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Costs of maternal care revealed through body condition in Northern Resident killer whales *(Orcinus orca)*

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In species with prolonged parental investment, extended care imposes considerable costs. In Northern Resident killer whales (*Orcinus orca*), maternal investment is demanding due to long gestation, extended lactation, and lifelong care of non-dispersing offspring. Using 10 years of aerial images, we assessed whether reproduction and maternal care affected body condition in 66 reproductive-aged females. Females in late pregnancy had significantly higher body condition than those not pregnant or with unsuccessful pregnancies, while females in the first two years of lactation had significantly lower condition. By year three, body condition rebounded, coinciding with weaning. To evaluate long-term costs, we analyzed body condition in 75 adult females relative to: (1) number of living offspring (life-long parental care hypothesis), (2) lifetime births (successive reproduction hypothesis), and (3) number of living sons (expensive sons hypothesis), while accounting for prey abundance. Maternal condition declined with increasing numbers of living offspring and lifetime births, independent of Pacific Salmon Commission Chinook salmon (*Oncorhynchus tshawytscha*) abundance index. Living offspring was the strongest predictor of the reproductive history covariates, supporting the life-long parental care hypothesis. We found no support for the expensive sons hypothesis. These findings highlight energetic costs of extended maternal investment in long-lived, socially complex species.

Keywords Photogrammetry, Parental investment, Drone, Cetacean, Reproduction, Orcinus orca

Identifying factors that can limit reproduction and survival of breeding individuals is a critical goal in the conservation management of wildlife. Among these limitations are costs associated with parental care. While breeding individuals can increase the survival of their offspring by providing care, this may limit the parent's ability to invest in producing future offspring[1]. Parental investment may extend over long periods; for example, investment can start before conception through pre-emptive resource gathering[2] and, in some social taxa, continue well after offspring reach sexual maturity[3].

Theory predicts that parents can maximise their reproductive success by achieving an optimal balance between the number of offspring and investment in individual offspring[4,5]. This prediction is consistent with studies demonstrating that increased reproductive output is linked to reduced offspring mass[6], lower offspring and parent survival[7], and diminished parental fitness[8–10]. Investment in individual offspring may also depend on factors such as offspring quality or the time required for offspring to reach independence, with parents allocating more resources to higher-quality offspring and those likely to become independent sooner[11,12]. The costs associated with parental investment can also increase when resources are scarce[13–15].

In mammals, females experience considerable demands related to gestation and post-partum care[16]. Pregnancy imposes energetic costs[17,18], which are amplified for species with complex fetal development[19]. Reproduction-related fluctuations in female size and body condition have been observed in large mammals

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with longer gestation periods[20–26]. Post-parturition demands can be even greater than those experienced during gestation due to the high physiological costs of lactation[3,27]. In species with male-biased sexual dimorphism, studies have demonstrated that a mother's health and/or future reproductive output may decline after raising sons than daughters[28–30]. This effect is likely greatest in species that continue to invest in their offspring up to and even beyond maturity. Investment beyond sexual maturity can occur when offspring do not disperse from the geographic range of one or both parents, and may include assistance with predator vigilance and defence, foraging assistance, grooming, and even direct provisioning of food[31,32].

Fish-eating Resident killer whales (RKWs; *Orcinus orca*) invest in extensive maternal care. Investment continues past weaning and even after sexual maturity of their offspring, and imposes enduring costs[30]. RKW females demonstrate a long reproductive investment period, with gestation lasting approximately 16 to 18 months[33,34], followed by approximately three years of lactation[35–37]. After weaning, maternal care continues through the lifelong sharing of their prey[38,39]. Adult daughters receive less provisioning as they age and raise their own offspring, whereas adult males continue to be provisioned more substantially by their mothers throughout their lives[39]. RKW mothers face especially pronounced costs from bearing male offspring due to this lifelong investment. Weiss et al.[30] found that mothers with at least one son have a 70% lower annual probability of producing a viable calf compared to females without offspring, whereas having daughters had no effect on reproductive success. Recent studies have focused on the costs of RKW maternal care on the future reproductive success of females[30] and kin fitness[40,41], but it is unknown how this reproductive investment and the cumulative investment of long-term care influences more readily observed measures, such as a female's body condition.

RKWs face additional challenges in provisioning offspring due to declines in the abundance and size of their primary prey, Chinook salmon (*Oncorhynchus tshawytscha*). RKW fecundity, survival, and social structure depends on Chinook salmon abundance and availability[42–50]. How prey abundance may additionally or interactively affect the intrinsic costs in body condition imposed by reproduction is critical for the development of conservation plans to promote RKW recovery.

Given the costly nature of maternal care in RKWs, we reasoned that a mother's body condition would be influenced by the physiological demands associated with maternal investment. Accordingly, our objective was to investigate how maternal investment, from pregnancy to post-weaning care and long-term provisioning of offspring, might affect the physical condition of RKW mothers. To examine this possibility, we analyzed a 10-year dataset of aerial images of Northern Resident killer whales (NRKWs). Listed as Threatened in Canada under the *Species at Risk Act*[51], the 341-member population of NRKWs (population size as of 2022[52]; belong to one of two RKW populations ranging from Washington State, USA, to southern Alaska, USA[53]. We investigated: (1) how maternal investment affects female body condition throughout the reproductive cycle (17.5-month pregnancy and three-year nursing period) and (2) how female body condition is influenced by prolonged investment associated with both the number and sex of offspring she has over her reproductive lifetime. We predicted that females would gain fat throughout pregnancy, followed by a decrease in body condition postpartum due to the energetic costs of lactation.

In considering the implications of lifetime investment, we reasoned that associations between female body condition and the number of offspring produced by a female is likely the result of prolonged parental care and/or nutritional demands from successive reproductive events. To evaluate these possibilities, we considered both the number of living offspring a female had (life-long parental care hypothesis) and the total number of births (number of living and dead offspring; successive reproductive events hypothesis). Given the influence of offspring sex on female fitness[30], we also examined the cost of having sons compared to daughters (expensive son hypothesis) on female condition. We predicted that female body condition would be more strongly associated with the number of living offspring than with the number of births, as the considerable birthing intervals in NRKWs (4.88 years[36], may reduce the costs of successive reproductive events. We also predicted that the number of living sons a female has would have a stronger association with reduced body condition than the number of living daughters. In light of evidence that RKW fecundity, survival, and body condition is influenced by Chinook salmon abundance[42–44,48], we also examined the effects of lifetime maternal investment on female condition under varying abundance of the key prey species. We predicted that any negative associations between a mother's body condition and the number and/or sex of her offspring would be more pronounced during years of lower Chinook salmon abundance.

