Lactation performance in polar bears is associated with fasting time and energetic state

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ABSTRACT: Females must continually make resource allocation decisions because of fitness trade-offs between self-maintenance and investment in current offspring, yet factors underpinning these decisions are unresolved. Polar bears *Ursus maritimus* face considerable allocation challenges when seasonal sea-ice melt precludes access to prey for several months, and females rely solely on energy stores to cover their own energetic needs and provision offspring. We tested how female polar bears regulate lactation during onshore fasting (i.e. capital breeding) and determined the consequences of moderated lactation for females and cubs. Overall, milk energy declined, and lactation was more likely to cease with longer time fasting. Lactation was partially mediated by maternal energetic state and depended on litter characteristics. Milk energy declined more sharply with fasting time (~2.6 times more strongly) in females with 2 offspring compared to those with 1. Females with cubs-of-the-year produced higher energy milk than those with yearlings, and their milk energy also increased more strongly with maternal energy density. Milk energy declines benefited females via reduced depletion of maternal energy reserves, but cub growth decreased. Altered lactation investment likely has consequences for both female survival and the fate of offspring, which could scale up to influence population dynamics. Given that Arctic warming means polar bears across much of their range will experience longer periods without access to primary prey, our results underscore how lactation will likely become increasingly compromised.

KEY WORDS: *Ursus maritimus* · Sea ice · Arctic · Climate change · Life-history tactics · Capital breeding

1. INTRODUCTION

During their lifetime, animals must manage allocation of their limited resources between competing processes (Stearns 1992). Allocation decisions based on internal physiological state and external conditions lead to life-history trade-offs, for example, between current and future reproduction (Roff 1992). In mammals, high energetic costs associated with milk production (Oftedal & Gittleman 1989, Thometz et al. 2016) mean that during lactation, females must balance resource investment in current offspring (and the fitness benefits associated with offspring growth and survival) with the costs to their own body condition, survival, and potential fitness gains from subsequent reproductive efforts. The challenges of optimal energy allocation are particularly acute for species that cover the energetic costs of lactation

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using accumulated body reserves i.e., species that occupy the 'capital breeding' end of the continuum in maternal energy management, as opposed to meeting reproductive costs by continual foraging, i.e., 'income breeding' (Jönsson 1997, Stephens et al. 2009).

Polar bears *Ursus maritimus* are an example of a long-lived mammal that provisions offspring with lipid-rich, high-energy milk, while also facing long periods of food scarcity. Along with phocid seals, mysticete whales, and other ursids (Oftedal 1993), polar bears can lactate while fasting, relying entirely on their stored energy reserves to support both their own needs and the needs of their offspring (Atkinson & Ramsay 1995, Oftedal 2000). Females give birth and nurse their altricial cubs while fasting in winter dens for 3-4 mo (Ramsay & Stirling 1988). During the subsequent prolonged weaning period that can typically last up to ~2.5 yr, accessibility of their key prey, seals, varies seasonally. Prey are abundant during seal pupping in the late spring but typically become scarcer in the summer and autumn due to unfavourable hunting conditions and shifts in prey distribution (Smith 1980, Stirling & Øritsland 1995, Galicia et al. 2020). In the southern extent of their range (e.g. Hudson Bay, Canada), polar bears are forced onto land when sea ice melts annually in the summer and must fast for several months until the ice returns with winter freeze-up. As such, across their reproductive cycle, female polar bears alternate between a capital breeding strategy (catabolising energy stored prior to fasting to support reproduction) and an income breeding strategy (fuelling reproductive investment by concurrent feeding while on sea ice) (Jönsson 1997, Stephens et al. 2009). Energy reserves accumulated from feeding on lipid-rich seals mean females can typically sustain considerable mass loss while fasting — for example, ranging from 1.0 to 1.49 kg d^{-1} for females with offspring onshore in the Western Hudson Bay subpopulation (Arnould & Ramsay 1994, Pilfold et al. 2016).

For long-lived iteroparous species, reproductive efforts during periods of food scarcity must be balanced against a female's own requirements for survival (and against costs to her future reproductive capacity) (Bunnell & Tait 1981, Stearns 1992, McNamara & Houston 1996). Polar bears adjust their reproductive investment to cope with the energetic constraints imposed by the variable Arctic environment. For example, delayed blastocyst implantation and short gestation times mean that females can abandon a pregnancy before parturition with minimal incurred cost (Derocher et al. 1992), and litter

size at den emergence can be predicted from female energy density at den entry (Molnár et al. 2011). Litter size in spring and autumn also increases with maternal age (peaking around 14–16 yr of age), which may reflect age-related increases in maternal body mass (Derocher & Stirling 1994). Along with reduced milk energy output reported in females with older offspring (Arnould & Ramsay 1994), some individuals cease lactation during prolonged fasting, while others continue lactating under similar conditions (Derocher et al. 1993). Given that cubs must devote energy toward structural growth but have not yet built the substantial energy reserves (i.e. adipose tissue) needed to sustain them through periods of food scarcity, a decline in maternal provisioning during the fasting period may impact offspring growth and survival, with consequences for recruitment. This reliance on maternal milk is particularly acute for cubs-of-the-year (COY), which have the highest skeletal growth rates (Arnould & Ramsay 1994) but smallest adipose deposits of all age classes (Pond et al. 1992).

