONS

Northern elephant seals exhibit both fertility and maternal effect senescence. The rates of decline for these two processes (i.e. how rapidly fertility and offspring survival decline with maternal age) were not different from each other. Theory predicts maternal effect senescence should evolve to be more rapid than fertility senescence (Moorad & Nussey, 2015); similar analyses with larger sample sizes and more species are necessary to fully test this hypothesis. Furthermore, maternal effect senescence had a substantially larger impact on offspring production than fertility senescence. Although maternal effect senescence is relatively understudied, it appears to be highly prevalent, as it has been detected in 93% of studied populations (Ivimey-Cook & Moorad, 2020). Our results show that population growth rates for age-structured populations may be overestimated if only fertility senescence is considered.

AUTHOR CONTRIBUTIONS

Roxanne S. Beltran, Allison R. Payne and Patrick W. Robinson conceived the ideas and designed methodology; Allison R. Payne, Patrick W. Robinson, Cara M. O. Munro, Kelli Ong, Adrien Bastidas, Alegra O. Negrete, Brecken Theders, Bryn Stillwell, Danissa Coffey, Elijah Schweitzer, Elise Baugh, Jasmine Salazar, Keenan Chau-Pech, Mason Rodrigues, Mimi Chavez, Savanna Wright, Sofia Rivas, R Condit, Joanne Reiter, Daniel P. Costa and Roxanne S. Beltran collected the data; Allison R. Payne, Max F. Czapanskiy, A. Marm Kilpatrick and Roxanne S. Beltran analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data and code available from the Dryad Digital Repository https://doi.org/10.5061/dryad.pg4f4qrx1 (Payne et al., 2024). Code is also available on GitHub (https://github.com/allisonpayne/sealaging).

ETHICAL APPROVAL

All research procedures were conducted under the National Marine Fisheries Service (NMFS) marine mammal permits 23188, 19108 and 14636. Animal care was authorized through the University of California, Santa Cruz Institutional Animal Care and Use Committee (IACUC). All projects were approved by the California State Park System and the University of California Natural Reserve System.

ORCID

Allison R. Payne https://orcid.org/0009-0001-6107-4252
Max F. Czapanskiy https://orcid.org/0000-0002-6302-905X
A. Marm Kilpatrick https://orcid.org/0000-0002-3612-5775
Patrick W. Robinson https://orcid.org/0000-0003-3957-8347
Cara M. O. Munro https://orcid.org/0009-0005-6971-8509
Brecken Theders https://orcid.org/0009-0003-3056-5221
Bryn Stillwell https://orcid.org/0009-0006-9021-6527
Danissa Coffey https://orcid.org/0000-0001-7032-130X
Elijah Schweitzer https://orcid.org/0009-0000-3998-5650
Elise Baugh https://orcid.org/0009-0002-2849-2441
Mimi Chavez https://orcid.org/0009-0000-0789-7314
Sofia Rivas https://orcid.org/0009-0000-0707-0333
Joanne Reiter https://orcid.org/0009-0009-1215-940X
Daniel P. Costa https://orcid.org/0000-0002-0233-5782
Roxanne S. Beltran https://orcid.org/0000-0002-8520-1105

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Coefficients for analyses with different threshold age breakpoints on a log scale.

Figure S2. Comparison of the coefficients (estimate and 95% CI) for age, among post-senescent animals, for H1 (fertility senescence) and H2a (offspring survival) for the base model and models including selective appearance, selective disappearance, or both.

Figure S3. The probability that an animal was observed decreased throughout the animal's lifetime.

Table S1. Covariates for all models (fertility senescence, maternal-effect senescence, sex ratio, and phenology).

Table S2. Results for quadratic models.

Table S3. AIC comparisons of the quadratic and breakpoint models for the analyses with significant results (H1, fertility senescence and H2a, offspring survival). Both models have the same number of degrees of freedom.

Table S4. AIC weights for threshold ages 6–14 for each hypothesis using the breakpoint model.

Table S5. Fitted model for H1 (fertility senescence).

Table S6. Fitted model for H2a (maternal effect senescence: offspring survival).

Table S7. Fitted model for H2b (maternal effect senescence: offspring recruitment).

Table S8. Fitted model for H3 (offspring sex ratio).

Table S9. Fitted model for H4 (phenology).

Table S10. Fitted models accounting for selective appearance, disappearance, and combined for hypotheses with significant results (H1 and H2a).

Table S11. Fitted model for biological age.

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