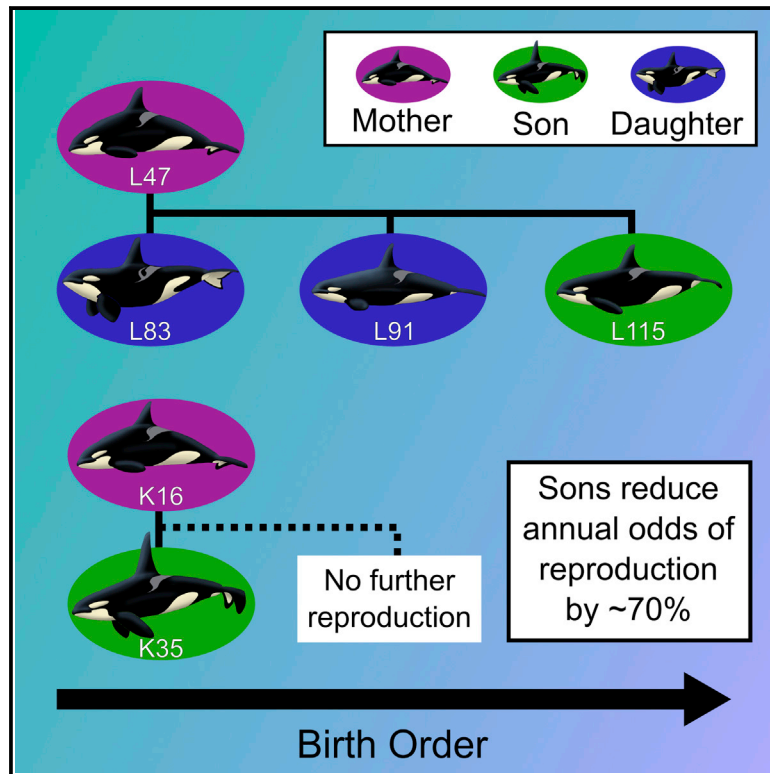# Costly lifetime maternal investment in killer whales

Graphical abstract

Authors

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In brief

Killer whale mothers are known to provide survival benefits to their adult offspring, especially their sons. Weiss et al. show that providing these benefits comes at a significant reproductive cost to mothers. These costs imply lifetime parental investment in killer whales, an extreme and unique life history strategy.

Highlights

- Providing care to weaned sons reduces female killer whales' reproductive output

- These effects cannot be explained by lactation costs or group composition

- Sons do not become less costly as they grow older

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Report

Costly lifetime maternal investment in killer whales

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SUMMARY

Parents often sacrifice their own future reproductive success to boost the survival of their offspring, a phenomenon referred to as parental investment. In several social mammals, mothers continue to improve the survival of their offspring well into adulthood;[1–5] however, whether this extended care comes at a reproductive costs to mothers, and therefore represents maternal investment, is not well understood. We tested whether lifetime maternal care is a form of parental investment in fish-eating "resident" killer whales. Adult killer whales, particularly males, are known to receive survival benefits from their mothers;[3] however, whether this comes at a cost to mothers' reproductive success is not known. Using multiple decades of complete census data from the "southern resident" population, we found a strong negative correlation between females' number of surviving weaned sons and their annual probability of producing a viable calf. This negative effect did not attenuate as sons grew older, and the cost of sons could not be explained by long-term costs of lactation or group composition effects, supporting the hypothesis that caring for adult sons is reproductively costly. This is the first direct evidence of lifetime maternal investment in an iteroparous animal, revealing a previously unknown life history strategy.

RESULTS AND DISCUSSION

Periods of parental investment, in which parents sacrifice future reproduction to improve the survival of their offspring, are a fundamental feature of animal life histories.[6,7] In some species, offspring continue to gain survival benefits from maternal presence long after weaning, and sometimes for their entire lives,[1–5] indicating extended and potentially lifelong maternal care. Whether this lifetime care represents a form of parental investment is poorly understood, as the costs (or lack thereof) of this care to mothers' future reproductive success are rarely quantified. In primates, including humans, it is generally thought that long term mother-offspring bonds provide mutual benefits, shortening maternal inter-birth intervals,[8] increasing maternal survival,[9] or boosting the survival of younger siblings,[8,10,11] and thus may represent maternal care, but not necessarily investment.[12] A lack of data on the reproductive costs or benefits of extended maternal care in other taxa hampers our understanding of how this life history strategy evolved.