Despite the importance of female lactation performance to recruitment and population demographics, there is considerable uncertainty surrounding when polar bears reduce or cease investment in lactation when fasting (Molnár et al. 2020, Miller et al. 2022), and the underlying factors that moderate lactation effort remain unresolved. This dearth of information regarding processes governing polar bear lactation is of particular concern given that rapid sea-ice loss across the Arctic is forcing many subpopulations to undertake longer fasting periods, and likely placing added nutritional stress on females with offspring (Stirling & Derocher 2012).

Here, we aimed to establish how fasting time and energetic state affect lactation in polar bears. We measured the body composition and milk energy content of female polar bears with offspring, which were captured while fasting on land for varying periods. Using a Bayesian hierarchical approach to model energetic status and milk composition, we tested how milk energy content and cessation of lactation were related to fast duration and maternal energy stores. We expected that females would be more likely to reduce the energy content of their milk and to cease lactation with increased time spent fasting, and that this relationship would be underpinned by maternal energy status. We also explored the effects of additional factors we considered potentially important in determining lactation patterns (maternal age, litter size, and cub age class). Because we expected reduced allocation to lactation to arise as an energy-saving mechanism, we then tested whether

declining milk energy content buffered the depletion of energy reserves by females fasting on land using data from bears with offspring that were recaptured within the same season. Finally, to determine consequences for offspring, we explored how reduced maternal investment in lactation impacted offspring mass loss and growth.

2. MATERIALS AND METHODS

2.1. Data collection

Adult female polar bears with accompanying offspring were captured during the ice-free period from 30 July to 2 November in 1989 and 1992–1994 while onshore on the western coast of Hudson Bay between the Churchill and Nelson rivers (57° 00′ to 58° 50′ N; 92° 25′ to 94° 15′ W). Bears were located via aerial search, captured non-selectively, and immobilized using standard procedures (8 mg Telazol administered per kg of estimated body mass; Stirling et al. 1989). Straight-line body length was recorded following standard procedure, and bears were weighed (± 0.45 kg) in a nylon net using an electronic load cell suspended from a tripod. Age was estimated from annuli in the cementum of a vestigial premolar tooth or by cross-referencing ID numbers of marked individuals with capture records. Litter size, and offspring body mass and straight-line body length were recorded, along with age class of offspring (COY [<1 yr old] were distinguished from yearlings [between 1 and 2 yr old] based on body size and tooth eruption). No captured females were accompanied by 2 yr olds. Total body lipids were estimated via isotopic dilution following standard procedures outlined by Farley & Robbins (1994) and described in detail by Atkinson & Ramsay (1995). For more information on data collection procedures, see Atkinson (1996) and Atkinson & Ramsay (1995).

2.2. Lactation performance

Adult females were given an intra-muscular injection of 2.5 ml oxytocin and nipples were cleaned of debris. After 5 min, milk was manually expressed from mammary glands. Individual mammary glands were evacuated as extensively as possible with milk pooled into a single sample for each bear. Samples were frozen at −20 °C until subsequent analysis. Two subsamples of 2–4 g were taken from each thawed milk sample and dried at 90 °C. Dry mass as a per-

centage of wet weight was calculated for each subsample, and the mean across subsamples was taken as the milk solid content (%) for that sample. On 9 occasions, milk could not be expressed from a female's mammae. Although the absence of milk could be due to low milk production and recent cub suckling, the nipples of these bears showed no sign of recent suckling and their mammae were regressed or smaller compared to bears that did produce milk. We thus considered these bears to be non-lactating (possibly due to mammary involution). Seven non-lactating females were accompanied by yearlings, and 2 were accompanied by COY.

Total body lipids and milk solids were measured in 24 individual bears, with some individuals captured more than once in the same year and among years (mean ± SD interval between within-year captures = 54 ± 19 d; average date of first capture 30 August, recapture 24 October), giving 41 total observations of body composition and lactation performance (23 samples from females with COY, 18 with yearlings) (Table 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m720p175_supp.pdf). Bears lost an average of 40.1 ± 25.5 kg of body mass between within-season captures with daily mass loss rates of 0.72 ± 0.25 kg).

2.3. Analysis

All analyses were carried out using R 3.2.0 (R Core Team 2021). We used published summary data on percentage milk solids and milk energy content in female polar bears (Derocher et al. 1993) to derive the following linear relationship: log(milk energy) = 1.33 + 2.92 × proportion milk solids, which we used to calculate gross milk energy (kJ g^{-1}) from proportion milk solids. We developed 6 models for our analyses: the first 2 models assessed whether lactation was affected by fasting time and maternal body condition, the third model tested whether changes in lactation investment affected maternal energy loss rates, and the final 3 models assessed the impact of altered maternal lactation investment on offspring.

