Maternal traits and ecological conditions shape mother-offspring association in a capital breeding mammal

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AMJ, MJP, and RSB conceived the ideas and designed methodology; AMJ, MJP, ARP, MHM, PWR, DPC, and RSB collected the data; AMJ, MJP, MHM, AMK, and RSB analysed the data; AMJ and MJP led the writing of the manuscript, and AMK, MHM, ARP, PWR, DPC, and RSB provided review and editing on all drafts of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Code will be made available on Dryad at https://doi.org/10.5061/dryad.hmgqnkb03 and is currently available on GitHub (https://github.com/UCSCBeltranLab/eseal_MOA.git).

NOVELTY STATEMENT

Maternal investment in wild populations is typically inferred from reproductive outcomes, and the behavioral mechanisms underlying variation remain poorly understood. Using 30 years of longitudinal data from known-age northern elephant seals, we quantify mother-offspring association as a novel behavioral dimension of maternal investment and demonstrate that it is shaped by both intrinsic and extrinsic drivers and consequential for offspring quality. We show that maternal behavior varies across individual lifetimes and ecological conditions, we provide a potential mechanism through which maternal state and environmental variation influence reproductive performance. By integrating behavioral and demographic data, our work identifies meaningful behavioral variation as a medium that may be overlooked when offspring outcomes alone are considered.

ABSTRACT

Maternal investment is central to life history theory and population dynamics. However, variation in maternal behaviors mediating investment, and the drivers and consequences of such variation, remain poorly understood. Using 30 years of data from 565 northern elephant seals (*Mirounga angustirostris*), we evaluated the intrinsic and extrinsic factors influencing mother-offspring association, calculated as the proportion of days a female was observed near a pup during lactation. Offspring weaning mass increased with mother-offspring association, linking variation in this behavioral metric to offspring quality. Despite high mother-offspring association across the population, association increased with maternal age until 8 years and pupping experience until five previous pups, declining thereafter, and decreased with local seal density and extreme wave and tide events. These findings highlight behavioral variation as a potential mechanism through which maternal state and ecological conditions shape offspring quality, such that even small behavioral deviations can have profound consequences for reproductive performance.

INTRODUCTION

Reproductive investment is central to an organism's life history and carries consequences for current and future fitness of both the parent and offspring (Hamel et al. 2010; Smith & Fretwell 1974). Maternal investment in the offspring's early life, particularly during the dependency period, can have cascading effects on long-term recruitment into the breeding population, reproductive success, and fecundity (Lummaa 2003; Moore et al. 2015). Consequently, variation in maternal investment can scale up to populations, influencing lineages through heritable maternal effects (Moore et al. 2019) and population dynamics (Benton et al. 2005, 2008; Payne et al. 2025). In wild populations, maternal investment is often inferred using cumulative outcomes such as offspring growth, survival, or lifetime reproductive success, which may obscure potentially meaningful variation in the behaviors through which mothers allocate resources to offspring. Behavior may represent an important mechanistic link between intrinsic and ecological variation and reproductive performance, yet these pathways remain poorly understood in long-lived species due to limited data across individual lifetimes. Thus, approaches that quantify behaviors underlying investment across individual lifetimes are critical for revealing processes that may be overlooked when reproductive outcomes alone are considered.

A combination of intrinsic characteristics and ecological context may influence maternal investment by altering both behavioral and physiological processes (Forslund & Pärt 1995; Garroway & Broders 2007; Badger et al. 2020). Age commonly influences investment through a combination of physiological and life-history changes, with improvements for young individuals as they gain experience and increase in body size as described by the constraint hypothesis (Curio 1983). Older individuals may also exhibit declines in parental behavior as a consequence of senescence (Descamps et al. 2008; Payne et al. 2025); for example, blue-footed boobies' (*Sula*

nebouxii) nest defensive strategy increases for young parents and declines progressively after prime age (Ortega et al. 2017). Additionally, individuals may exhibit simultaneous increases in some metrics of reproductive performance while undergoing declines in other metrics. For example, female moose (*Alces alces*) exhibit senescence in parental care, but compensate by increasing offspring birth mass with age (Ericsson et al., 2001), though the specific behavioral mechanisms resulting in a decline in parental care remain unknown. Furthermore, previous maternal experience can influence investment independently of age, with costs of reproduction accumulating after multiple successive breeding attempts (Weladji et al., 2008; Moyes et al., 2011). In addition to intrinsic drivers, extrinsic variation can modulate investment through both annual (Lynch & Ennis, 1983) and seasonal ecological conditions (Fortuna et al., 2021; Plard et al., 2021). Thus, examining how behaviors vary across individual lifetimes and ecological conditions may reveal the mechanisms through which intrinsic and extrinsic variation translate into differences in reproductive performance.

In mammals, lactation is typically the most energetically costly period of investment, during which females expend substantial energy while continuously adjusting their resource allocation to offspring, making this period particularly sensitive to intrinsic and external conditions (Clutton-Brock et al., 1989). During the postnatal care period, maternal care directly impacts investment by facilitating energy allocation and offspring protection (Gittleman & Thompson, 1988). Because size at weaning is often a strong predictor of later-life success (Théoret-Gosselin et al., 2015), maternal effort during lactation can have substantial impacts on offspring fitness. Beyond energetic investment, maternal behaviors may buffer against environmental variability during lactation by providing protection from extrinsic disturbances (Grew et al., 2019). While postnatal maternal allocation has traditionally been assessed by

measuring offspring mass gain from birth to weaning (Gittleman & Thompson, 1988) or lactation duration (Dahle & Swenson, 2003; Huijsmans et al., 2024), fewer studies have examined how behaviors during this critical period shape investment outcomes.

Animals with capital breeding life history strategies rely on stored energy reserves accumulated prior to breeding and generally fast throughout lactation, resulting in brief but energetically costly periods of maternal investment with limited behavioral flexibility (Houston et al., 2007). Unlike income breeders that can compensate for variation in offspring demand through increased foraging effort (Stephens et al., 2014), even minor disruptions to maternal care in these systems may have cascading effects on offspring survival and lifetime reproductive success (Costa, 1993). Capital breeders therefore provide an ideal system for examining the consequences of postnatal maternal care because opportunities to compensate for disruptions are limited. One useful metric for detecting fine-scale changes in postnatal maternal behavior is mother-offspring association, which has previously been defined using spatial or social association between a mother and her offspring (Guinness et al., 1979; Holekamp et al., 1997; Szabo & Duffus, 2008). Because efficient energy transfer, protection from disturbance, and avoidance of prolonged separations require mothers and offspring to remain associated throughout lactation, mother-offspring association is likely an important behavioral dimension facilitating investment for capital breeders. However, the extent to which individuals vary in mother-offspring association, the factors driving its variation, and its consequences for offspring quality remain poorly understood.

Northern elephant seals (*Mirounga angustirostris*) are well-suited to quantify the drivers and consequences of mother-offspring association because previous work has documented both intrinsic and extrinsic drivers of reproductive performance and offspring quality. As extreme

capital breeders, maternal care is constrained to a short (<1 month) nursing period (Costa et al., 1986) during which females allocate substantial resources to a single pup while fasting on land (Ortiz et al., 1984). Since small reductions in energy transfer can decrease offspring condition and separations frequently result in pup mortality, maintaining association throughout lactation is likely a key factor in successfully weaning a pup (Riedman & Le Boeuf, 1982). Moreover, offspring with greater mass at weaning are more likely to survive to breeding age (Le Boeuf et al., 2019), suggesting that mother-offspring association may provide a mechanistic link between maternal behavior and offspring quality, and ultimately fitness. Previous work has shown that several metrics of reproductive success in elephant seals are shaped by both intrinsic and extrinsic factors. Offspring survival and weaning mass increase with maternal age until approximately 9 years old before declining in older females (Le Boeuf et al., 2019; Payne et al., 2025), while reproductive experience has also been shown to influence offspring quality independently of age due to factors such as recruitment age (Reiter & Le Boeuf, 1991) and skipped years of breeding (Huber, 1987). In addition to these maternal characteristics, environmental conditions such as local density and extreme wave events can disrupt mother-pup associations and increase pup mortality (Reiter et al., 1981; Riedman & Le Boeuf, 1982). Because studies using fine-scale observations are constrained by relatively short periods of data collection on a limited number of individuals (Le Boeuf et al., 1972; Riedman & Le Boeuf, 1982; Hooper et al., 2019) less is known about how behaviors mediating investment vary both within the lactation period and across individual lifetimes.

Our goal was to examine the influences of intrinsic and extrinsic mechanisms affecting mother-offspring association in a species with extreme lactation constraints. We used long-term near daily observational data on adult female northern elephant seals (Beltran et al., 2024) to

calculate mother-offspring association as the proportion of observation days a female was sighted with a pup during lactation. We first measured the correlation between mother-offspring association and offspring weaning mass. We hypothesized that weaning mass would increase with mother-offspring association, reflecting a mechanistic link from maternal behavior to energy allocation and offspring fitness (H1). We then examined intrinsic and extrinsic factors influencing mother-offspring association, including age, reproductive experience, breeding site crowding, and extreme environmental events (waves and tides). We hypothesized that mother-offspring association would increase with age (H2a) and previous pupping experience (H2b), as females grow larger and gain experience. We predicted that mother-offspring association would decrease with seal density, given the negative impact of population density on offspring weaning mass previously observed in this population (Holser et al., 2021) (H3a). Similarly, we hypothesized that mother-offspring association would decrease with environmental disturbances (the number of yearly extreme wave and tide events) (H3b). This framework allows us to evaluate a behavioral mechanism mediating offspring quality and the drivers of its variation.