Fish-eating "resident" killer whales (*Orcinus orca*) exhibit an extreme example of extended maternal care. In these populations, maternal presence enhances survival across the lifespan, particularly for males.[3] These benefits are likely derived at least in part from maternal ecological knowledge and leadership during foraging[13] and directed food sharing.[14,15] Although the survival benefits that mothers provide their offspring in this system are well-established, it is not known whether this behavior is reproductively costly to mothers. If females pay no reproductive cost to help their offspring, then this relationship may be similar to the mutualistic relationships found between mothers and adult offspring in some primate societies.[12] However, if lifetime care for offspring does impose reproductive costs on mothers, then this relationship would be an example of lifetime maternal investment, a strategy not yet documented in iteroparous animals.

We investigated the costs of lifetime maternal care in killer whales using a long-term study of the "southern resident" population, consisting of a complete census of the population every year since 1976. We predicted that females with more surviving, weaned offspring would be less likely to successfully reproduce in a given year, and that these effects would be larger when those offspring were male, as mothers preferentially support male offspring.[3] We further hypothesized that these effects would be independent of sons' age, reflecting males' lifelong dependence on their mothers.

We collated data on known-aged southern resident females (n = 40) from 1982 until 2021. After excluding whale-years in which
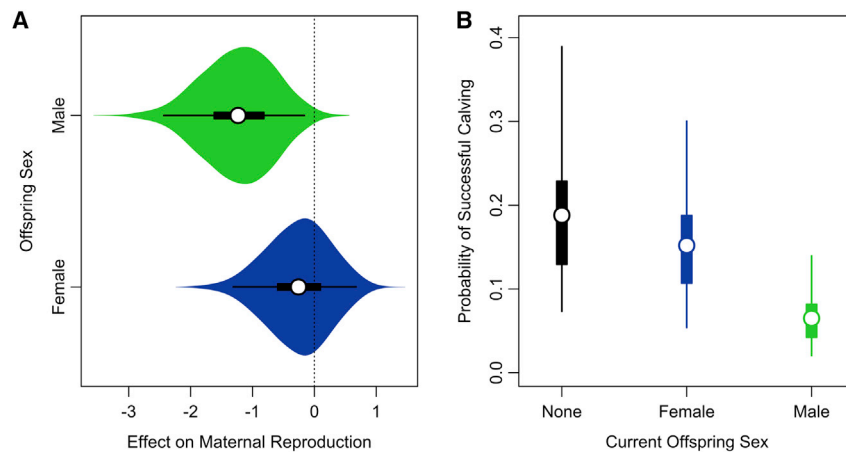
Figure 1. Male killer whales impose reproductive costs on their mothers

(A) Posterior distributions of male (green) and female (blue) offspring effects on maternal reproductive success. Violins indicate densities, thin and wide rectangles represent 50% and 95% credible intervals, respectively, and points indicate posterior mean estimates. Note that the effects are in logit space, and thus indicate an effect on females' annual log-odds of successful calving.

(B) Posterior conditional effects of male and female offspring on maternal annual recruitment probability. Points indicate the predicted probability of success for hypothetical 21-year-old females with, from left to right, no offspring, a single weaned daughter, or a single weaned son. Error bars indicate 50% and 95% credible intervals as in (A).

females could not have reproduced (see STAR Methods for details), our dataset contained 636 whale-years and 67 documented births. Due to high neonate mortality in this population,[16] we considered a birth "successful" if the calf survived its first year of life. Of the 67 births, 54 calves survived their first year and were therefore considered cases of successful reproduction.

We analyzed the costs of caring for weaned offspring using Bayesian logistic regression models. These models all had a Bernoulli error structure, predicting whether females successfully reproduced in a given year. All models included terms accounting for age-specific reproductive output, individual-level variation, across-year trends, and within-year correlations (see STAR Methods for details).