Materials and methods

Study population and data collection

From 2014 to 2023, we conducted three to five-week field seasons (August to September) along Northeastern Vancouver Island, British Columbia within Kwakwaka'wakw territories (Northern boundary: 51° 19' 55" N, Southern boundary: 49° 58' 36" N; Supplementary Fig. 1) to collect aerial images of NRKWs as part of a long-term health assessment study. We performed additional two-week field efforts on the Central Coast of British Columbia in June 2019, July 2022, and July 2023, within Gitga'at, Kitasoo/Xai'xais, Heiltsuk, and Wuikinuxv territories (Northern boundary: 53° 45' 59" N, Southern boundary: 51° 19' 56" N; Supplementary Fig. 1) to photograph as many of the NRKW population as possible. We conducted field work during summer months to avoid potentially confounding seasonal effects on body condition[54] and to capture annual snapshots when body condition is likely most robust[48]. All field activities were carried out under research permits from Fisheries and Oceans Canada.

We located NRKWs by visual and acoustic scans (~ 10 nautical mile acoustic range hydrophone), with search efforts guided by local sightings shared via VHF radio from mariners and tourism operators. We collected lateral identification images with a DSLR camera and telephoto lens (300 mm and 400 mm maximum range) by approaching the whales at 30–100 m with our research vessels (8.2 m motor vessel (2014–2022), 15.5 m motor vessel (2019 Central Coast sampling), and a 20 m sailing vessel with a 4.2 m tender (2022 Central Coast sampling; 2023 both study areas sampling). We cross-referenced the images with published photo-identification catalogues[55–58], as well as our own aerial catalogues, to identify individual whales. We used demographic information (including sex, birth year, death year [if applicable], identity of the whale's mother, and matrilineal grouping) for every individual from the same catalogues. Sex designations for individuals and calf-mother relationships were confirmed in the catalogues only when supported by direct evidence. Visual confirmation included observations of ventral skin pigmentation, characteristic dorsal-fin sprouting in maturing males, and the presence of a closely associated new calf indicating a reproductive female and mother-offspring relation[57]. In some cases, genetic analyses provided additional verification[57]. Although occasional misclassification is possible, established field protocols and consistent morphological and behavioural indicators make such errors uncommon.

To evaluate body condition of NRKWs from aerial photographs, we used Remotely Piloted Aircraft Systems (RPASs or 'drones') following protocols established by Durban et al.[59]. Detailed description of the RPAS equipment we used can be found in Supplementary Table 1. The RPAS flew 25 to 40 m above the whales, with a gimbal camera oriented at 90 degrees to take photographs from directly above the surfacing whales. We took precautions to minimize potential disturbance to whales following recommendations from Durban et al.[59], and Aubin et al.[60]: maintaining RPAS altitude at a minimum of 25 m and monitoring for avoidant behaviours, which were never observed. Although we frequently conducted multiple flights over individual whales to ensure an adequate number of images for photogrammetric analysis, we limited total flight time over an individual whale to 30 min per day. During RPAS operations, the vessel remained within 400 m of the whales, moving slowly behind or parallel to them. Over the 10 years of field work, the research teams conducted 766 RPAS flights during 177 encounters with NRKWs. We photographed 82 females (age 10 and above, see Methods below), with 52 females sampled across multiple years and an average of 24 females sampled in each year.

Photogrammetric analysis

We evaluated body condition through photogrammetric measurements of each whale's anterior region. When small, toothed whales become nutritionally stressed, they lose adipose tissue behind the cranium which can be a reliable indicator of declines in body condition[23,61,62]. Such declines have been correlated with nutritional status and survivorship in Southern Resident killer whales[23,48,54]. Using the *ImageJ* software package (https://imagej.net/), we estimated each whale's body condition by measuring its eye patch ratio (as per Fearnbach et al.[54] using the following formula (Eq. 1):

$$Eye\ patch\ ratio\ = \frac{Distance\ between\ 75\%\ length\ of\ eye\ patches}{Distance\ between\ anterior\ edges\ of\ eye\ patches} \tag{1}$$

Eye patch ratio has been used as a proxy for the nutritional status of killer whales and is a sensitive measure of body condition[48,54]. Lower values indicate less fat behind the cranium, which is associated with increased probability of mortality[48]. We selected aerial images where the whale's eye patches were in focus, each end of the eye patches were visible above the water surface, and the whale had no discernable tilt in body axis or head.

We calculated the annual mean eye patch ratio for a whale using all suitable images from that sampling year (median number of images per whale = 5.0, ranging from 1 to 46 images). Repeated measurements of the same individual taken from different images in the same year were highly consistent; within-subject coefficients of variation ranged 0.0003 to 0.03, with a median of 0.01. As this is substantially lower than the variation observed across individuals in each year of the study (0.02–0.04, median 0.03), we do not believe that measurement error significantly influenced our results. For whales that were sampled in different months, we pooled images from all sampling months to calculate their annual mean eye patch ratio, given that sampling month had no significant effect on eye patch ratio during our three-month sampling window (See Supplementary Methods and Supplementary Fig. 2).

Assessing body condition throughout the reproductive cycle

To assess how the reproductive cycle might influence female body condition, all females of reproductive age were assigned one of six reproductive statuses in each year they were measured (described in Robinson & Visona-Kelly[63]). We considered all females between 10 years (the youngest age a killer whale typically produces its first viable calf[36] and 42 years to be of reproductive age, in addition to females of 42–48 years old who had a current calf[52]. While there are infrequent reports of females becoming pregnant at younger ages, these definitions align with observed pregnancies in our dataset, where the youngest females to give birth would have become pregnant at 10–11 years old and the oldest females to give birth became pregnant at 46 years old. This resulted in a sample size of 207 whale-by-year observations representing 66 unique individuals. Due to the 17.5-month gestation period of killer whales[33,34], females were considered 'pregnant - late stages' in the year before they were first seen with a calf and 'pregnant - early stages' the previous year. For example, a female that was first seen with a calf between the 2019 and 2020 field seasons would be designated as 'pregnant - late stages' in 2019 and 'pregnant - early stages' in 2018. Lactating females were categorized into 'lactating year 1' for the year a calf was born, and 'lactating year 2' and 'lactating year 3' for the following two years until calves are weaned[35]. Miscarriage rates for the closely related Southern Resident killer whales have been estimated as high as 69%[46,64]. Therefore, we assigned all other reproductive-aged females as 'non-pregnant/unsuccessful pregnancy', to account for the possibility that whales in this category could have been pregnant when measured and later miscarried. Reproductive statuses were confirmed through annual population censuses[58]. Three females were visually identified as pregnant from drone imagery based on visually-apparent increased mid-section width, a known indicator of pregnancy in killer whales and other dolphins[65,66]. However, their pregnancies were not confirmed by calf presence the following year, so we excluded these observations from analysis. Post-menopausal females (42–48 years without a current calf or older than 48 years, according to the definition used in the Fisheries and Oceans Canada population census[52]) were excluded from this analysis due to their inability to breed.