METHODS

Study site and field methods

We studied the northern elephant seal population at Año Nuevo, California using three decades of near daily observations from a mark-recapture program (Le Boeuf et al., 2019). Each year, alphanumeric flipper tags were placed on 94–349 weaned pups, creating a cohort of known-age individuals that were subsequently followed across their lifetimes (Le Boeuf et al., 2019). During the breeding season (approximately from December 1 through March 15 each year (Le Boeuf et

al., 1972), we searched the beach for tagged individuals nearly every day, to estimate the day of arrival (from an at-sea foraging trip), birth, and departure (Beltran et al., 2024). We recorded each tagged female's unique tag number (AnimalID) (from which we could calculate her age), pup status (present = 1, absent = 0, unknown = NA) and colony location. At approximately 18 days post-parturition, we applied hair bleach to temporarily mark pups with a unique identifier to link them to their mothers. This marker allowed us to locate pups after weaning to attach a flipper tag and weigh them.

Quantification of mother-offspring association

Mother-offspring association was calculated as the proportion of days a mother was seen with one pup out of the total number of observation days post-birth in a given year. The pup's estimated birth date was defined as the first day a female was seen with a pup in the breeding season (Fig. 1a). To balance uncertainty in estimated birth dates with a robust sample across ages and years we included mother–pup pairs whose estimated pupping date was within 7 days of the previous sighting. Results were qualitatively unchanged when analyses were repeated using a more conservative 3-day criterion (Table S1). In a small number of cases (0.02% of all sightings), females were observed with multiple pups or had uncertain pup status. Because our aim was to measure the proportion of days the mother was seen with versus without a pup, we filtered observations to those where the mother had a pup status of either 0 or 1. We only included mother-pup pairs with at least 14 observation days after the estimated pup birth date, which is at least half of the average 26.8-day lactation period (Costa et al., 1986).

Offspring weaning mass

Offspring were weighed in the field using a canvas bag that was suspended from a scale on a tripod (Holser et al., 2021; Condit et al., 2024) within 0–71 days after weaning**.** We weighed offspring in all years except 2000 and 2009. We corrected weaning mass using the formula $M = M_0^{kt}$, where M is the corrected mass at weaning, M_0 is the observed mass, t is the number of days since weaning, and k = 0.00596 per day is the rate constant of mass loss (Le Boeuf & Crocker, 2005).

Seal density estimates

We divided the breeding area into 35 locations (Figure 4a). We assigned each seal to the location where she was observed for more than half of her total observations in a given breeding season. We only included adult females in the seal density estimates, because other ages and sexes move between locations much more than adult females (Reiter et al., 1981). If individuals were observed equally in multiple beach locations, we assigned the seal to the denser location. We estimated seal density for each location using imagery from annual UAS drone surveys conducted at peak breeding (January 26 to 31) when the density of seals is highest each year. We flew pre-programmed transects over the colony at an altitude of ~45 m, covering ~0.25 km^2 total area (Molly McEntee, Patrick Robinson, *personal communication*), to capture aerial photographs from directly above the seals and created georeferenced orthomosaics for each survey in Pix4Dmapper (v4.7, Pix4D SA). We identified seals in images using Picterra, a machine learning platform, with an image segmentation approach (see Infantes et al., 2022; Carroll et al., 2025) and created polygons covering the footprint area of each seal and assigned each seal an age class (adults and pups) and sex based on polygon area. Using the *sf* package in R (Pebesma & Bivand,

2023), we calculated seal density for each breeding location as the average number of adult females within a 10 m radius of each female's centroid.

Extreme wave and tide events

We extracted tide and wave data for each breeding season to examine the effects of environmental disturbance. Because mother-pup pairs are exposed to the tide line, high tides in conjunction with powerful waves during storms can result in separations. We obtained wave height and dominant period data from the National Data Buoy Center station 46042 from 1996-2023 (the buoy stopped transmitting after 2023) (National Data Buoy Center, 1996–2023). We obtained tide height data from National Oceanic and Atmospheric Administration water level records for the closest station (Monterey, 9413450) (National Oceanic and Atmospheric Administration, 1996–2023). Wave power was calculated using the simplified equation (Özger et al., 2004): wave power = 0.49 * wave height² * dominant wave period, where wave power is measured in kilowatts per meter of wave crest, wave height in meters, and dominant wave period in seconds. Wave and tide datasets were converted to UTC date and time and joined by exact date and hour. We defined an extreme wave and tide event as an hour with co-occurring wave and tide conditions exceeding the 90th percentile of observations across the full study period, corresponding to wave power ≥ 110.84 kW/m and tide height ≥ 5.03 ft. An extreme wave and tide event was therefore recorded when both thresholds were exceeded simultaneously.

Statistical Analyses

All models were fit with the *lme4* package (version 2.0-1, Bates et al., 2015) and model assumptions were checked using the *DHARMa* package (version 0.4.7, Hartig, 2016) in R version 4.3.3 (R Core Team, 2024).

i) Offspring fitness model

To examine the effects of mother-offspring association on offspring fitness, we used weaning mass as our response variable because it strongly predicts offspring survival and recruitment, which contributes to future lifetime reproductive success (Le Boeuf et al., 2019). Using data from 1996–2025, we fit a linear mixed effects model (LMM) to weaning mass with mother-offspring association and maternal age as predictors (n = 499 seal-year observations of 348 seals). Maternal age was included in this model to account for previously documented strong effects of maternal age on offspring weaning mass (Holser et al., 2021; Le Boeuf et al., 2019). Individual and year were included as random effects.

To interpret the biological effect of mother-offspring association on weaning mass, we compared the model-estimated effect of a 10% increase in mother-offspring association to a theoretical benchmark: the weaning mass change expected from a 10% reduction in total milk intake. We estimated the theoretical benchmark by integrating predicted milk intake across lactation (McHuron 2026), assuming linear pup growth from 40 kg at birth to 131.4 kg at weaning (Ortiz *et al.* 1984), and converting the milk intake to pup mass gain using a 66.7% milk retention efficiency (Ortiz *et al.* 1984).

ii) Mother-offspring association models

We estimated the effects of maternal age, pupping experience, seal density, and extreme wave and tide events on mother-offspring association using generalized linear mixed effects models (GLMMs) with a binomial distribution and logit link. Mother-offspring association was the response variable and each female-year observation was a data point. We included individual and year as random effects in all of the models to account for the non-independence of observations and variation between years.

We first fit a series of generalized linear mixed models (GLMMs) with mother-offspring association as the response using the full dataset from 1996–2025 (n = 936 seal-year observations of 565 seals). Following Payne et al. (2025), we fit a piecewise segmented regression model, and chose a threshold of 8 years old based on a comparison of threshold ages between 5 and 14 using Akaike's Information Criterion (Table S2). We then compared the results of the breakpoint model to a quadratic and linear model, of which the breakpoint model had the lowest Akaike's Information Criterion (AIC; Akaike, 1973; Table S3). The final model included a binary age variable known as "age class" that encoded whether seals were considered old (i.e. seals aged 8 and older) or young (i.e. seals younger than 8 years old), allowing the slope (coefficient) to vary before and after the age threshold (Payne et al., 2025). Numerical age was centered at the 8-year threshold (e.g., a 8 year old seal was coded as age = 0), so that the intercept represented the expected response at the threshold age while maintaining a continuous age effect (Berman et al., 2008; Tompkins & Anderson, 2019).

Maternal age and pupping experience were highly collinear (Pearson's $r = 0.91$, $p < 0.001$) and therefore were not included as predictors in the same models. We examined experience-related patterns using a separate model with the same structure as the age model (n = 936 seal-year observations of 565 seals). We evaluated the fit of the model for pupping experience for this dataset as before, with a breakpoint model that had the lowest AIC (Table S4) using a threshold at 5 previous pups (Table S5). See the supplementary material for sensitivity analyses evaluating alternative thresholds for age and experience (Fig. S4; Fig. S5).

Next, to examine extrinsic influences on mother-offspring association, we used the subset of years for which both seal density and wave and tide data were available (2016–2023; n = 293 seal-year observations of 188 seals). We fit two sets of models using data from 2016–2023: one

including maternal age, and the other including previous pupping experience. Both included seal density and the number of extreme wave and tide events. We compared threshold, linear, and quadratic forms for age and experience in these models based on thresholds derived from the full dataset. For both of these models, linear forms of age and experience were supported by AIC comparison (Table S6; Table S7).

RESULTS

Our selected sample from 1996–2025 included 565 individual adult female seals that were observed in one or more years for a total of 936 female-years collected across 16,895 re-sightings. Mean mother-offspring association high across the population (mean ± SD; 0.95 ± 0.13) and 68% (636 out of 936) of females were sighted with a pup during every lactation observation day (Fig. 1b).