Sons, but not daughters, reduce their mother's subsequent reproductive success

Our first model (Model 1) tested whether male and female offspring reduced their mother's future reproductive success. In addition to the terms outlined above, we included females' number of surviving weaned sons and daughters in each year as predictors in the model. We found strong statistical evidence that sons imposed biologically significant reproductive costs ($\beta_{\text{sons}} = -1.23 \pm 0.59$, 95% CI = [$-2.44$, -0.16], posterior P($\beta_{\text{sons}} < 0$) = 0.99, Figure 1). In contrast, we did not find evidence that daughters influenced their mothers' reproductive success ($\beta_{\text{daughters}} = -0.26 \pm 0.52$, 95% CI = [$-1.32$, 0.68], posterior P($\beta_{\text{daughters}} < 0$) = 0.67, Figure 1). Contrast analysis provided clear evidence that the effect of sons was more negative than the effect of daughters ($\beta_{\text{sons}} - \beta_{\text{daughters}} = -0.98 \pm 0.49$, 95% CI = [$-2.00$, -0.05], posterior P($\beta_{\text{sons}} < \beta_{\text{daughters}}$) = 0.98).

The effect of sons cannot be explained by lactation costs or group composition

We considered two processes that could lead to the apparent costs of sons without continued maternal investment. First, correlations between number of surviving sons and reproductive output could arise if male group members are generally costly. This is particularly probable as males have greater energetic requirements[17] and are less likely to perform cooperative behaviors.[13,15] Second, raising an offspring to weaning is itself

energetically costly, and females may bias this early investment towards sons. If this early investment has long-term consequences, this could generate a negative correlation between females' number of sons and annual reproductive success, even in the absence of continued investment. To examine these possibilities, we fit a model (Model 2) including the number of surviving sons, the number of sons previously weaned but no longer alive, and the number of other weaned males in each females' matriline as predictors of annual reproductive success. Surviving sons were once again found to have a negative effect on maternal reproduction, without any reduction in effect size from Model 1 ($\beta_{\text{sons}} = -1.09 \pm 0.49$, 95% CI = [$-2.12$, -0.21], posterior P($\beta_{\text{sons}} < 0$) = 0.99). In contrast, sons that were no longer alive had no clear impact on reproduction, with a small and uncertain positive estimated effect ($\beta_{\text{dead}} = 0.09 \pm 0.86$, 95% CI = [$-1.77$, 1.64], posterior P($\beta_{\text{dead}} < 0$) = 0.44). Similarly, we found no clear effect of non-son male group members on female reproduction ($\beta_{\text{group}} = 0.10 \pm 0.23$, 95% CI = [$-0.35$, 0.57], posterior P($\beta_{\text{group}} < 0$) = 0.33). Though the estimated effect of dead sons had high variance, there was still moderately strong evidence that surviving sons had a more negative effect than dead sons ($\beta_{\text{sons}} - \beta_{\text{dead}} = -1.18 \pm 0.92$, 95% CI = [$-2.94$, 0.72], posterior P($\beta_{\text{sons}} < \beta_{\text{dead}}$) = 0.90). There was also very strong evidence that the effect of sons was stronger than that of other male group members ($\beta_{\text{sons}} - \beta_{\text{group}} = -1.19 \pm 0.57$, 95% CI = [$-2.38$, -0.19], posterior P($\beta_{\text{sons}} < \beta_{\text{group}}$) = 0.99).