We then constructed a linear mixed effects model to examine how body condition might relate to the reproductive cycle. Specifically, we used the R package glmmTMB[67], with reproductive status (i.e., non-pregnant/ unsuccessful pregnancy, early-stage pregnant, late-stage pregnant, lactating year 1, lactating year 2, lactating year 3) as a fixed explanatory variable and eye patch ratio as a response variable. This analysis also provided an opportunity to identify consecutive stages of the RKW reproductive cycle that presented similar distributions of eye-patch ratios. Specifically, we used the outputs of this model to reduce our covariate set in subsequent analyses (see Methods below) by combining consecutive reproductive stages that had similar effects on RKW body condition into three reproductive stages. To account for changes in eye patch ratio as whales age[48], we included a fixed effect of female age, fit as a cubic natural spline (Supplementary Fig. 3). Due to the repeated measurement of the same individuals in successive sampling years, we included whale identity and matriline identity as random effects. We also included year-level random intercepts that followed a first-order autoregressive (AR1) model, allowing us to quantify inter-annual variation in body condition across the entire study population. More specifically, we assumed that year-level random intercepts followed a multivariate Gaussian distribution where each component (i.e., the effect associated with each year) was only correlated with components for the previous and following years. To assess the validity of model assumptions, we examined residual plots using the R package DHARMa[68], and tested normality of the eye patch ratio by assessing histograms and a Cullen and Frey graph with 1,000 bootstrap replicates.

Assessing impacts of lifetime maternal care on body condition

We examined the effects of lifetime maternal investment (i.e., investment during reproduction and life-long provisioning) on adult female body condition (age 12 or greater[36,39]). Using data from 225 whale-by-year observations of 75 unique individuals, we regressed NRKW eye patch ratios against a suite of biological and demographic predictors. A summary of each adult female's reproductive history can be found in Supplementary Table 2. We included reproductive status as a categorical covariate using a simplified classification based on results from the analysis outlined in above: We designated females as 'pregnant' the year immediately preceding a calf's birth and combined all 'lactating year 1' and 'lactating year 2' females into a single 'lactating' category (see Results for more details). We included a cubic natural spline for age as a fixed effect (Supplementary Fig. 3), and individual and matriline identity as random effects.

We also included the Pacific Salmon Commission's annual ocean catch abundance index from 2014 to 2023 in our models[69], which estimate salmon abundance relative to levels measured in 1979–1982. This metric has been shown to correlate with NRKW mortality and fecundity[42,43]. We averaged the annual abundance indices across three areas (Southeastern Alaska, Northern British Columbia, and West Coast Vancouver Island), given that the NRKW range includes all three areas[53,70].

We constructed four predictors related to offspring characteristics and included them as covariates in our models. These were: (1) number of known births (sum of the number of living and dead offspring), (2) number of living offspring, (3) the number of living sons, and (4) the number of living daughters a mature female had in a given year. We included interactions between each of these offspring covariates and age to account for any relationships between prolonged maternal care and body condition that were influenced by a female's age and experience. We also included interaction terms between salmon abundance and our four offspring covariates. Interactions between the abundance index and social factors have been observed in the context of mortality in previous studies. Specifically, when salmon abundance was low, lower social connectivity and lack of matriline leadership was associated with higher mortality[45,71,72]. Strong positive correlations between some of our offspring covariates (e.g., "number of births" and "number of living offspring": $R^2 = 0.91$, Supplementary Fig. 4) prohibited us from including these variables in the same model. Instead, we constructed a set of four candidate models for our analysis on adult females based on a priori hypotheses (Table 1). To directly test whether rearing sons is more costly to a mother's body condition than rearing daughters, we performed an additional analysis in which we included the total number of offspring as a covariate in the expensive sons and expensive daughters models (See Supplementary Methods and Supplementary Tables 3, 4).

Null Model	
Null	1 + random effects (whale ID and matriline ID)
Number of living offspring model (Life-long parental care hypothesis)	
1	Number of offspring + number of offspring X age + number of offspring X salmon + salmon + reproductive status + age
Number of births model (Successive reproductive events hypothesis)	
2	Number of births + number of births X age + number of births X salmon + salmon + reproductive status + age
Number of living sons model (Expensive sons hypothesis)	
3	Number of sons + number of sons X age + number of sons X salmon + salmon + reproductive status + age
Number of living daughters model (Expensive daughters hypothesis)	
4	Number of daughters + number of daughters X age + number of daughters X salmon + salmon + reproductive status + age

Table 1. List of candidate models for analysis on the body condition of adult female Northern resident killer Whales. Models 1 to 4 include random effects of Whale ID and matriline ID. Interaction terms are denoted with an 'X'.

We used the R package glmmTMB[67] to design Gaussian linear mixed-effects regression models to fit the data. All statistical analyses were conducted using the programming software R 4.2.3[73]. We evaluated our candidate models using the Akaike Information Criteria (AIC)[74], considering models within two AIC points of the top performing model (lowest AIC) as competitive, unless simpler models had lower ΔAIC (the difference in AIC between each model and the best model) than more complex models[74,75]. We validated model performance using the R package DHARMa[68] and assessed the influence of covariates by evaluating coefficient estimates and their 95% confidence intervals within our top models. To aid interpretation, we used the R package ggeffects[76] to generate predicted values for body condition across three representative age values using: the mean age of females in our dataset (28.9 years), mean age plus one standard deviation (40.9 years), and mean age minus one standard deviation (17.0 years).