Impact of mother-offspring association on offspring weaning mass

Weaning mass increased significantly with mother-offspring association and maternal age (Table S8; Fig. 2). An increase in mother-offspring association from 0.85 to 0.95 corresponded to an approximate 3.8 kg (95% CI: 1.3–6.3 kg) increase in weaning mass. In comparison, a theoretical 10% increase in milk intake across lactation was estimated to increase pup mass by 6.9 kg; our model's estimate represents roughly 55% of this benchmark.

Mother-offspring association exhibits a nonlinear relationship with maternal age and reproductive experience

Maternal age was a strong predictor of mother-offspring association. Mother-offspring association was lowest in the youngest seals, and increased from approximately 0.9 (95% CI:

0.86–0.93) at 3 years old to 0.97 (95% CI: 0.95–0.98) at the threshold age of 8 years after which it exhibited a slight non-significant decline among older seals (8–21; Table S9; Fig. 3a). Mother-offspring association also increased strongly for inexperienced seals, but in contrast to the maternal age model in the same years, mother-offspring association exhibited a significant decline with pupping experience after the threshold of 5 previous pups (Table S10; Fig. 3c). Predicted mother-offspring association increased from 0.93 (95% CI: 0.90–0.95 for first-time breeders to 0.97 (95% CI: 0.95–0.98) at the threshold of 5 previous pups, after which it declined to 0.92 (95% CI: 0.84–0.98) for females with 15 previous pups.

Intrinsic and extrinsic factors impact mother-offspring association from 2016–2023

In the subset model (2016–2023) including both age and extrinsic predictors, mother-offspring association increased with continuous maternal age (Table S11; Fig. 3b). Similarly to maternal age, mother-offspring association increased with pupping experience in the parallel 2016–2023 subset model (Table S12; Fig. 3d). Mother-offspring association decreased with both seal density and the number of annual extreme wave and tide events (Table S11; Table S12; Fig. 4b; Fig. 4c).

DISCUSSION

Our findings demonstrate that behavioral variation can provide insight into mechanisms underlying maternal investment that are not captured by reproductive outcomes alone. Our results indicate that mother-offspring association contributes significantly to weaning mass, and relatively small deviations in behavior corresponds to meaningful variation in offspring quality. The proportion of days a mother was observed with a pup increased with maternal age: youngest mothers had the lowest mother-offspring association, rapidly improving until a threshold of 8

years old, after which association remained consistently high in older mothers. Similarly, mother-offspring association improved up to a threshold of 5 previous births, but was followed by a decline consistent with experience-related senescence. Mother-offspring association was also lower for seals under higher seal density and extreme weather events. Taken together, these results provide evidence that mother-offspring association may be a key, understudied dimension underlying variation in reproductive success.

Mothers who were more frequently observed with a pup throughout lactation weaned heavier pups, supporting H1. Weaning mass has previously been identified as a strong predictor of first-year survival and subsequent fitness outcomes, such as probability of recruitment (McMahon et al., 2000; Le Boeuf et al., 2019). Therefore, even small deviations in maternal behavior during the lactation period can have profound implications for offspring fitness. Previous studies have shown that offspring weaning mass varies between individual mothers (Condit et al., 2024) and increases strongly with maternal age (Oosthuizen et al., 2015; Holser et al., 2021). We extend this work by providing evidence that mother-offspring association is a potential behavioral mechanism through which intrinsic variation shapes energy allocation and offspring outcomes. Consistent with impacts on offspring growth, our model-predicted 3.8 kg increase in weaning mass was approximately half of the 6.9 kg increase expected if a 10% increase in mother-offspring association translated proportionally into milk intake. This suggests mother-offspring association substantially contributes to investment, but that observations of mothers without pups do not necessarily represent complete losses of nursing. A plausible alternative is that mothers and pups may compensate for separation by increasing nursing frequency. Furthermore, our estimates of the effects of mother-offspring association on offspring outcomes are likely conservative because pups in poor condition (very small or injured) are less

likely to be selected for weighing. However, early offspring mortality is difficult to detect using the current mark-recapture dataset because pups are marked later in their lactation period to reduce disturbance during critical survival bottlenecks. Further research on the consequences of mother-offspring association for pup survival will require more fine-scale observations of pup separations and mortality.

The observed high population-level mother-offspring association suggests that opportunities for behavioral variation during lactation are strongly constrained in this system. This is consistent with the strong maternal attendance characteristic of fasting phocids, where females spend the majority of the brief lactation period in close proximity to their offspring, and prolonged mother-offspring separations can compromise pup survival (Costa & Maresh, 2022). Due to the extreme constraints of the lactation period in elephant seals, there may be greater capacity for behavioral flexibility in the choice of whether or not to produce a pup rather than how much to invest after lactation has begun. Consequently, individuals may instead exhibit greater plasticity in other reproductive traits that preclude reproductive allocation, such as skipped breeding, as an adaptive strategy for recovering physiologically after costly bouts of reproduction (Shaw & Levin, 2013; Griffen, 2018). Because mother-offspring association exhibits limited behavioral flexibility, the variation we detected may reflect constraints posed by intrinsic maternal limitations (i.e., inexperience in younger mothers) and environmental pressures, rather than mothers adjusting their investment during lactation.

A large body of research supports strong age-related maternal effects across species, which has important implications for the value of specific age classes to population growth (Kroeger et al., 2020). Our results support hypothesis H2a that young mothers strongly improve in mother-offspring association as they grow older, followed by a plateau in mothers above age 8

as they approach the mother-offspring association ceiling. Our evidence for an increase in mother-offspring association among younger seals aligns with previously described patterns of increasing offspring weaning mass and success as elephant seal mothers age (Le Boeuf et al., 2019), suggesting that improvements in association may represent one mechanism contributing to age-related variation in reproductive performance. Improvements in mother-offspring association for young and inexperienced mothers may reflect a combination of behavioral and physiological changes. For example, optimization of pupping location may confer areas with topographical advantages, such as lower tide exposure. Increased dominance or aggression among older mothers (Riedman & Le Boeuf, 1982; Sydeman et al., 1991) and larger body size may allow for these females to better maintain their position in a harem.

Despite high collinearity between maternal age and experience, individuals exhibit some variation in reproductive experience from what is expected for a directly proportional age-experience relationship (Fig. S1). We found that mother-offspring association increased with reproductive experience, supporting H2b, but found evidence for an experience-related decline in mother-offspring association after a threshold of 5 previous births. This decline may result from an inability to regain body condition or accumulation of stressors across multiple reproductive events, which suggests that skipped breeding may become increasingly beneficial for maximizing association to each pup, though it comes with the trade-off of not producing any offspring during that year. Distinguishing reproductive costs from compensatory breeding strategies remains an important area for future work.

Extrinsic conditions of the breeding site negatively influenced mother-offspring association, supporting H3a. The decrease in mother-offspring association with increasing location density suggests that local crowding of the breeding area imposes limitations on a

mother's ability to maintain association with her pup. High-density breeding locations may lower mother-offspring association through increased aggression from female or male seals which may result in separations or pups getting trampled (Riedman & Le Boeuf, 1982). Similar patterns have been detected in offspring weaning mass, which decreased under higher colony density on an annual basis for the population (Holser et al., 2021). Our results expand upon these results by further disentangling these effects by examining the influence of each mother's pupping site within the colony and support mother-offspring association as a potential mechanism underlying reductions in weaning mass in high colony density conditions.

Years with greater numbers of extreme wave and tide events were associated with reduced mother-offspring association, providing evidence for H3b. Extreme storm surge conditions may elevate the risk of pup drowning (Reiter et al., 1981), particularly when pups are young, thereby increasing separation or pup mortality. One of the worst years for mother-offspring association was 2023, which corresponded to a strong El Niño year, where the Año Nuevo colony was impacted by intense storms during early January, corresponding with a time when many pups were very small and vulnerable to drowning. Because extrinsic early-life conditions can influence an individual's fitness across their lifetime (Marshall et al., 2017), increasing local environmental variability may have consequences for offspring that extend beyond the breeding season. Our finding extends a growing body of literature suggesting that extreme weather events can have severe impacts on breeding outcomes across taxa by amplifying existing pressures (Sojitra et al., 2026). Furthermore, as the intensity and frequency of coastal storms are projected to increase with climate change (Dettinger, 2011; Huang & Swain, 2022), understanding how maternal behaviors respond to such disturbances may be critical for predicting their consequences for reproductive performance.

Several limitations should be considered when interpreting the drivers and consequences of mother-offspring association in this study. We could not always confidently assess that a pup sighted with a female was the female's biological offspring. While our analysis partially mitigated this limitation by selecting mother-offspring units with high resight detections, future studies integrating pedigree analyses with detailed behavioral observations could improve the identification of mother-pup pairs and enable more accurate monitoring throughout lactation. Furthermore, maternal behaviors that mediate offspring growth may occur simultaneously with physiological factors, such as fat content in the milk, which we were unable to measure. Future work that combines physiological measurements with long-term behavioral data can elucidate how these mechanisms jointly influence maternal allocation.