Sons do not become less costly with age

We next sought to establish whether sons remain costly throughout their lives, or if these costs diminish as they grew older. If the latter were the case, it would indicate extended, but not lifelong, maternal investment. To examine this, we fit a model (Model 3) which allowed the effect that males exerted on their mothers' reproductive success to vary with age, while accounting for mothers' age-specific reproductive rates (see STAR Methods). We found no evidence that sons became less costly as they grew older ($\beta_{\text{son age}} = -0.04 \pm 0.07$, 95% CI = [$-0.18$, 0.07], posterior P($\beta_{\text{son age}} > 0$) = 0.28) and the model posterior indicated males were consistently costly regardless of age (Figure 2).
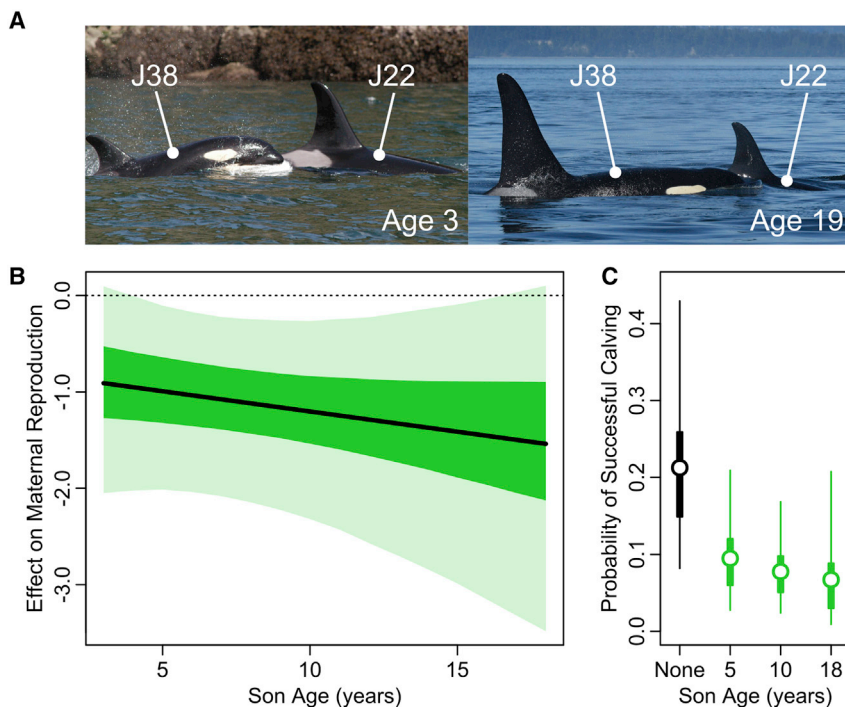
A

B

C

Figure 2. Sons do not become less costly with age

(A) Males maintain lifelong close associations with mothers, even as they reach physical maturity. Photographs show female J22 associating with son J38 (born 2003) when J38 was 3 and 19 years old. Photographs by D.K.E.

(B) Estimated relationship between son age and effect on maternal reproduction. Black line indicates posterior mean, and light and dark shading indicates 95% and 50% credible intervals. Dotted line indicates an effect of zero. Note that the effects are in logit space, and thus indicate an effect on females' log-odds of successful calving.

(C) Posterior conditional effects of sons of different ages on maternal reproduction. Posterior estimates are the estimated annual recruitment probabilities for a hypothetical 30-year-old female with, from left to right, no sons, a single 5-year-old son, a single 10-year-old son, and a single 18-year-old son. Points indicate posterior means, while thick and thin error bars indicate 50% and 95% credible intervals, respectively.

DISCUSSION

Our analysis demonstrates that the long-term survival benefits that southern resident killer whale females provide to their sons come at a significant cost to their own reproductive success. To our knowledge, this is the first direct evidence of lifetime maternal investment in any iteroparous animal.

Our results align with theoretical predictions of maternal investment and life history in species with bisexual philopatry and out-group mating. In killer whales, daughters reproduce within their mother's group, which can potentially lead to reproductive conflict that is costly for the older generation female.[18] In contrast, the offspring of sons will typically be born in other matrilines (although rare cases of within-matriline mating have been recorded), where they are less likely to compete with the male's mother or her kin.[19] Theory therefore predicts that, when help can be directed to particular offspring, females should preferentially provision sons.[20] The indirect fitness benefits of boosting adult son survival likely contribute to selection for longer lifespans in female killer whales, while late-life reproductive conflict with daughters exerts selective pressure against extended reproductive lifespans.[3,18] Our results expand this picture of killer whale life history evolution, suggesting that the indirect benefits of improving sons' survival are significant enough to outweigh substantial costs to females' reproductive success across their lifespan.

Although our analysis cannot disentangle the precise mechanisms underlying females' reduced reproduction while caring for sons, we hypothesize that this pattern is at least in part driven by the costs of provisioning sons through directed prey sharing. Female reproductive success in this population is highly dependent on prey availability[21] and females' nutritional state,[22] and thus reductions in food intake due to prey sharing are likely to have significant impacts on females' reproductive success. The role of resource availability and maternal condition in determining levels of maternal investment across offspring's lifespans could be further explored by analysis of individual body condition and physiology,[22,23] as well as comparison to other populations, particularly the nearby "northern" resident community and the sympatric Bigg's (formerly "transient") killer whale population. These populations have similar life history to the southern residents[24] but are less resource limited. Such analyses could test whether predictions from theoretical models of maternal condition and sex-biased maternal investment hold true for the extreme case of lifetime investment.[25]

The southern resident killer whales have been in decline since the early 1990s, with 73 individuals alive at the time of writing. The effects we report here could have important implications for population-level reproductive rates. Specifically, if a large portion of reproductive-aged females have one or more surviving sons, we would expect the population's reproductive capacity to be reduced. Through the last 5 decades, the portion of potentially reproductive females with at least one son has varied from less than 30% to nearly 80%, with 63% of potentially reproductive females having sons as of the beginning of 2022. Future work should investigate whether these patterns may have contributed to past demographic trends, and whether these effects may have implications for future population viability.