2.3.1. Estimating time spent fasting

We calculated time spent fasting as the difference between capture date and the date that polar bears were expected to have arrived onshore each year, estimated to be 27 d after the sea-ice extent in West-

Table 1. Overview of milk samples collected from female polar bears with 1 or 2 offspring, classed as either cubs-of-the-year or yearlings. Total number of milk samples (including recaptures) are given by year, with number of individual bears shown in brackets alongside. Also shown is maternal mass, age range of females, and number of females that were considered above prime reproductive age

Year	Onshore date	Litter size = 1		Litter size = 2	
		Cub-of-the-year	Yearling	Cub-of-the-year	Yearling
1989	2 August	3 (3)	1 (1)	2 (2)	3 (3)
1992	25 August	2 (1)	6 (3)	–	2 (1)
1993	3 August	4 (2)	2 (1)	–	–
1994	5 August	6 (3)	2 (1)	6 (3)	2 (1)
Maternal mass ± SD (kg)		214.9 ± 33.4	205.4 ± 46.1	208.9 ± 32.8	200.0 ± 23.6
Maternal age range (yr)		6–21	9–24	7–17	10–18
Females ≥ 18 yr		1	3	0	1

ern Hudson Bay dropped below 30% in a given year (previously identified as a critical threshold when bears generally abandon the receding ice, move ashore, and begin fasting — see Molnár et al. 2020 for a detailed explanation of sea-ice threshold calculations and associated mechanisms underlying polar bear migration). The estimated date of onshore arrival may not be the exact date that a bear stops feeding (e.g. 1 bear was caught on land 4 d before that year's critical threshold value) but we considered days since arriving onshore to be a conservative approximation of accumulated fasting time.

2.3.2. Estimating energy density

Because our goal was to determine the energetic constraints to polar bear lactation, we estimated individual body condition in terms of energy density (i.e. storage energy per unit of lean body mass) using a body composition model previously developed for polar bears (Molnár et al. 2009). The model calculates an individual polar bear's storage energy (MJ) using total body mass, straight-line body length, and estimates of the proportion of storage that consists of lipid. We used measurements of total body lipids, body mass, and straight-line body length on captured bears to re-parameterize the model for each bear in our data set, allowing us to account for individual variation in body composition. Briefly, we first calculated γ, i.e. the proportion of storage energy that is stored in lipid reserves, at each capture following Molnár et al. (2009) (their Eq. 15). We then developed a hierarchical Bayesian measurement error model for γ that was incorporated in subsequent models (see below) to estimate energy density as a predictor variable. The measurement error model assumed

that there was a single, true value of γ for each bear j (assuming strong homeostasis; Kooijman 2010), and any within-individual variation in γ stemmed from sampling/observation error, where:

$$\gamma_{obs_{i,j}} \sim \text{Beta}[\gamma_{true_j} \times \phi, (1 - \gamma_{true_j})\phi]$$
$$\gamma_{true_j} \sim \text{Beta}(\chi, \tau)$$
$$\chi \sim \text{Beta}(1, 1)$$
$$\tau \sim \text{HalfCauchy}(0, 5)$$

(1)

We assumed there is a true, latent random variable γ_{true_j} for the jth bear, with the observed proportion $\gamma_{obs_{i,j}}$ for the ith sample drawn from a beta distribution (reparametrized in terms of its mean γ_{true} and precision ϕ by moment matching from the shape parameters α and β). We modelled γ_{true_j} as also being drawn from a Beta distribution with hierarchical priors. To aid in identifiability, we fixed the precision of $\gamma_{obs_{i,j}}$ at $\phi = 5000$ (i.e. equal to an SD of 0.014). We used the estimated γ_{true_j} value for each adult bear to calculate total storage energy (MJ) and total lean body mass (kg) at each capture following Molnár et al. (2009) (their Eqs. 9, 11, 12, 13A) and then calculated energy density (MJ kg^{-1}) as the ratio of total storage energy to lean body mass. We calculated the body composition of offspring similarly but assumed that the value for γ could vary between captures in growing bears, and thus did not incorporate the measurement error model for offspring.