Long-term monitoring of known-age animals provides a rare opportunity to examine behavioral mechanisms underlying reproductive investment across an individual's lifetime and between years of varying environmental conditions. Our results demonstrate that mother-offspring association mediates postnatal maternal investment and exhibits biologically important variation. Although this extreme life-history strategy pushes mother-offspring association near its upper bound, intrinsic and extrinsic conditions drive predictable deviations from this apparent optimum. Younger mothers may be less able to buffer environmental disturbances, whereas older mothers maintain high mother-offspring association, which may confer resilience to environmental variability. In contrast, experience-related declines suggest that cumulative reproductive costs may eventually constrain a female's ability to sustain high investment. By disentangling the effects of age and experience, our findings highlight how learning, optimization, and reproductive costs shape behavioral investment across the lifespan.

By linking mother-offspring association to offspring fitness, we demonstrate that even highly constrained reproductive behaviors retain biologically meaningful variation and that fine-scale behavioral traits can provide insight into mechanisms linking maternal state, environmental conditions, and offspring quality. Similar age-dependent patterns in parental care and reproductive trade-offs have been documented across birds, mammals, and other long-lived taxa, suggesting that learning effects and costs of reproduction may be common features of investment, and behavioral mediators of such effects should be tested more broadly. Our findings suggest that important variation in maternal investment may be overlooked when reproductive outcomes alone are considered, highlighting the value of integrating behavioral and demographic perspectives. Understanding these behavioral mechanisms will become increasingly important for predicting how reproductive performance responds to increasing environmental variability and ultimately influences population resilience in long-lived species.

ETHICAL APPROVAL

All research activities were conducted under the National Marine Fisheries Service (NMFS) marine mammal permits (numbers: 786–1463, 87–143, 14636, 19108, 23188, and 28742). 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.

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FIGURES

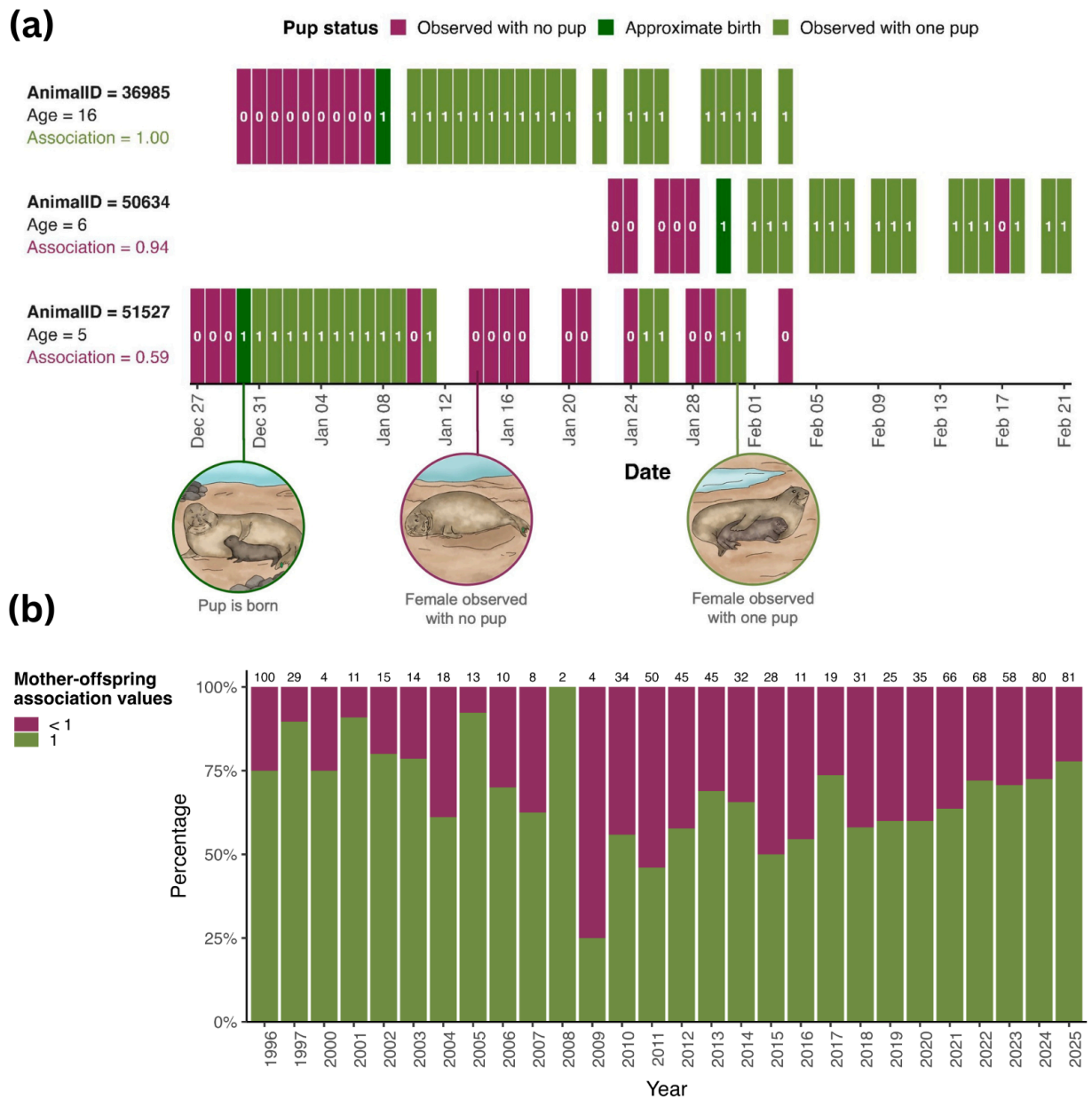

Figure 1. (a) Sample of breeding season observation data for three known-age adult female seals included in the study. Magenta boxes represent an observation with no pup (0), light green boxes represent an observation with a pup (1) and the dark green box represents the estimated birth date of the pup. Blank boxes indicate that the adult female was not observed on that day. **(b)** Distribution of mother-offspring association values across years. Stacked bars are colored by the

percentage of females with mother-offspring associations of exactly one (in green; every lactation observation was with a pup) versus females with mother-offspring associations below one (in magenta; seen at least once with no pup during lactation). Sample sizes for each year are included along the top axis. Illustrations by Harlow Knott.

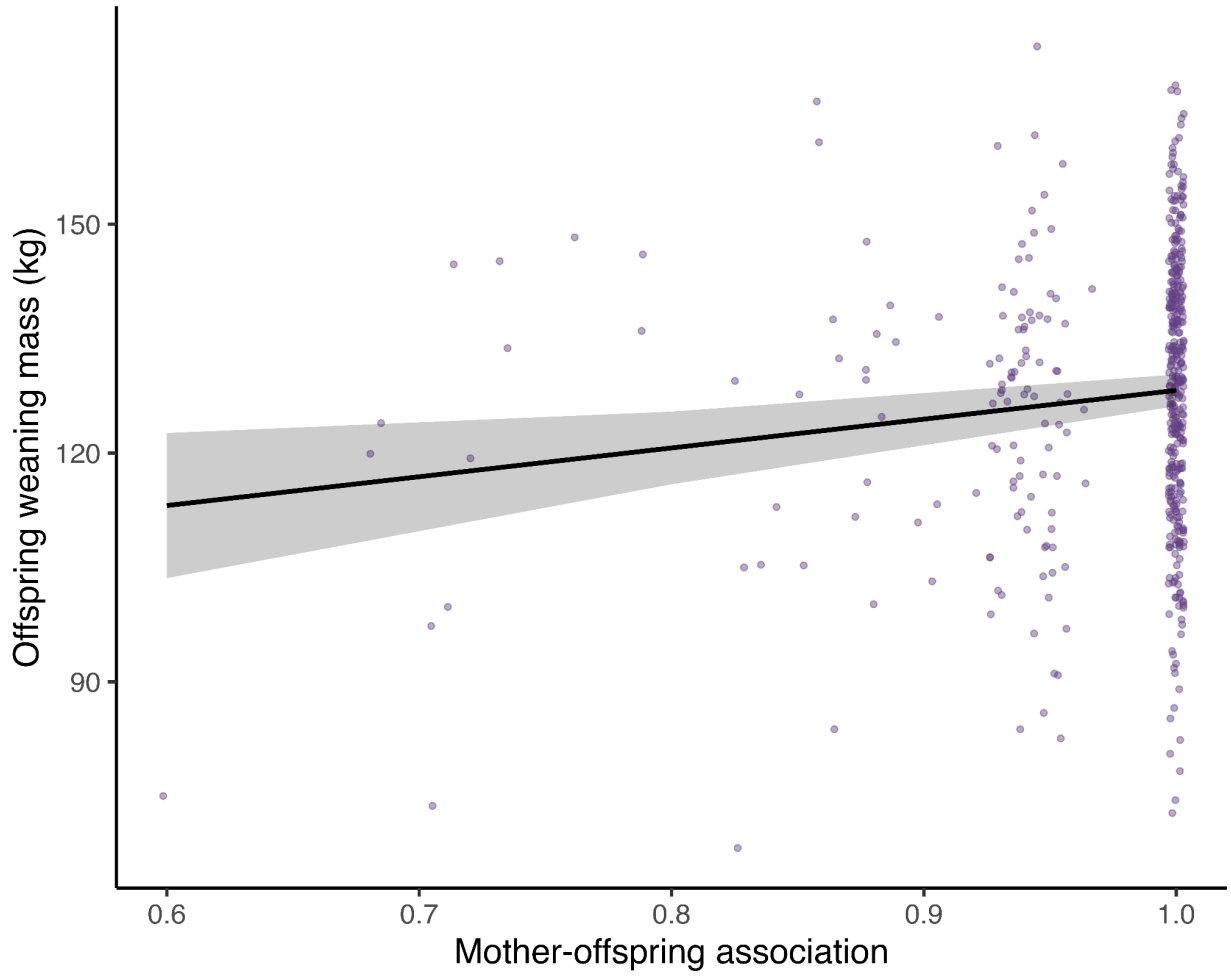

Figure 2. Weaning mass increased significantly with the proportion of the lactation period a mother was observed with a pup. Points represent individual observations, the solid line shows model-predicted weaning mass, and the shaded ribbon represents the 95% confidence interval of the fitted model.