Because intense investment in sons is predicted for systems with bisexual philopatry and primarily out-group mating, we predict that lifetime investment may occur in other toothed whales with similar demographic patterns to resident killer whales, such as pilot whales (*Globicephala* spp.)[26–28] and false killer whales (*Pseudorca crassidens*),[29] as well as other killer whale

populations. In addition to having similar demography, these species, like resident killer whales, exhibit significant sexual size dimorphism,[30] which may contribute to selection for greater maternal investment in sons to meet males' higher energetic requirements. Studies of these species' life histories should seek to not only establish whether females boost the survival of their mature offspring, but whether females pay a reproductive cost to do so. Further work in other species where mature offspring are known to benefit from maternal presence should similarly analyze the reproductive costs mothers pay to provide this care. Data on the taxonomic and ecological distribution of lifetime maternal investment will be crucial to understanding the evolution of this extreme life history strategy.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.12.057.

AUTHOR CONTRIBUTIONS

M.N.W., D.P.C., and D.K.E. conceived of the project. M.N.W. conducted statistical analysis, with input from D.W.F., S.E., and D.P.C.. Field work was conducted by K.C.B., D.K.E., M.N.W., and M.L.K.N. M.N.W. drafted the initial version of the manuscript, and all authors contributed to subsequent drafts. Funding was acquired by D.P.C., D.W.F., M.A.C., R.A.J., S.E., and K.C.B.

DECLARATION OF INTERESTS

The authors declare they have no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in their field of research or within their geographical location. One or more of the authors of this paper self-identifies as living with a disability. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw data	This paper	https://doi.org/10.5281/zenodo.7457806
Software and algorithms		
R	R Core Team[31]	www.r-project.org
Brms	Burkner et al.[32]	https://cran.r-project.org/web/packages/brms/
Rstan	Stan Development Team[33]	https://cran.r-project.org/web/packages/rstan/
Stan	Stan Development Team[34]	https://mc-stan.org

RESOURCE AVAILABILITY

Material availability
This study did not generate new unique reagents.

Lead contact
Further information and requests for methods and materials should be directed to and will be fulfilled by the lead contact, Michael Weiss (michael@whaleresearch.com).

Data and code availability
All data and code necessary to replicate analyses in this study have been deposited on Zenodo (https://doi.org/10.5281/zenodo.7457806).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

This study is based on demographic data collected from the southern resident killer whale population in the inland waters of Washington, USA, and British Columbia, Canada. Permits to conduct photographic surveys of the population were granted by the USA National Oceanic and Atmospheric Administration (NOAA/NMFS P33, GA14A, 532-1822, 15569, 21238) and the Department of Fisheries and Oceans Canada (DFO SARA 388).

METHOD DETAILS

Southern resident killer whale demographic data was derived from a long-term field study conducted by the Center for Whale Research. This study uses photographic identification of individuals to complete a full census of the population every year, and determines the mothers of new calves based on close associations between calves and reproductive females.[35] This method has since been validated genetically.[19] The birth years of individuals born since 1973 are known with certainty. We only analyzed data from known-aged females, both so that age-specific reproductive output could be properly accounted for and to ensure that we were correctly determining the number and characteristics of females' offspring as well as their prior reproductive history. As females are not reproductive until at least 9 years old, we utilized data from 1982 to 2021 in our analysis.

We excluded years immediately following an observed birth, as killer whales' 18 month gestation period makes birth in these years impossible.[21] We did not include females in the year of their death. Further examination showed that no female in our dataset had a calf while lactating (i.e. had a surviving calf younger than 3 years old[36]). We therefore also excluded these years of data in our analysis. Finally, we excluded females older than 45 years old from our analysis, as killer whale females past this age are post-reproductive.[24] We considered a female to have successfully reproduced in a given year if she was observed with a new calf in that year and the calf survived its first year of life.