2.3.3. Lactation analysis

We used a Bayesian hierarchical modelling approach to test potential factors we considered likely to influence lactation, in combination with a directed acyclic graph to consider relationships between pre-

dictor variables and to decide on model structure. Our first model structure (Model 1) included milk energy (kJ g^{-1}) as the response variable, (positive, continuous), and included the following independent variables: days since onshore arrival, litter size (categorical, coded using sum contrasts where −0.5 was a litter of 1, and 0.5 was a litter of 2), offspring age class (categorical, coded using sum contrasts and −0.5 for COY and 0.5 for yearlings), maternal energy density (MJ kg^{-1}); maternal age (years), and litter mass (kg) (Table 2). All continuous variables were standardized to have a mean = 0 and standard deviation = 1, and we included the Bayesian measurement error described above when calculating energy density. We included interactions between days onshore and offspring age, and between days onshore and litter size to assess whether effects of fasting time depended on the age or the number of accompanying offspring. Since our aim was to test if energetic state underpinned lactation responses to fasting time on land, we also built a second model (Model 2) that excluded days onshore as an explanatory variable but otherwise followed the same structure (with energy density used in place of days onshore in the interaction terms) (Table 2). By conditioning on days onshore, Model 1 also tests for causal effects of energy density independent of fasting period, while Model 2 deliberately excludes days onshore to test for the mediating effect of energy density i.e. days onshore might impact lactation if females reduce energy output when incoming energy is low (a direct effect of fasting time on lactation) or because their energy reserves are increasingly depleted when fasting on land (fasting time affects energy density, which impacts lactation).

Although milk energy (kJ g^{-1}) was a positive, continuous variable $y_{ij} > 0$, we assumed y_{ij} could also take on true values of zero when a female was not lactating (i.e. bears with cubs from which no milk could be obtained). The subscript ij refers to the ith observation for bear j, and n_j is the number of observations for bear j ($n_j = 1$ or 2). Because the data were a mixture of true zeros and positive continuous values bounded by zero, we used a log-normal hurdle model to allow modelling of both the zero data and the continuous y_{ij} data. The continuous data were assumed to follow a log-normal distribution, parameterized in terms of its location μ, and scale σ. For the 'hurdle' part of the model, we let z_{ij} be a random variable describing lactation status of females with cubs: 1 if a female was lactating and 0 if not, with errors assumed to follow a Bernoulli distribution with probability p_{ij}. The general model for gross milk energy y_{ij} is then given by:

$$y_{ij} \begin{cases} 0 & z_{ij} = 0, \\ \text{LogNormal}(\mu_{ij}, \sigma) & z_{ij} = 1 \end{cases} \quad (2)$$

The probability of lactation p_{ij} was modelled as a logistic function of independent variables x_l (predictor variables and interaction terms listed in Table 2), and the location parameter for milk energy μ_{ij} was modelled as a function of x_k:

$$p_{ij} = \frac{\exp(\Psi_{0,j} + \sum_{l=1}^{n_l} \Psi_l x_{l_{ij}})}{1 + \exp(\Psi_{0,j} + \sum_{l=1}^{n_l} \Psi_l x_{l_{ij}})}$$

$$\mu_{ij} = \beta_{0,j} + \sum_{k=1}^{n_k} \beta_k x_{k_{ij}}) \quad (3)$$

Table 2. Structure of the 6 models used in our analyses to assess female lactation investment and the effects of altered lactation investment on females and offspring

Model structures
Assessing female lactation investment
1 Maternal milk energy ~ days onshore × litter size + days onshore × cub age + maternal energy density + maternal age + litter mass
2 Maternal milk energy ~ maternal energy density × litter size + maternal energy density × cub age + maternal age + litter mass
Assessing maternal responses to altered lactation investment
3 Change in maternal storage energy ~ change in maternal milk energy + capture interval + initial maternal energy density
Assessing offspring responses to altered lactation investment
4 Change in offspring mass ~ change in maternal milk energy + capture interval + initial offspring mass
5 Change in offspring storage energy ~ change in maternal milk energy + capture interval + initial offspring energy density
6 Change in offspring length ~ change in maternal milk energy + capture interval + initial offspring length

The parameters $_{0,j}$ and $\beta_{0,j}$ were assumed to be drawn from a population with respective means of $\mu_{_0}$, μ_{β_0} and variance $\sigma_{_0}$, σ_{β_0} (i.e. individual variation among bears in the average milk energy content was treated as a 'random effect', borrowing strength from the hierarchical model structure) (Gelman et al. 2013). Additional variation in y_{ij} was modelled as sampling error, σ (Hobbs & Hooten 2015).

The joint and posterior distributions of the full hierarchical model were given by:

$$[\boldsymbol{\beta}, \sigma, \boldsymbol{\psi}, \boldsymbol{z}, \sigma_{\beta_0}, \sigma_{\psi_0}, \chi, \tau \mid \boldsymbol{y}, \boldsymbol{\gamma}] \propto$$

$$\prod_{j=1}^{24}\prod_{i=1}^{n_j} \text{LogNormal}(y_{ij} \mid \mu_{ij} \times z_{ij}, \sigma)\ \text{Bernoulli}(z_{ij} \mid p_{ij})$$

$$\times \text{Beta}(\gamma_{obs\,i,j} \mid \gamma_{true\,j} \times \phi, (1 - \gamma_{true\,j})\phi) \times \text{Beta}(\gamma_{true\,j} \mid \chi, \tau)$$