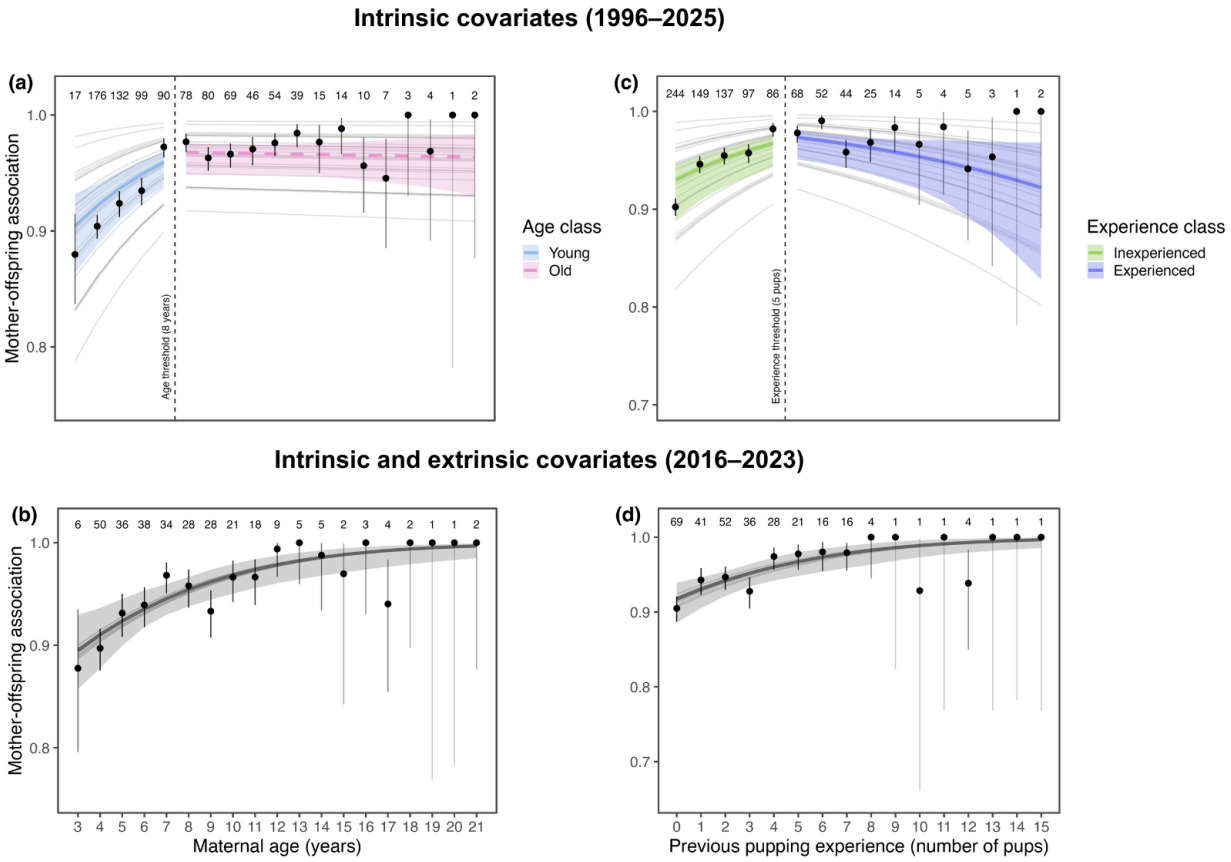

Figure 3. Mother-offspring association plotted against maternal age and experience for the age-specific and full-covariate models. **(a)** Mother-offspring association plotted against maternal age using the full dataset (1996–2025) with a segmented regression model, without environmental covariates. **(b)** mother-offspring association plotted against age (2016–2023) used in the models containing seal density and extreme wave and tide events. **(c)** Breakpoint effect of previous pupping experience on mother-offspring association from the full dataset (1996–2025) model and **(d)** continuous effect of previous pupping experience on mother-offspring association from the subset (2016–2023) model. Black points and error bars show the raw data mean and 95% CI of mother-offspring association for each age and experience level, respectively. Sample sizes for each age or experience level are included along the top axes. Thin grey lines show the

model-predicted responses for individual years. Thick lines show the post-stratified model-predicted mean response, obtained by varying the focal predictor (age or pupping experience) while retaining the observed values of all other model predictors, with solid lines representing significant results and dashed lines representing non-significant results. Shaded areas show the 95% confidence intervals from parametric bootstrapping.

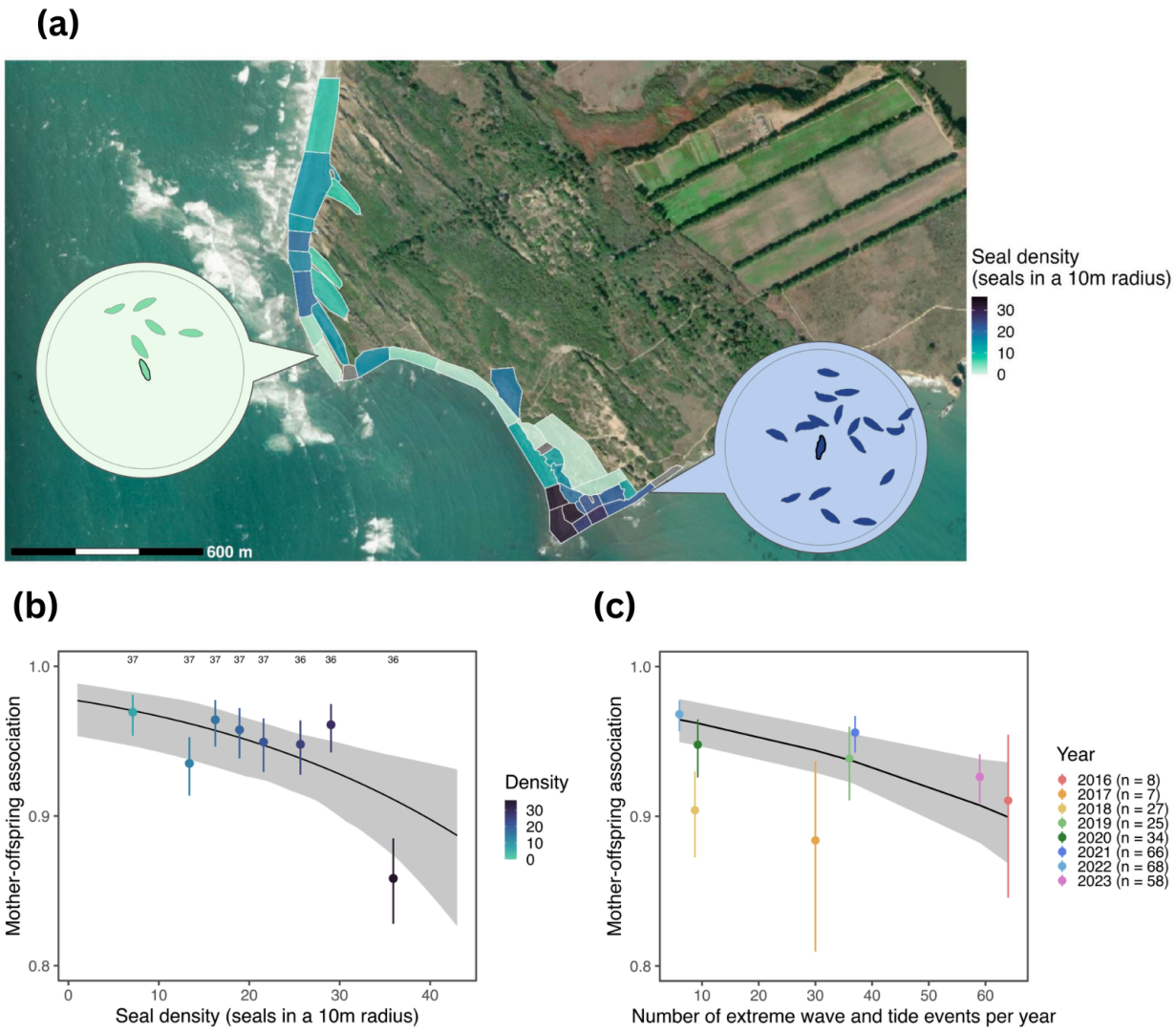

Figure 4. (a) Map of the divisions of the breeding area at Año Nuevo Reserve, with examples of the 10-m radius density count for a centroid seal in a high density location (dark blue) and a low

density location (light teal). The colony spans approximately 2 kilometers alongshore. **(b)** Mother-offspring association plotted against local seal density. Data from individual seal-years were binned into 8 groups for display. **(c)** Mother-offspring association plotted against the annual number of extreme wave and tide events. Data was binned by year. Point error bars show the observed mean and 95% binomial confidence intervals from the raw data. Thick solid lines show the post-stratified model-predicted mean response, generated by varying the focal predictor (density or extreme wave and tide events) while retaining the observed values of all other model predictors. Shaded areas show the 95% confidence intervals from parametric bootstrapping. See figures S2 and S3 for versions displaying the unbinned data.