Results

Influence of the reproductive cycle on female body condition

Eye patch ratio showed significant associations with reproductive status (Table 2; Fig. 1). Whereas we found no difference in eye patch ratio between reproductive-aged females that were not pregnant/had unsuccessful pregnancies and females in the early stages of pregnancy (> 1 year before the birth of their calf), females in the later stages of pregnancy (< 1 year before the birth of a calf) had significantly higher eye patch ratios than non-pregnant females/females that had unsuccessful pregnancies (Coefficient = 0.020, Z = 5.38, $p < 0.001$; Table 2; Fig. 1). Following parturition, females showed a steep decline in eye patch ratio, decreasing to significantly lower values than non-pregnant females (Coefficient = −0.010, Z = −2.71, $p = 0.007$; Table 2; Fig. 1). Eye patch ratios remained significantly lower in females in their second year of lactation compared with non-pregnant females/females that had unsuccessful pregnancies (Coefficient = −0.012, Z = −3.01, $p = 0.003$; Table 2; Fig. 1), but showed no difference in the third year of lactation (Table 2; Fig. 1).

Influence of lifetime maternal investment on female condition

We found evidence that an adult female's body condition was influenced by characteristics of her living offspring and reproductive history. Multi-model inference suggested that the model containing the number of living offspring a female had best explained variation in body condition (AIC weight = 0.73, Table 3), and was the only competitive model in the model set. This top model explained 87% of the variation, with fixed effects explaining 27% of the variation (marginal $R^2 = 0.27$). The influence of the Pacific Salmon Commission Chinook abundance covariate on body condition was modest; we observed a slight but negative association (Supplementary Fig. 5), and no interaction term that included Chinook abundance had a detectable influence on body condition (coefficient = 0.002, Z = 0.66, $p = 0.51$) (Supplementary Fig. 6). The coefficient related to Chinook abundance was greater than that relating to the number of living offspring (Fig. 2). However, given we did not scale our coefficients, this finding does not directly indicate that Chinook had a larger effect on a female's body condition.

Eye patch ratio was negatively associated with the number of living offspring (coefficient = −0.011, Z = −2.06, $p = 0.04$) and number of births a reproductive female had (coefficient = −0.008, Z = −1.53, $p = 0.13$) (Figs. 2 and 3). There was no significant interaction between number of living offspring and age (coefficient = 0.011, Z = 0.61, $p = 0.54$) or between number of births and age (coefficient = 0.009, Z = 0.64, $p = 0.52$) (Fig. 3). For the average age of adult females in the dataset (age 29), there was a negative association between body condition and number of living offspring a female had (slope = −0.008, 95% CI: −0.014 to −0.003), with a similar pattern among older adult females (age = 41, slope = −0.006, 95% CI: −0.011 to −0.001). The number of births a female had was negatively associated with body condition for averaged aged females (age = 29, slope = −0.007, 95% CI: −0.013 to −0.002) and older adult females (age = 41, slope = −0.006, 95% CI: −0.010 to −0.001).

While the total number of offspring influenced body condition in adult females, the number of living sons or daughters considered separately did not. However, the number of living daughters had a stronger negative association with a female's body condition than the number of living sons (Supplementary Fig. 7). These patterns were consistent across adult female age. For average aged females (age 29), the number of living sons was weakly

Fixed effect	Estimate	SE	Z value	*p* value
Intercept	1.146	0.007	158.03	**< 0.001**
Age (1st degree)	0.081	0.014	5.79	**< 0.001**
Age (2nd degree)	0.037	0.014	2.64	**0.01**
Reproductive status:				
Pregnant - early stages	0.004	0.004	0.99	0.32
Pregnant - late stages	0.020	0.004	5.38	**< 0.001**
Lactating year 1	−0.010	0.004	−2.71	**0.007**
Lactating year 2	−0.012	0.004	−3.01	**0.003**
Lactating year 3	−0.007	0.004	−1.84	0.07

Table 2. Fixed effects from linear mixed effects model examining how body condition varies across reproductive stages of reproductive-aged female Northern resident killer whales ($n = 207$ whale-by-year observations, 66 individuals). Statistically robust effects (i.e., $p < 0.05$) are highlighted in bold. For the fixed effect of reproductive status, regression coefficients indicate comparisons between each factor level (i.e., reproductive stage) and non-pregnant females/females that had unsuccessful pregnancies.