$$\times \text{Beta}(\chi \mid 1, 1)\ \text{Half Cauchy}(\tau \mid 0, 5)$$

$$\times \text{Normal}(\beta_{0,j} \mid \mu_{\beta_0}, \sigma_{\beta_0})$$

$$\times \text{Normal}(\psi_{0,j} \mid \mu_{\psi_0}, \sigma_{\psi_0})$$

$$\times \prod_{k=1}^{n_k}\text{Normal}(\beta_k \mid 0, 0.5) \tag{4}$$

$$\times \text{Normal}(\mu_{\beta_0} \mid 2, 0.5)\text{Half Cauchy}(\sigma_{\beta_0} \mid 0, 5)$$

$$\times \text{Half Cauchy}(\sigma \mid 0, 5)$$

$$\times \prod_{l=1}^{n_l}\text{Normal}(\psi_l \mid 0, 1)$$

$$\times \text{Normal}(\mu_{\psi_0} \mid 0, 1.5)\text{Half Cauchy}(\sigma_{\psi_0} \mid 0, 5)$$

2.3.4. Energetic savings by females

To test if reduced milk energy content was associated with reduced energy loss for females, we built a third Bayesian model (Model 3) using a subset of lactating bears that were recaptured within the same fasting season (n = 14). After accounting for initial differences in energy density, we expected females that decreased their milk energy content between captures would lose storage energy at lower rates than females that maintained greater milk energy content (i.e. females that reduced the energetic content of their milk the most would lose a smaller amount of stored energy between captures). The model was structured: storage energy loss (MJ) ~ milk energy reduction (kJ g^{-1}) + capture interval (d) + initial energy density (MJ kg^{-1}) (Table 1). All variables were continuous and standardized prior to fitting, and we incorporated the same Bayesian measurement error model as described above when estimating storage energy loss. Although storage energy declined between captures for all bears in our study, we assumed that energy loss was a continuous variable s_j that could take on positive or negative values (i.e. bears could theoretically increase storage energy between captures e.g. by feeding on terrestrial foods). We assumed s_j followed a normal distribution with mean μ_s and scale σ_s, and we modelled μ_{s_j} as a linear function of independent variables x_h (listed in Table 2):

$$\mu_{s_j} = \beta_{s_0} + \sum_{h=1}^{h}\beta_{s_h} x_{h_j} \tag{5}$$

The joint and posterior distributions of Model 3 were then given by:

$$[\boldsymbol{\beta_s}, \sigma_s, \chi, \tau \mid \boldsymbol{s}, \boldsymbol{\gamma}] \propto \prod_{j=1}^{14}\prod_{i=1}^{n_j}\text{Normal}(s_j \mid \mu_{s_j}, \sigma_s)$$

$$\times \text{Beta}[\gamma_{obs\,i,j} \mid \gamma_{true\,j} \times \phi, (1 - \gamma_{true\,j})\phi] \times \text{Beta}(\gamma_{true\,j} \mid \chi, \tau)$$

$$\times \text{Beta}(\chi \mid 1, 1)\ \text{Half Cauchy}(\tau \mid 0, 5) \tag{6}$$

$$\times \prod_{h=0}^{3}\text{Normal}(\beta_{s_h} \mid 0, 1)$$

$$\times \text{Half Cauchy}(\sigma_s \mid 0, 5)$$

2.3.5. Effects of lactation on offspring

Lastly, we tested if offspring were affected by changes in lactation performance by modelling the difference in body mass, storage energy, and straight-line body length in offspring that were recaptured in the same season (n = 18) in response to changes in maternal milk energy content over the same period. We expected that a greater reduction in maternal milk energy would be associated with greater losses in offspring body mass and storage energy, and smaller increases in straight-line body length between recaptures. The 3 models for offspring responses were structured similarly, with either the difference in body mass (kg), storage energy (MJ), or straight-line body length (cm) as the response variable, and maternal milk energy reduction (kJ g^{-1}) and capture interval (days) as predictor variables (Table 2). We also included either the offspring's initial body mass, energy density, or straight-line body length in each model to account for initial differences in size/body composition. Observed differences in body mass $c_{m,j}$ and storage energy $c_{s,j}$ for the jth cub were modelled as continuous variables (Models 4 and 5, respectively), which we assumed could take on positive or negative values. Both variables were assumed to follow normal distributions,

parameterized by the mean μ_c and scale σ_c. We modelled μ_c in each model as a linear function of independent variables x_h (Table 2), where:

$$\mu_{c_j} = \beta_{c_0} + \sum_{h=1}^{n_h} \beta_{c_h} x_{h_j} \tag{7}$$

The joint and posterior distribution for each model (where c represents either c_m or c_s) was then given by:

$$
\begin{aligned}
[\boldsymbol{\beta_c}, \sigma_c | \boldsymbol{c}] &\propto \prod_{j=1}^{18} \text{Normal}(c_j \mid \mu_{c_j}, \sigma_c) \\
&\times \prod_{h=0}^{3} \text{Normal}(\beta_{c_h} \mid 0, 1) \\
&\times \text{Half Cauchy}(\sigma_c \mid 0, 5)
\end{aligned} \tag{8}
$$