SUPPLEMENTARY INFORMATION

Table S1. Model outputs for the sensitivity analyses using a more conservative pup birth date precision threshold (≤ 3 days). Results were qualitatively consistent with the primary analyses using a 7-day pupping date precision threshold.

Model	Predictor	Estimate	SE	Z	P-value
Weaning mass	Intercept	70.296	12.46	5.643	3.0×10^{-8}
	Mother-offspring association	35.996	12.84	2.804	0.0053
	Maternal age	2.734	0.24	11.391	1.0×10^{-26}
	Random effect: AnimalID	97.865			
	Random effect: Year	7.614			
	Random effect: Residual	160.621			
Maternal age, 1996–2025	Intercept	4.653	0.24	19.388	10.0×10^{-84}
	Maternal age : Pre-threshold (< 8 years)	2.798	0.49	5.716	1.0×10^{-8}
	Maternal age : Post-threshold (≥ 8 years)	-0.179	0.41	-0.439	0.6606
	Random effect: AnimalID	3.014			

	Random effect: Year	0.643			
Pupping experience, 1996–2025	Intercept	4.946	0.26	19.208	3.0×10^{-82}
	Previous pupping experience : Pre-threshold (< 5 previous pups)	2.539	0.41	6.228	5.0×10^{-10}
	Previous pupping experience : Post-threshold (≥ 5 previous pups)	-1.922	0.68	-2.835	0.0046
	Random effect: AnimalID	3.105			
	Random effect: Year	0.725			
Maternal age, 2016–2023	Intercept	4.811	0.57	8.428	4.0×10^{-17}
	Maternal age	0.19	0.05	3.582	3.0×10^{-4}
	Seal density	-0.064	0.01	-4.408	1.0×10^{-5}
	Number of extreme wave and tide events	-0.027	0.01	-3.67	2.0×10^{-4}
	Random effect: AnimalID	3.122			
	Random effect: Year	0.059			

Pupping experience, 2016–2023	Intercept	5.69	0.5	11.371	6.0×10^{-30}
	Previous pupping experience	0.209	0.06	3.259	0.0011
	Seal density	-0.064	0.01	-4.367	1.0×10^{-5}
	Number of extreme wave and tide events	-0.027	0.01	-3.494	5.0×10^{-4}
	Random effect: AnimalID	3.187			
	Random effect: Year	0.076			

Table S2. AIC comparison and weights for threshold ages 5-14 for the full dataset breakpoint model (1996–2025). The highest AIC weight among the threshold ages is bold.

Threshold ages	AIC	ΔAIC	AIC weight
5	2,552.1	11.33	0.002
6	2,551.8	11.01	0.002
7	2,545.0	4.26	0.054
8	**2,540.7**	**0.00**	**0.452**
9	2,541.6	0.83	0.298
10	2,544.1	3.33	0.086
11	2,547.0	6.23	0.020
12	2,547.1	6.34	0.019
13	2,545.8	5.09	0.036
14	2,546.1	5.31	0.032

Table S3. AIC comparison between linear, quadratic, and threshold age predictors for the full dataset model (1996–2025).

Model	AIC	ΔAIC	AIC weight
Threshold	**2,723.8**	**0.00**	**0.733**
Quadratic	2,725.9	2.02	0.267
Linear	2,740.7	16.83	0.000

Table S4. AIC comparison between linear, quadratic, and threshold pupping experience predictors for the full dataset model (1996–2025).

Model	AIC	ΔAIC	AIC weight
Threshold	**2,545.2**	**0.00**	**0.981**
Quadratic	2,553.1	7.86	0.019
Linear	2,561.9	16.69	0.000

Table S5. AIC comparison and weights for threshold experience levels of 1-11 for the full dataset breakpoint model (1996–2025). The highest AIC weight among the threshold experience levels is bold.

Threshold experience levels	AIC	ΔAIC	AIC weight
1	2,554.8	9.54	0.005
2	2,556.3	11.06	0.002
3	2,554.7	9.47	0.005
4	2,546.3	1.04	0.351
5	**2,545.2**	**0.00**	**0.590**
6	2,550.4	5.14	0.045
7	2,560.5	15.31	0.000
8	2,560.7	15.47	0.000
9	2,560.8	15.58	0.000
10	2,562.4	17.20	0.000
11	2,563.3	18.03	0.000

Table S6. AIC comparison between linear, quadratic, and threshold age predictors for the subset dataset model (2016–2023).

Model	AIC	ΔAIC	AIC weight
Linear	**780.3**	**0.00**	**0.554**
Quadratic	782.0	1.70	0.237
Threshold	782.3	1.94	0.210

Table S7. AIC comparison between linear, quadratic, and threshold pupping experience predictors for the subset model (2016–2023).

Model	AIC	ΔAIC	AIC weight
Linear	**784.7**	**0.00**	**0.564**
Quadratic	786.6	1.88	0.221
Threshold	786.7	1.93	0.215

Table S8. Fitted model (LMM) output for the effects of maternal age and mother-offspring association on offspring weaning mass.

Predictor	Estimate	SE	Z	P-value
Intercept	70.924	12.28	5.776	1.0×10^{-8}
Mother-offspring association	37.758	12.65	2.985	0.0030
Maternal age	2.439	0.22	10.978	3.0×10^{-25}
Random effect: AnimalID	94.456			
Random effect: Year	6.764			
Random effect: Residual	161.648			

Table S9. Fitted model (GLMM) output from the 1996–2025 piecewise segmented regression for maternal age.

Predictor	Estimate	SE	Z	P-value
Intercept	4.67	0.24	19.868	8.0×10^{-88}
Maternal age : Pre-threshold (< 8 years)	2.803	0.48	5.887	4.0×10^{-9}
Maternal age : Post-threshold (≥ 8 years)	-0.111	0.38	-0.289	0.7727
Random effect: AnimalID	2.981			
Random effect: Year	0.623			

Table S10. Fitted model (GLMM) output from the 1996–2025 piecewise segmented regression for previous pupping experience.

Predictor	Estimate	SE	Z	P-value
Intercept	4.916	0.25	19.586	2.0×10^{-85}
Previous pupping experience : Pre-threshold (< 5 previous pups)	2.419	0.4	6.12	9.0×10^{-10}
Previous pupping experience : Post-threshold (≥ 5 previous pups)	-1.35	0.62	-2.187	0.0288
Random effect: AnimalID	3.053			
Random effect: Year	0.706			

Table S11. Fitted model (GLMM) output from the 2016–2023 model with maternal age.

Predictor	Estimate	SE	Z	P-value
Intercept	4.174	0.49	8.446	3.0×10^{-17}
Maternal age	0.231	0.05	4.408	1.0×10^{-5}
Seal density	-0.05	0.01	-3.718	2.0×10^{-4}
Number of extreme wave and tide events	-0.025	0.01	-4.075	5.0×10^{-5}
Random effect: AnimalID	3.01			
Random effect: Year	0.019			

Table S12. Fitted model (GLMM) output from the 2016–2023 model with previous pupping experience.