Offspring sex was determined based either on genital coloration, or retrospectively based on sexual dimorphism that develops during puberty.[16] We considered an offspring to be alive for a year if they were born prior to that year and died either during or after that year.

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical analysis was carried out in R.[31] Following Ward et al.[21] all models treated whether a female i successfully reproduced in year t as a Bernoulli random variable ($B_{t,i}$), with a logit function linking birth probability to our predictors. Our first model (Model 1) considered the effects of both male and female offspring. This model had the form:

$$B_{t,i} \sim \text{Bernoulli}(p_{t,i}) \tag{Equation 1}$$

$$\text{logit}(p_{t,i}) = \beta_0 + \beta_1\text{sons}_{t,i} + \beta_2\text{daughters}_{t,i} + f_1(\text{age}_{t,i}) + f_2(t) + \delta_t + \varepsilon_i$$

$$\delta_t \sim N(0, \sigma_\delta)$$

$$\varepsilon_i \sim N(0, \sigma_\varepsilon)$$

Here, $p_{t,i}$ is the estimated birth probability for individual i in year t, the β represent fixed effects, and sons$_{t,i}$ and daughters$_{t,i}$ are individual i's number of surviving sons and daughters in year t, respectively. The term $f_1(\text{age}_{t,i})$ is an estimated smooth function for age, controlling for age-specific reproductive output, while $f_2(t)$ is a smooth function over year, accounting for across-year trends in fecundity over the study period as well as temporal autocorrelation between years. We additionally include random effects for year (δ_t) and individual (ε_i), with estimated standard deviations σ, which model within-year correlations not accounted for by temporal trends and individual variation in annual reproductive success, respectively.

Next, we fit a model (Model 2) to determine whether the estimated effect of males on reproductive success could be explained by long-term effects of raising sons to weaning, or from general effects of male group members:

$$\text{logit}(p_{t,i}) = \beta_0 + \beta_1\text{sons}_{t,i} + \beta_2\text{dead}_{t,i} + \beta_3\text{group}_{t,i} + f_1(\text{age}_{t,i}) + f_2(t) + \delta_t + \varepsilon_i \tag{Equation 2}$$

Here, dead$_{t,i}$ is the number of sons that female i had raised to weaning prior to year t, but were deceased by year t, and group$_{t,i}$ is the number of weaned males alive in female i's matriline in year t other than her sons. Matrilines were defined following Parsons et al.[37] as a set of whales with a known shared maternal ancestor, as these sets of whales tend to be in near-constant association. The structure of the random effects were the same as in Model 1.

Finally, to determine if the cost of sons was dependent on their age, we fit a model (Model 3) that incorporated the sum of the ages of all sons as a predictor

$$\text{logit}(p_{t,i}) = \beta_0 + \beta_1\text{sons}_{t,i} + \beta_2\text{total son age}_{t,i} + f_1(\text{age}_{t,i}) + f_2(t) + \delta_t + \varepsilon_i \tag{Equation 3}$$

This is equivalent to letting the effect of each son vary linearly as a function of their age. To demonstrate this, consider if we were to re-write (3) with a single term representing the effect of sons on a females' reproductive success ($\varphi_{t,i}$):

$$\text{logit}(p_{t,i}) = \beta_0 + \varphi_{t,i} + f_1(\text{age}_{t,i}) + f_2(t) + \delta_t + \varepsilon_i \tag{Equation 4}$$

If we assume the effect of sons is additive, and that the effect of each son has a linear relationship with the son's age, we can write

$$\varphi_{t,i} = \sum_{k=1}^{\text{sons}_{t,i}} (\beta_1 + \beta_2\text{son age}_{t,k}) \tag{Equation 5}$$

Re-arranging (5), we arrive at

$$\varphi_{t,i} = \beta_1\text{sons}_{t,i} + \beta_2 \sum_{k=1}^{\text{sons}_{t,i}} \text{son age}_{t,k} \tag{Equation 6}$$

By substituting (6) into expression (4), we re-derive the original model formula in (3). Thus, estimates for β_1 and β_2 in Model 3 represent the baseline effect of sons on reproduction (at age 0) and the relationship of this effect with age, respectively.