We assumed the observed difference in straight-line body length $c_{l,i}$ (Model 6) followed a Poisson distribution (as a linear function of predictors with a log link), given that observations could take on positive or zero values only, i.e. assuming cubs could not decrease in length between recaptures, and because the observed data consisted of discrete values (straight-line body length was measured to the nearest cm). Three cubs were recorded as being slightly shorter than their initial capture lengths, so we assumed that these cubs had not grown and set their difference in length to zero. The joint and posterior distribution for difference in straight-line body length was then given by:

$$
\begin{aligned}
\lambda_j &= \exp(\beta_{c_0} + \sum_{h=1}^{n_h} \beta_{c_h} x_{h_j}) \\
[\boldsymbol{\beta_c} | \boldsymbol{c}] &\propto \prod_{j=1}^{18} \text{Poisson}(c_{l_j} \mid \lambda_j) \\
&\times \text{Normal}(\beta_{c_0} \mid 0, 1) \\
&\times \prod_{h=1}^{3} \text{LogNormal}(\beta_{c_h} \mid 0, 0.5)
\end{aligned} \tag{9}
$$

2.3.6. Model fitting

Posterior distributions for the parameters of the Bayesian models were estimated using Hamiltonian Monte Carlo sampling in Stan via the R package *rstan* (Stan Development Team 2021). We used prior predictive simulations to establish regularizing priors and limit overfitting. To compare models with and without interaction terms, we used leave-one-out (LOO) information criteria, computed from the log-likelihood of the posterior samples via the R package *loo* (Vehtari et al. 2022). Models were run with 4 Markov Chain Monte Carlo chains, each with an ini-

tial adaptation phase of 1000 iterations and a sampling phase of 10 000 iterations (giving 40 000 total samples of the posterior distribution). Good chain mixing was indicated by visual inspection of trace plots and density plots, and convergence was confirmed by Gelman-Ruben statistics of $\hat{R} < 1.01$ and high numbers of effective sample sizes. We carried out additional posterior predictive checks to assess lack of fit between the models and the data (Gabry et al. 2019), implemented via the *bayesplot* R package (Gabry & Mahr 2022). Pareto's K values from LOO comparisons (with moment matching) were acceptable for all models. Following McElreath (2020), we report 89% compatibility (credible) intervals. We also report the magnitude of overlap between the posterior parameter distribution and zero (i.e. the probability of direction) as an index of the strength of evidence for a parameter's influence on the response. A smaller overlap with zero indicates stronger evidence for the presence of an effect, though in keeping with Bayesian philosophy, we do not define any (subjective) hard limit for the probability of direction.

3. RESULTS

In agreement with our expectations, maternal energy density was negatively correlated with days since onshore arrival (Pearson's r = −0.49; t = −3.51, df = 39, p = 0.001), and females with a litter of 1 cub tended to be of higher energy density than those with 2 cubs (Fig. 1A; 89% CI = −4.79; −1.38). Females with COY were of similar energy density to those with yearlings (Fig. 1B; 89% CI = −1.29; 2.03).

3.1. Associations between lactation and days since arrival onshore (Model 1)

In Model 1 (with days onshore), LOO Information Criteria indicated the most parsimonious model retained an interaction between days onshore and litter size (Table S2). Lactation probability declined with days since onshore arrival (overlap with zero for $\psi_{\text{days onshore}} < 0.01$; Fig. 2A, Fig. S1), with no clear difference between litter sizes (overlap with zero for $\psi_{\text{litter size}} = 0.40$). Gross milk energy also declined with days onshore (Fig. 2B; see β parameters in Table 3). This decline in milk energy depended on litter size (overlap with zero for $\beta_{\text{days onshore} \times \text{litter size}} = 0.03$; Fig. S1B) and was steeper for females with litters of 2 cubs than those with 1 cub (Fig. 2B). Cub age class also affected lactation
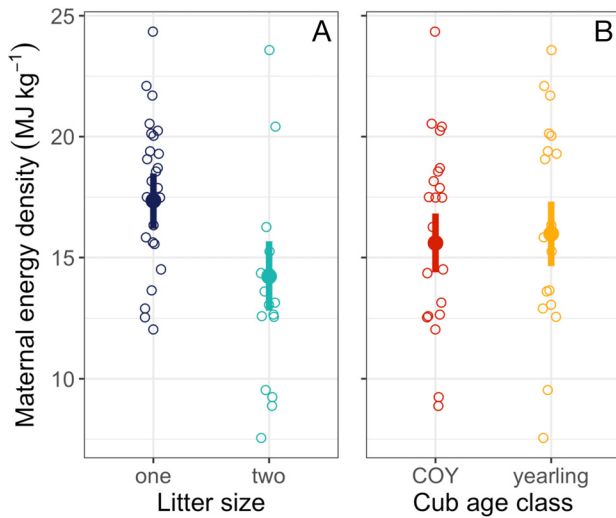
Fig. 1. Energy density of fasting female polar bears captured onshore in Western Hudson Bay with (A) litters of 1 or 2 offspring; and (B) accompanied by cubs-of-the-year (COY) or yearlings. Hollow circles show estimated energy density (mean of the posterior distribution for each individual, predicted at the average number of days since onshore arrival: 39 d). Filled circles represent overall mean maternal energy density and the bars show 89% credible intervals