Predictor	Estimate	SE	Z	P-value
Intercept	5.199	0.44	11.913	1.0×10^{-32}
Previous pupping experience	0.248	0.06	3.919	9.0×10^{-5}
Seal density	-0.049	0.01	-3.579	3.0×10^{-4}
Number of extreme wave and tide events	-0.025	0.01	-3.785	2.0×10^{-4}
Random effect: AnimalID	3.05			
Random effect: Year	0.034			

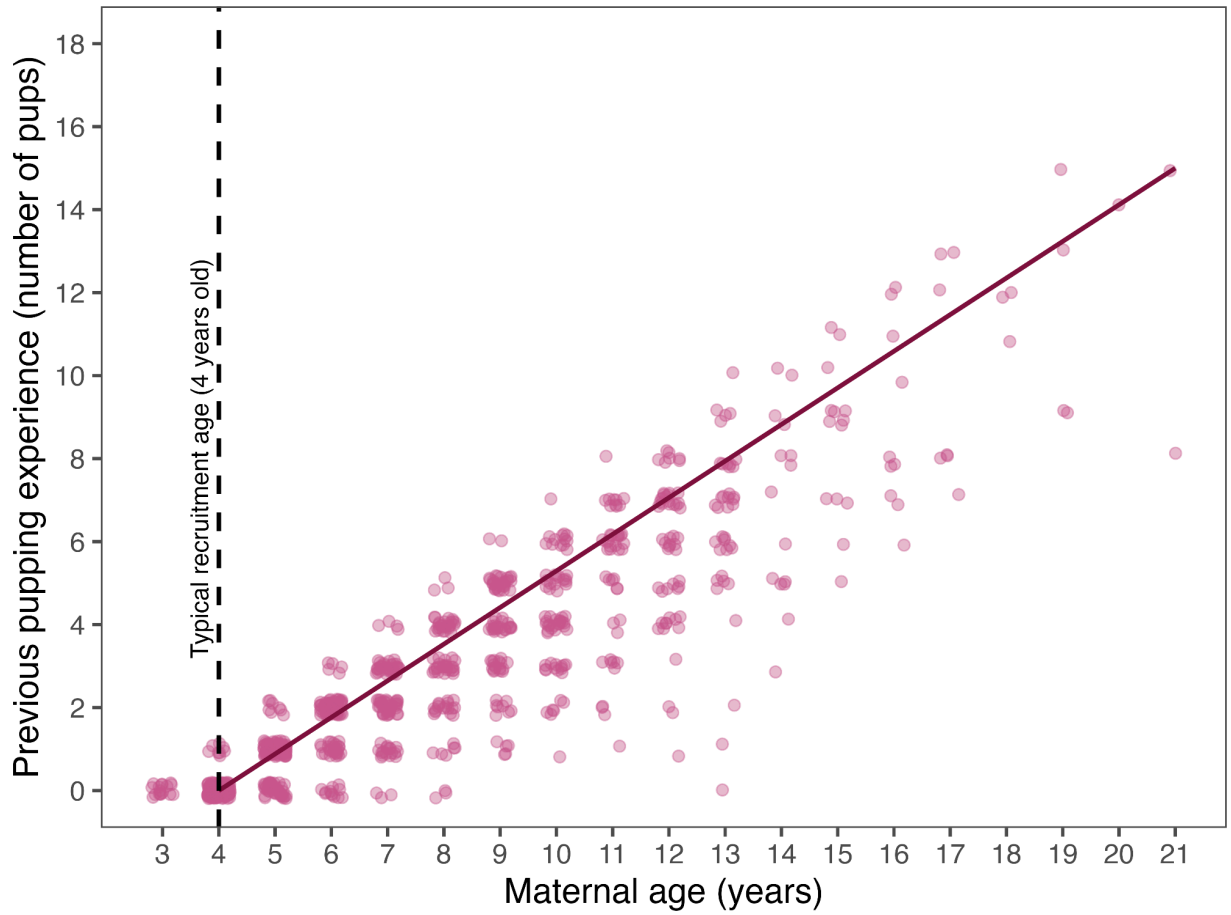

Figure S1. Females vary substantially in previous pupping experience within each age, despite a high correlation coefficient of 0.91. Each point represents the cumulative number of previous pups for an individual female at a given age. The typical recruitment age is represented by a vertical dashed line at age 4. The solid line represents the expected reproductive experience trajectory for a female that recruits at age 4 and produces a pup every subsequent year.

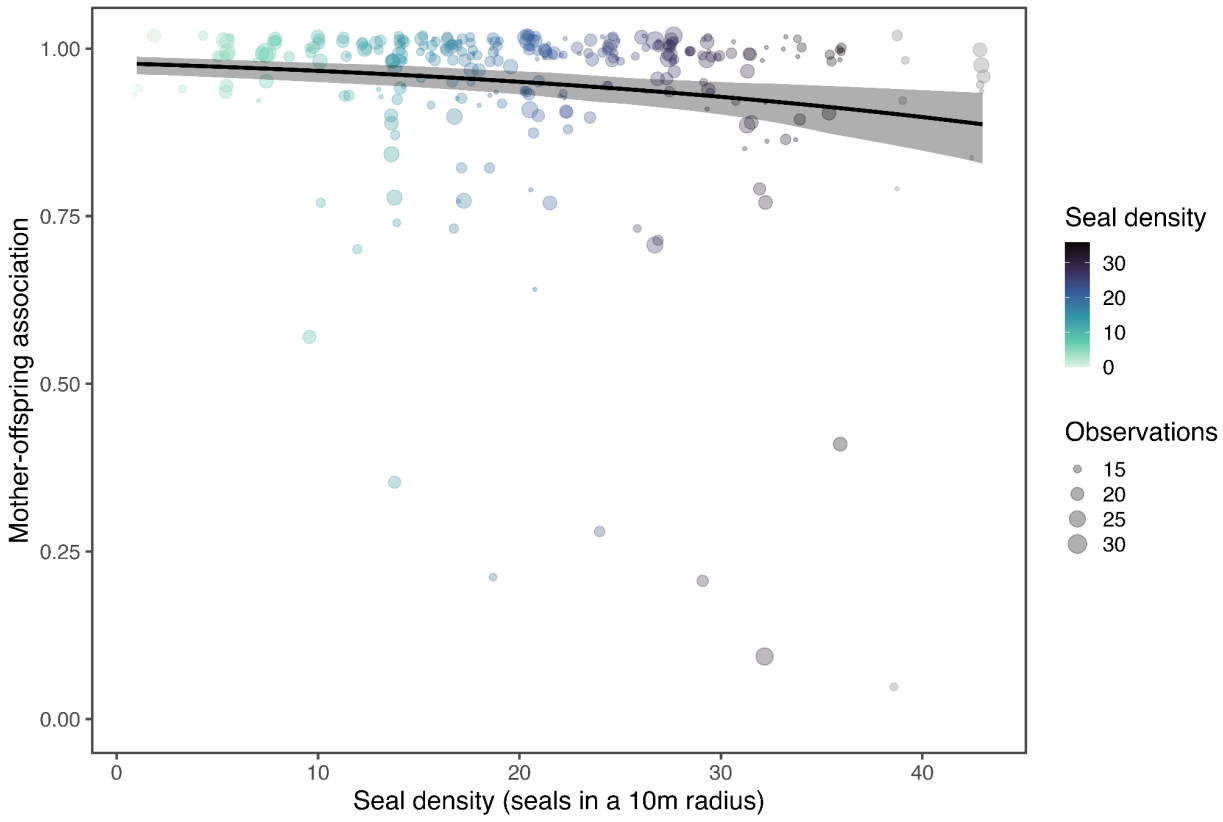

Figure S2. Unbinned version of Figure 4b, with mother-offspring association plotted against local seal density. Each point represents an individual seal, with point sizes weighted by total resight observations.

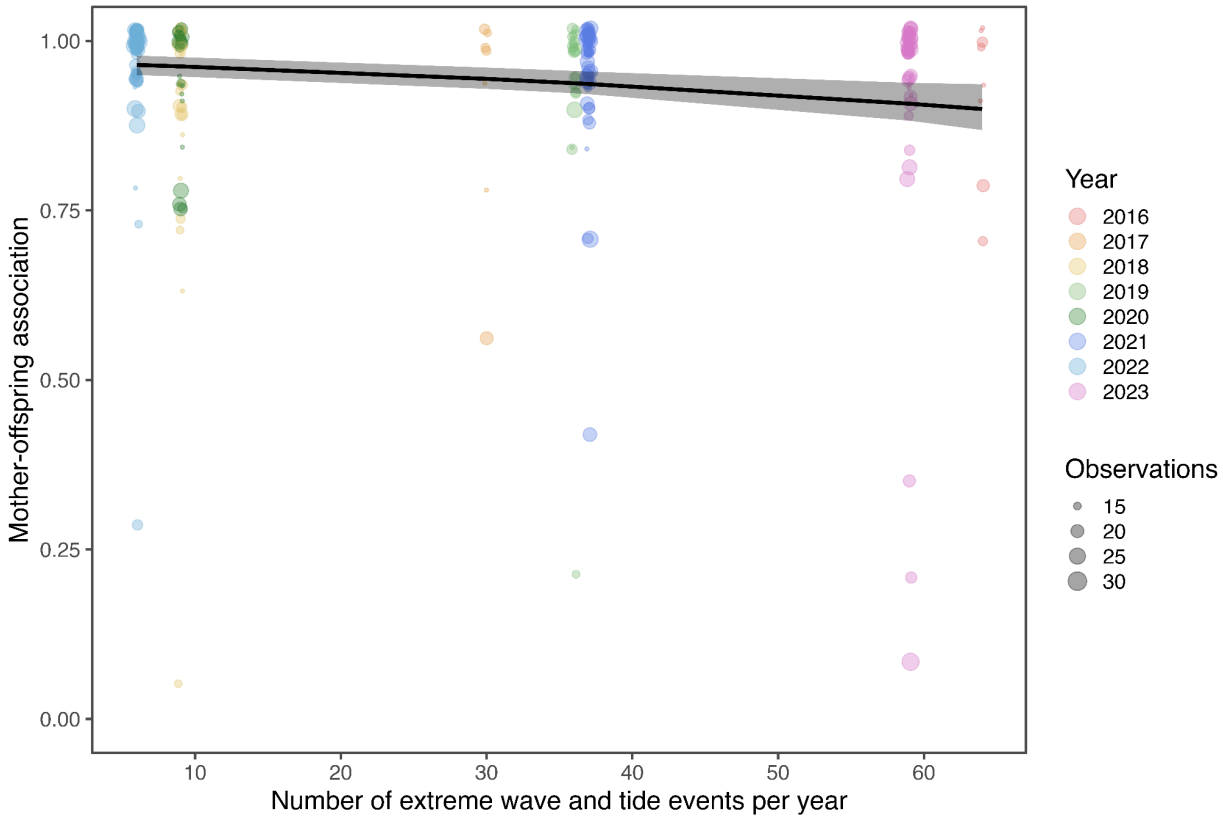

Figure S3. Unbinned version of Figure 4c, with mother-offspring association plotted against the number of extreme wave and tide events per year. Each point represents an individual seal, with point sizes weighted by total resight observations.