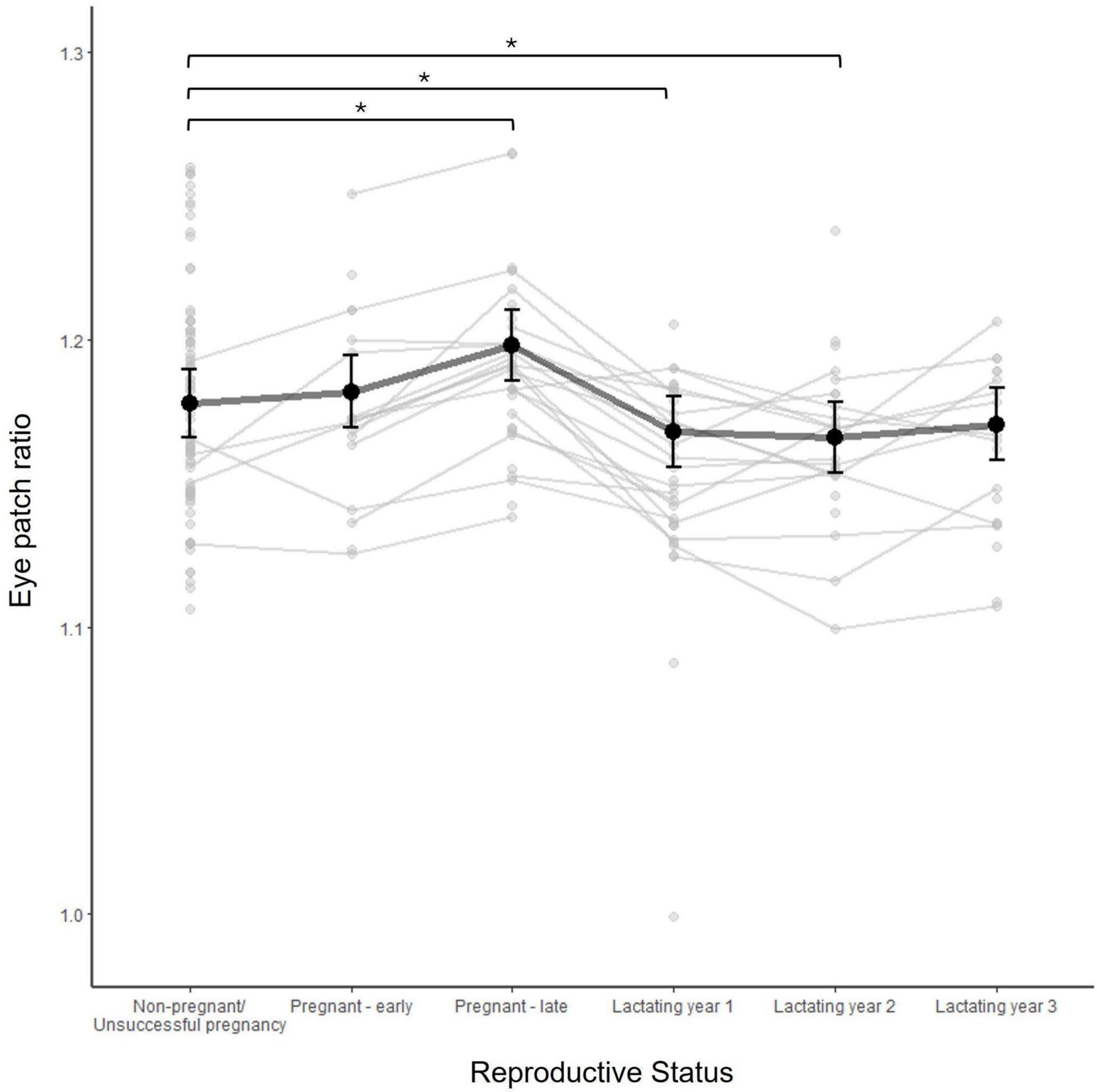

Fig. 1. Marginal effects (black points) of each reproductive stage on eye patch ratio (i.e., body condition) in reproductive-aged female Northern Resident killer whales, as estimated from the model presented in Table 1. Error bars depict 95% confidence intervals ($n = 207$ whale-by-year observations, 66 individuals). Asterisks indicate reproductive states for which eye patch ratio differed significantly ($p < 0.05$) from non-pregnant females/females that had unsuccessful pregnancies. Grey points represent annual mean eye patch ratio values for each female measured at each reproductive stage. Points representing individual females that were measured in consecutive years are linked by grey lines, and the black line links marginal effects for each reproductive stage.

associated with an adult female's body condition (slope = 0.001, 95% CI: −0.007 to 0.008; Coefficient = −0.007, Z = −0.87, $p = 0.38$). Whereas the number of living daughters had a stronger negative association on an adult female's body condition than the number of living sons, and had a significantly negative slope for average aged females (age = 29, slope = −0.008, 95% CI: −0.014 to −0.002), the overall effect of the number of living daughters was not a significant predictor of adult female body condition (Coefficient = −0.01, Z = −1.18, $p = 0.24$) nor was the interaction between age and number of living daughters (Coefficient = 0.03, Z = 1.32, $p = 0.19$). Our supplementary analysis also found that neither the number of living sons nor the number of living daughters significantly influenced an adult female's body condition (Supplementary Table 4).

Model #	Hypothesis	Reproductive history covariate	K	AICc	Δ AICc	AICc weight	Marginal R^2
1	Life-long parental care	Number of living offspring	13	246.56	0.00	0.73	0.27
2	Successive reproductive events	Number of births	13	249.78	3.22	0.15	0.25
4	Expensive daughters	Number of living daughters	13	250.39	3.84	0.11	0.24
3	Expensive sons	Number of living sons	13	253.53	6.98	0.02	0.20
Null		None	4	344.99	98.43	0.00	0.00

Table 3. Model selection results from analysis on adult female Northern resident killer whales ($n = 225$ whale-by-year observations, 75 individuals). Models varied by which reproductive history covariate was included. For each model, the reproductive history covariate it contained was also considered in interaction terms with age and salmon abundance. See Supplementary Table 2 for a full list of terms for each model in the model set. The top performing model is indicated in bold. K indicates the number of terms in the model including each degree of any natural spline covariate (accounting for age effects) and interactions with natural spline covariate.