performance (Fig. 2C, Table 3): gross milk energy was lower in females with yearlings (overlap with zero for $\beta_{cub\ age\ class}$ = 0.01; Fig. S1B); and there was some evidence that females with yearlings were more likely to stop lactating (overlap with zero for $\psi_{cub\ age\ class}$ = 0.15). There was no clear evidence for additional effects of maternal age (Fig. S2A), maternal energy density, or litter mass (Fig. S2B) on lactation (overlaps with zero: 0.49, 0.46, and 0.41, respectively; Fig. S1).

3.2. Associations between lactation and energetic state (Model 2)

According to LOO information criteria (Table S3), the most parsimonious version of Model 2 (with energy density) retained interactions between maternal energy density and cub age class. Lactation probability was positively related to maternal energy density (overlap with zero for $\psi_{energy\ density}$ = 0.02; Fig. S3). We also detected some evidence of an effect of cub age class on lactation probability (overlap with zero for $\psi_{cub\ age\ class}$ = 0.12), whereby females with yearlings were more likely to stop lactating than females with COY (Fig. 3A, Table 4). The gross milk energy produced by females was positively associated with maternal energy density, but the strength of this relationship depended on cub age class (over-

lap with zero for $\beta_{energy\ density\ \times\ cub\ age}$ = 0.06; Fig. S3B). Milk energy increased more strongly with energy density for females with COY than those with yearlings (Fig. 3B, Table 4). In agreement with Model 1, there was no clear evidence for an effect of maternal age (Fig. S4A) or litter mass (Fig. S4B) on lactation in Model 2 (overlaps with zero: 0.35 and 0.39, respectively; Fig. S3B, Table 4).

3.3. Milk energy reduction and maternal energy savings (Model 3)

After accounting for positive effects of capture interval and initial energy density, total storage energy loss was negatively associated with the observed reduction in milk energy between captures (Table 5; overlap with zero for $\beta_{s,\ \Delta\ milk\ energy}$ = 0.05; Fig. S5). Females that showed larger reductions in milk energy content between captures lost less storage energy during the recapture interval than females with smaller reductions in milk energy content (Fig. 4).

3.4. Effects of milk energy reduction on offspring (Models 4–6)

All offspring lost mass between recaptures, but we did not detect any effect of maternal milk energy reduction on offspring mass loss or storage energy loss (Table 6, Fig. S6A,B). However, offspring growth (change in body length) was positively associated with the difference in maternal milk energy content between recaptures (overlap with zero for $\beta_{c,\ \Delta\ milk\ energy}$ = 0; Table 6, Fig. 5, Fig. S6C). Offspring growth in length increased when females had smaller reductions in milk energy content.