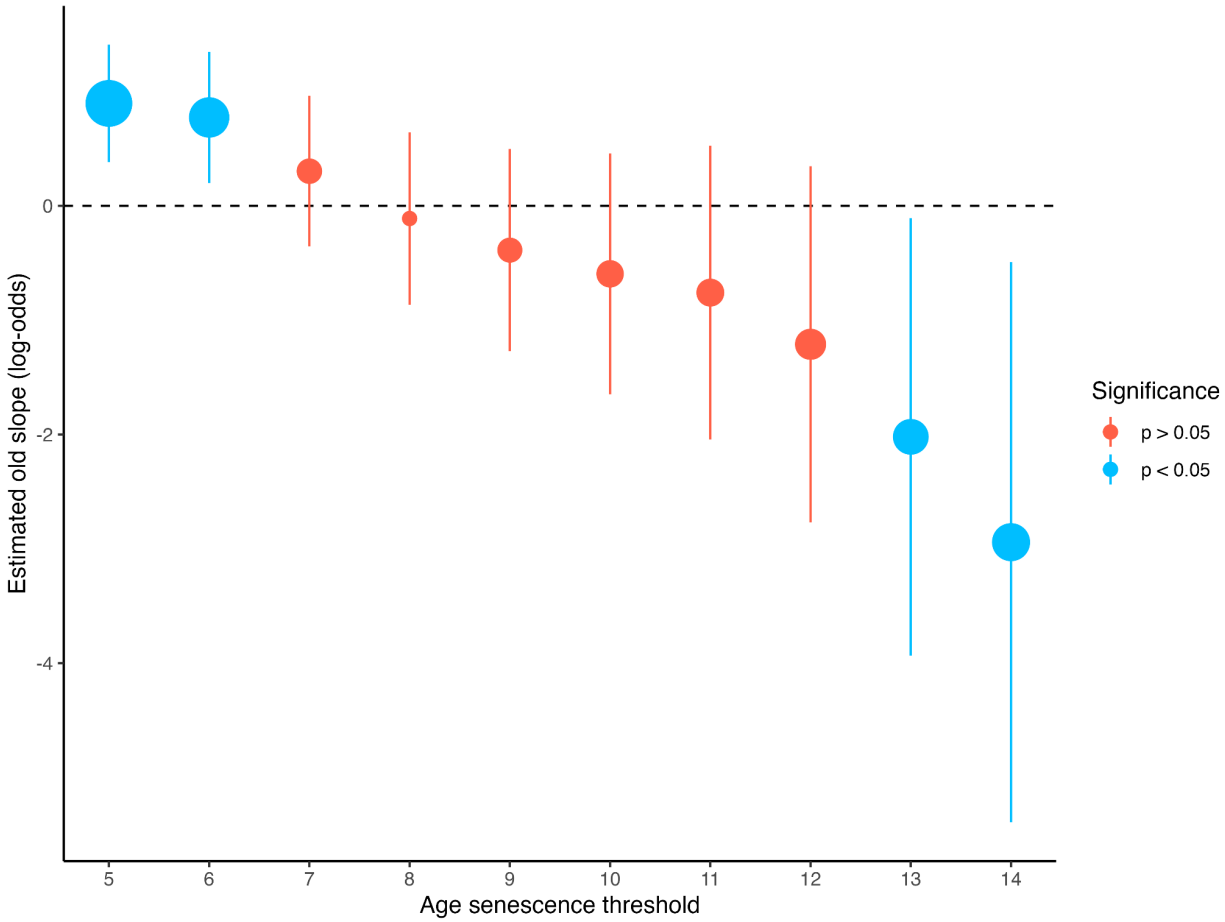

Figure S4. Coefficients for analyses with different threshold age breakpoints on a log scale. Threshold ages were fit to the model with the most data, from 1996–2025. The threshold age for the breakpoint is on the x-axis, and the coefficient of slope post-threshold (age class = old) is on the y-axis. Points represent p-values scaled by size, and CI ranges include the standard error, with significant results as blue points. A coefficient of zero is indicated by a dashed horizontal line. Only thresholds after age 12 showed significant senescence slopes.

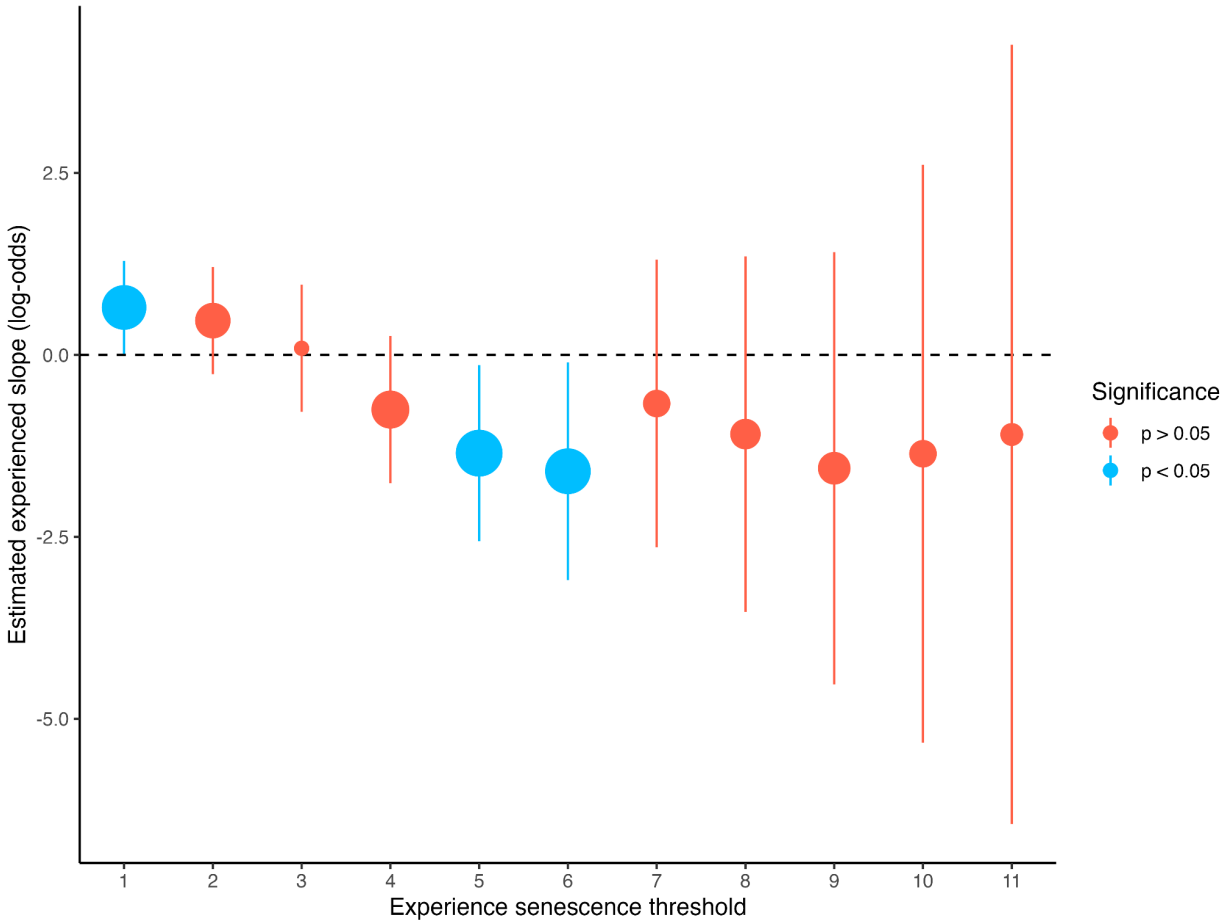

Figure S5. Coefficients for analyses with different threshold experience breakpoints on a log scale. Threshold experience levels were fit to the model with the most data, from 1996–2025. The threshold experience level for the breakpoint is on the x-axis, and the coefficient of slope post-threshold (experience class = experienced) is on the y-axis. Points represent p-values scaled by size, and CI ranges include the standard error, with significant results as blue points. A coefficient of zero is indicated by a dashed horizontal line.