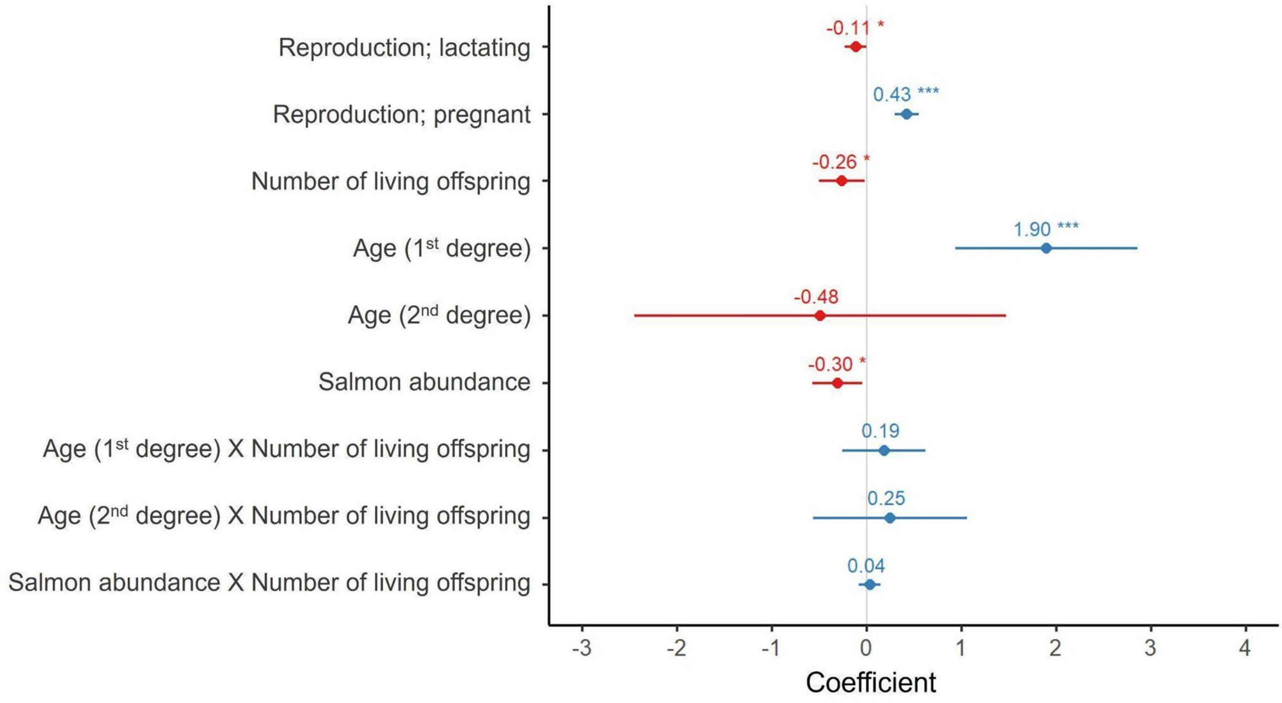

Fig. 2. Coefficients (dots) and 95% confidence intervals (lines) for fixed effects in the top performing model (Model # 1; Supplementary Table 3) for predicting eye patch ratio among adult female Northern Resident killer whales ($n = 225$ whale-by-year observations, 75 individuals). Coefficient values reflect scaled and centered eye patch ratio values. Predictor coefficients are associated with unscaled covariates (y axis) and the relative strength of evidence associated with each covariate is compared using p values. Symbols denote p values (*** = 0.0001, ** = 0.001, * = 0.01, · = 0.05). Blue values indicate positive associations, and red values indicate negative associations between predictors and eye patch ratios of adult females. Reproductive status categories denoted by ';' represent the level of the predictor variable compared to the base case level (not pregnant). Brackets around age terms represent the degree of natural spline function for age and 'X' indicates an interaction between predictors.

Discussion

Our analysis provides evidence that female killer whales incur physiological costs from investing in their non-dispersing offspring, attributable to their lifelong provisioning of offspring as well as reproduction, lactation, and neonatal care. An adult female's body condition increased during the later stages of pregnancy and declined to below baseline non-pregnant/unsuccessful pregnancy levels during the first two years of lactating. Our analysis also showed that a mother's body condition was negatively associated with the number of births and living offspring she had. However, the number of living offspring a female had was a stronger predictor of female body condition than the number of births she had, providing stronger support for the life-long parental care hypothesis over the successive reproductive events hypothesis. Contrary to our predictions, offspring sex did not significantly influence a mother's condition, providing no additional support for the expensive sons hypothesis. Additionally, neither of these patterns were influenced by the Pacific Salmon Commission's Chinook abundance

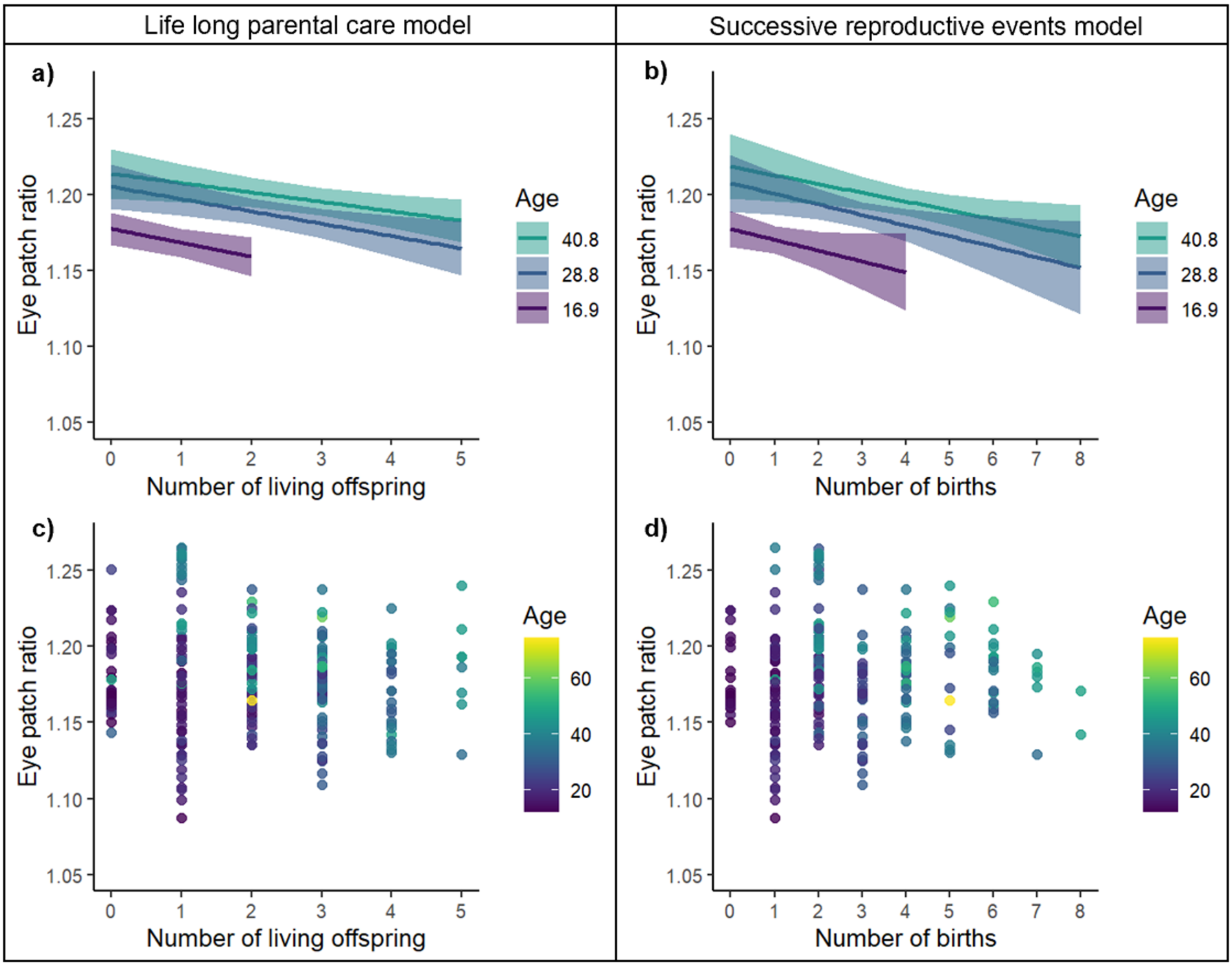

Fig. 3. Effect of number of living offspring (a and c; top performing model, Model #1: Life-long parental care) and number of births (b and d; second ranking model, Model #2: Successive reproductive events) a female had on the eye patch ratio of adult female Northern Resident killer whales by age from top two ranking models ($n = 225$ whale-by-year observations, 75 individuals). Results shown as model predicted eye patch ratio values (a and b) and raw data showing range of female eye patch ratios (c and d) as a function of model covariate by age. All other model terms are held constant at their mean. Age is represented visually as three categories: the mean age of females in the data set (28.8), mean age plus one standard deviation (40.7), and mean age minus one standard deviation (16.9). The model predicted values for females at age 16.9 are restricted to no more than two living offspring and no more than four births, as it is biologically unlikely that females of this age would have surpassed these values. Lines represent model predicted values and shaded areas represent 95% confidence intervals.