We estimated the posterior distribution for the parameters of these models using Hamiltonian Monte Carlo sampling in the R package brms,[32] which uses Stan to perform sampling.[33,34] Smooth functions were estimated as thin plate regression splines with a six-dimensional basis; increasing the basis dimension did not alter fixed effect estimates or the shape of the estimated smooths. As there is extremely limited information regarding social effects on fecundity in cetaceans, fixed effects were given broad, independent normal priors $N(0,10)$. The prior distributions for the standard deviations of smooths and random effects were set as broad half-t distributions $t(3,0,2.5)$. The prior for population-level intercepts (after centering predictors) was set to Logistic(0,1), as this results in a uniform distribution from 0 to 1 on the probability scale.

We conducted a sensitivity analysis to assess if our choice of fixed effects prior effected our inferences. We ran the same models with fixed effect prior distributions with standard deviations ranging from 1 to 10. Across all ranges of priors, we found consistent evidence for the main results of our initial analysis (see Table S1).

Posteriors were estimated across 4 independent chains, with 1500 iterations of sampling following 1500 iterations of warm-up. Convergence was checked by examining trace and density plots, and ensuring all potential scale reduction factors were below 1.01. We checked that all bulk and tail effective sample sizes were >1000 prior to interpreting posterior distributions of model parameters. Posterior predictive plots were used to ensure that our models predicted a reasonable number of births across the study. To avoid divergent transitions during sampling, the target proposal acceptance probability was set to 0.99. For Model 2, the sexes of some weaned matriline members were unknown. The whale-years in which a female had weaned matriline members of unknown sex ($n = 3$, 0.5% of the dataset) were therefore excluded when estimating Model 2.

The evidence for effects and their estimated size was evaluated from the posterior distributions of parameter estimates. We report the mean effect size and standard error ($\beta \pm$ SE), the 95% credible interval, and the posterior probability of the effect being in the hypothesized direction (the portion of posterior samples with the hypothesized sign).

Supplemental Information

Costly lifetime maternal

investment in killer whales

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		Fixed Effect Prior Distribution			
Model	**Parameter**	$N(0, 1)$	$N(0, 2.5)$	$N(0, 5)$	$N(0, 10)$
1	Sons	$\beta = -0.81 \pm 0.45$ $P(\beta < 0) = 0.97$	$\beta = -1.02 \pm 0.54$ $P(\beta < 0) = 0.98$	$\beta = -1.14 \pm 0.57$ $P(\beta < 0) = 0.99$	$\beta = -1.25 \pm 0.59$ $P(\beta < 0) = 0.99$
	Daughters	$\beta = 0.03 \pm 0.40$ $P(\beta < 0) = 0.43$	$\beta = -0.08 \pm 0.46$ $P(\beta < 0) = 0.54$	$\beta = -0.18 \pm 0.49$ $P(\beta < 0) = 0.62$	$\beta = -0.27 \pm 0.51$ $P(\beta < 0) = 0.68$
2	Sons	$\beta = -0.85 \pm 0.40$ $P(\beta < 0) = 0.99$	$\beta = -1.03 \pm 0.45$ $P(\beta < 0) = 0.99$	$\beta = -1.06 \pm 0.46$ $P(\beta < 0) > 0.99$	$\beta = -1.08 \pm 0.49$ $P(\beta < 0) > 0.99$
	Dead Sons	$\beta = 0.16 \pm 0.63$ $P(\beta < 0) = 0.39$	$\beta = 0.24 \pm 0.79$ $P(\beta < 0) = 0.41$	$\beta = 0.13 \pm 0.83$ $P(\beta < 0) = 0.42$	$\beta = 0.08 \pm 0.85$ $P(\beta < 0) = 0.44$
	Males in Group	$\beta = 0.06 \pm 0.22$ $P(\beta < 0) = 0.39$	$\beta = 0.09 \pm 0.23$ $P(\beta < 0) = 0.35$	$\beta = 0.09 \pm 0.23$ $P(\beta < 0) = 0.35$	$\beta = 0.10 \pm 0.23$ $P(\beta < 0) = 0.34$
3	Age Trend	$\beta = -0.06 \pm 0.07$ $P(\beta > 0) = 0.18$	$\beta = -0.05 \pm 0.07$ $P(\beta > 0) = 0.26$	$\beta = -0.04 \pm 0.07$ $P(\beta > 0) = 0.27$	$\beta = -0.04 \pm 0.07$ $P(\beta > 0) = 0.29$

Table S1. Sensitivity analysis of model priors, related to STAR Methods