index, suggesting that social factors were important regardless of the Chinook abundance index during the time of this study. We note that no years of considerably low Chinook abundance occurred during the course of our study, in contrast to the earlier timeframes examined by Ford et al.[43] and Ward et al.[42], who reported a strong relationship between Chinook salmon abundance and RKW mortality. Our results suggest that reproduction and the continual provisioning of non-dispersing offspring may limit a mother's ability to provision herself, and these physiological costs might impose further costs to maternal fitness and limit future reproduction.

Whereas the body condition of non-pregnant females or females that had unsuccessful pregnancies was similar to the body condition of females in the early stages of pregnancy, body condition was highest for those in late stages of pregnancy. This is consistent with patterns of gestational growth in other mammals; for example, meerkats (*Suricata suricatta*) exhibit a much lower rate of weight gain during the first half of gestation compared to the second half[77], likely reflecting the non-linear nature of foetal growth. The increase in fat reserves during late gestation may also reflect an increase in caloric intake to meet the higher energetic demands of this stage and to buffer against the upcoming costs of lactation. Studies of other toothed whales[78] and baleen whales[79,80] found that the energetic costs of gestation are far higher in the final months, which supports the explanation that females may need to increase caloric intake during later pregnancy, resulting in greater fat gain compared with early pregnancy.

Detection of early pregnancy in free-living cetacean species is challenging[81], and often requires biological samples[46] or measurements of aerial images[22,63,65,66]. As we relied on demographic data (i.e., the birth year of a documented calf) to determine pregnancies, we were unable to distinguish between non-pregnant females and females whose pregnancies ended in miscarriage or stillbirth. To address this limitation, we ran an additional model using a dataset that restricted the non-pregnant/unsuccessful pregnancy category to only include females measured in the year before a documented pregnancy and not nursing a current calf, which did not qualitatively change our results (Supplementary Table 4). Additionally, as the exact birth dates of NRKW calves are usually unknown, we assumed that females photographed in late summer with a new calf were pregnant for the two summers prior. Although RKWs can breed at any time of year, most calves are born between September and March[82], which aligns with a date of conception between late February and late August. However, in some cases where calves were born later, females may have been erroneously classified as in early pregnancy before conception actually occurred.

Our results suggest lactation imposes energetic demands on NRKW females. This pattern aligns with findings for Southern Resident killer whales[23,83]. During the first year of lactation, females displayed a steep decline in condition below non-pregnant levels, then on average, maintained a similar level in the second year, before seemingly recovering to pre-pregnancy body condition after the third year of lactation. These trends suggest that the energetic requirements of lactation impose physiological costs on female NRKWs that are not regained until at least two years post parturition. This likely reflects the timing of calf weaning[35,36,82]. Similar patterns have been documented in other mammals, such as caribou (*Rangifer tarandus*), where fat reserves did not begin to replenish until calf weaning was completed[84]. Interestingly, individual females exhibited substantial variation in this post-weaning recovery phase; some females showed a large increase in body condition, while most increased more modestly or even continued to decrease (Fig. 1). Such variation may simply reflect differences in the specific timing of birth and weaning across females sampled. For income breeders like toothed whales that rely on a consistent food supply during pregnancy and lactation, unfavourable environmental conditions can shorten the duration of maternal care[85,86], suggesting that annual conditions experienced by females in this prey-limited population may have played a role in the timing of their weaning and recovery. However, it could also result from variation in female 'quality'. In some species of ungulates, higher-quality females are better at managing the costs of pregnancy and lactation[87]. Age[88] and genetics[89] have been shown to influence maternal condition and reproductive resilience of female fur seals (*Arctocephalus pusillus*) and Blackface sheep (*Ovis aries*), while body length[90] has been demonstrated to have a positive relationship with lipid storage in humpback whales (*Megaptera novaeangliae*) and sperm whales (*Physeter macrocephalus*). The females in our dataset vary by both age and length[91]. However, RKWs are a highly social species, and it is plausible that social conditions (e.g., the presence of other female 'helpers') could also affect how much or quickly females recover after parturition and lactation.

Another limitation of our approach is that it was not possible to determine the exact age at which individual females become sexually mature or undergo menopause in a wild population of killer whales. While we aimed to use biologically reasonable thresholds for classifying reproductive-age females in NRKWs (see Methods), age at the onset of sexual maturity and menopause is likely to vary among individuals. Therefore, it is possible that some non-reproductive females were included in our sample. For example, A43 (a 33-year-old female when the study began in 2014) was classified as reproductive despite not giving birth to a documented calf since 1996. Interestingly, A43 accounts for the six highest eye patch ratios measured in our non-pregnant/unsuccessful pregnancy category during the study. Given substantial individual variation in 'baseline' body condition across individuals (Fig. 1), we cannot determine whether this is associated with early menopause, a lack of reproduction due to miscarriages, or simply morphological variation across individuals. However, restricting the dataset to only females that produced a documented calf during the study period did not meaningfully change our results (Supplementary Table 5).

Our results suggest that NRKW females with a higher reproductive output incur greater physiological costs. The number of living offspring was a stronger predictor of adult female body condition compared to the number of births a female had, suggesting that provisioning (via lactation and life-long prey sharing) may be more influential than the cumulative costs from successive births on a mother's body condition. However, these variables are highly correlated, and their similar slopes in relation to female body condition make it difficult to disentangle the relative influence of successive reproductive events.

It is possible that successive reproductive events impose costs to NRKW mothers. Although the considerable calving intervals of NRKWs (average 4.88[36]; may buffer the costs from successive births and lactation periods, cumulative costs from multiple reproduction events could still impact a female's physiological condition. Cumulative reproductive costs are well-documented in mammals, even those without lifelong parental care. In ungulates, mothers that produce more offspring early in life experience reduced survival and accelerated senescence[29,92]. In humans, which often demonstrate extended parental care, women with higher parity or reproductive rates have lower body fat and faster aging rates [93, but see 94, 95]. Given the negative effects of the number of births on female body condition, it is reasonable to infer that female NRKWs likely experience long-term physiological costs from successive reproductive investment as well. Future work should build on these findings, examining how physiological characteristics, such as body condition and body length, might relate to calving success, lactation duration, and the timing of reproductive senescence. Any patterns would provide greater clarity on the reproductive costs experienced by female RKWs.

Contrary to our expectations, offspring sex was not a strong predictor of female body condition. Instead, the number of living daughters was more negatively associated with maternal condition than the number of living sons. This may reflect higher costs of raising daughters, whose offspring remain in the maternal matriline and impose energetic demands of grandmaternal care[40]. Nevertheless, the finding that the number of living sons did not strongly predict maternal body condition in NRKWs is notable, given that caring for sons can reduce the future reproductive output of female SRKWs while daughters do not impose similar costs[30]. Potentially, the costs of rearing sons might only be reflected in a mother's future reproductive output rather than in a mother's body condition, as seen in bighorn sheep (*Ovis canadensis*[28]). Alternatively, NRKWs represent a growing population in comparison to the endangered Southern Resident killer whales[96], suggesting that stressors facing the NRKWs may be lower, and mothers may be able to raise energetically demanding sons with fewer consequences to their condition. Future research comparing maternal care and its associated costs across the two populations would improve our understanding of how environmental stressors influence NRKWs and SRKWs. Foraging and prey sharing dynamics of NRKW males may also differ from SRKWs, given that foraging capture rates of each age-sex class differ between the two populations[97]. However, male NRKWs appear to be more dependent on maternal provisioning, spend less time foraging than Southern Resident males, and have a lower prey capture rate[97], suggesting that NRKW males may in fact be more costly. If mothers divert investment from costly sons to meet their own nutritional needs or those of additional offspring, the resulting costs may be reflected in the son's body condition rather than the mother's, consistent with the recent evidence that immature and teenage males might receive less provisioning when their matriline has more dependent juveniles[98].

The influence of the Pacific Salmon Commission's Chinook abundance index on NRKW body condition was minimal during the study period. Overall, Chinook abundance showed only a weak association with body condition, and the relationship between body condition and the number of living offspring a female had did not depend on Chinook abundance. This is surprising, given that previous studies using the Pacific Salmon Commission index as a metric of prey abundance found it to be associated with mortality[43] and calving probability[42]. It is possible that variation in our measure of Chinook salmon abundance during the study period may have been insufficient to detect an effect on body condition, as previously discussed. We may not have detected any costs of raising sons if Chinook abundance was sufficient to meet those energetic demands. However, because female body condition declined with more living offspring regardless of Chinook abundance, we reason that the cost of raising sons should have been evident as well. Additionally or alternatively, the Pacific Salmon Commission's Chinook abundance index may not accurately reflect prey availability for NRKWs, as its temporal and geographic scale may not account for seasonal variation or adequately measure the abundance of specific salmon stocks of primary importance to this population[38,99]. Fine-scale measurements of prey abundance that reflect prey species composition, seasonal gaps in prey availability, and prey quality could reveal other relationships between prey availability and NRKW body condition.

Our study highlights the costs of lifetime maternal investment of offspring in NRKWs. The results suggest that reproduction and the continual provisioning of non-dispersing offspring may limit the extent to which a mother provisions herself. Further research is needed to understand how these physiological costs might affect the fitness of both mothers and offspring. Given that body condition is associated with survivorship in RKWs[48], it is possible that reproductive output influences maternal survival. However, the annual survival rates of NRKW adult females (99% in young reproductive females to 88% in post-reproductive females[96]) suggest that the cost of maternal care is unlikely to impact survival directly when environmental conditions are sufficiently favourable to allow the populations to grow, as it did during the period of our study[58]. Instead, the cumulative costs of reproduction and provisioning may reduce future reproductive output. Similar effects have been observed in elk (*Cervus canadensis*), where prior nursing periods limit future reproduction[100], and importantly in Southern Resident killer whales, where the energetic demands of raising sons decreases future reproduction[30]. Although further research is needed to understand how these costs impact the fitness of both mothers and offspring, our findings contribute to the growing body of literature on maternal investment.

Conservation management should consider the inherent challenges faced by NRKWs mothers. Environmental stressors, including increased noise pollution, contaminants, and reduced prey availability, could further burden reproductively valuable members of this threatened population[101]. Similar physiological costs of parental care have been documented for Southern Resident killer whales[22,23,83], an endangered and declining population with greater environmental stressors, and lower reproductive success compared to NRKWs[46,96,102], and expanded analyses are underway. Finally, applying well-studied behavioural concepts like parental investment to highly social systems can reveal the complexity and variety of reproductive behaviour and life history strategies.

Data availability

The datasets and code generated during and/or analysed during the current study are available in the "costs-of-maternal-care-NRKWs" repository, https://github.com/sharon-kay/costs-of-maternal-care-NRKWs, or can be requested from the corresponding author via e-mail: sharon.wc.kay@gmail.com.

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Author contributions

SK: Conceptualization; Data Curation; Funding Acquisition; Formal Analysis; Investigation; Methodology; Visualization; Writing – Original Draft Preparation, Writing – Review & Editing. AGR: Conceptualization; Data Curation; Formal Analysis; Investigation; Methodology; Project Administration; Visualization; Writing – Original Draft Preparation; Writing – Review & Editing. BCV: Conceptualization; Funding Acquisition; Investigation; Methodology; Project Administration; Writing – Original Draft Preparation; Writing – Review & Editing. LGB: Conceptualization; Funding Acquisition; Investigation; Methodology; Project Administration; Supervision; Writing – Extensive Review & Editing. PRT: Methodology; Formal Analysis; Validation; Writing – Review & Editing. GJS: Methodology; Writing – Review & Editing. HF: Investigation; Funding Acquisition; Writing – Review & Editing. JWD: Investigation; Funding Acquisition; Writing – Review & Editing. CTD: Conceptualization; Funding Acquisition; Methodology; Project Administration; Supervision; Writing – Extensive Review & Editing. All authors commented on previous versions of the manuscript and approved the final manuscript.

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Competing interests

The authors declare no competing interests.

Compliance with ethical standards

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Additional information

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