4. DISCUSSION

Our Bayesian hierarchical modelling approach identified a negative association between days since onshore arrival and both the gross milk energy produced by a female and the probability of lactation. Our second model aimed to explain the mechanism underpinning these observed relationships by testing whether similar trends were evident in a model that contained just maternal energy density (and covariates). Overall, our results suggested that the decline in female lactation performance was, at least partially, mediated by the energetic
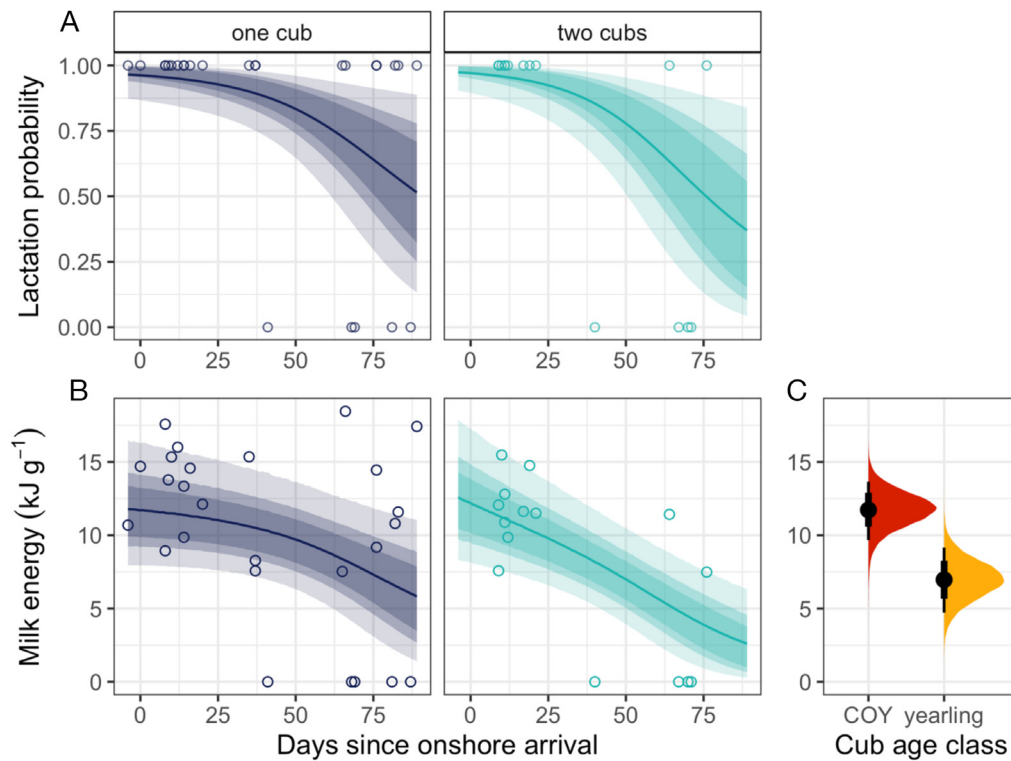
Fig. 2 (A) Lactation probability and (B) predicted gross milk energy of female polar bears as a function of litter size and days since onshore arrival, and (C) age of accompanying offspring. Lines in (A) and (B) show the mean of the posterior distribution and shaded areas show the prediction intervals from the first Bayesian hurdle model [Model 1], where (A) shows the zero process and (B) incorporates both the zero and continuous process (light, medium, and darker shading = 89, 67, 50% prediction intervals). Filled circles in (C) show the mean gross milk energy for females with cubs-of-the-year (COY) or yearlings, black bars show the credible intervals (thicker bar = 67% CI and thinner bar = 89% CI), and shaded areas show posterior distributions. Remaining variables were held at their mean values for predictions

state of the mother, but also by characteristics of her litter (cub age class, litter size). In keeping with expected life-history strategies for long-lived species (Gaillard & Yoccoz 2003, Hamel et al. 2010, Festa-Bianchet et al. 2019), females that reduced the energy content of their milk across the fasting period used less of their energy reserves, underscoring the benefits of reduced lactation for maternal energy savings at the expense of offspring growth.

4.1. Time spent fasting reduces lactation effort

The decline in lactation performance with days onshore was in line with our expectations, indicating that females reduce investment in lactation as the fasting season progresses. Predicted lactation probability at the start of the onshore period was close to 100% for both females with COY and yearlings. After ~3 mo on land, the probability of a female with COY lactating was 53% and dropped

as low as 35% for a female with yearlings. This result closely matches a previous report that only 38% of observed females with yearlings in Western Hudson Bay were still lactating by October (Derocher et al. 1993). In our study, females that were capable of sustained lactation nonetheless showed a declining investment in the energetic quality of milk produced as fasting time increased, and those with 2 cubs reduced their milk energy output more sharply with fasting time than those with a single cub, indicating that larger litters might exhaust the reserves a female can allocate earlier in the fasting period. This was further supported by females with litters of 2 in our study tending to be of lower maternal energy density overall (Fig. 1A). A reduction in milk energy output could potentially signal impending cessation of lactation due to the energetic strain of provisioning 2 cubs (Hurley 1989, Derocher et al. 1993), and may be a contributing factor in lower cub survival rates reported in larger litters for this subpopulation (Derocher & Stirling 1996).

Table 3. Mean, SD, and 89% credible intervals of the posterior distribution for the parameters of Model 1 (with days onshore; see Table 2) that describes lactation probability and gross milk energy (kJ g^{-1}) of female polar bears fasting onshore in Western Hudson Bay. Posterior distributions for the parameters of the Bayesian measurement error model for body composition are also shown. See Eqs. 1 and 3 for parameter descriptions

Parameter	Mean	SD	Lower 89%	Upper 89%
Lactation probability				
$\psi_{cub\ age\ class}$	0.931	0.910	−0.538	2.373
$\psi_{energy\ density}$	−0.386	0.700	−1.533	0.693
$\psi_{litter\ size}$	0.215	0.883	−1.203	1.637
$\psi_{days\ onshore}$	1.543	0.625	0.575	2.570
$\psi_{maternal\ age}$	−0.070	0.628	−1.049	0.941
$\psi_{litter\ mass}$	0.358	0.641	−0.665	1.384
$\psi_{days\ onshore\ \times\ litter\ size}$	0.374	0.791	−0.895	1.627
μ_{ψ_0}	−2.187	0.774	−3.506	−1.061
σ_{ψ_0}	2.127	1.493	0.277	4.772
Gross milk energy				
$\beta_{cub\ age\ class}$	−0.413	0.180	−0.694	−0.122
$\beta_{energy\ density}$	0.005	0.057	−0.086	0.097
$\beta_{litter\ size}$	−0.200	0.128	−0.400	0.007
$\beta_{days\ onshore}$	−0.114	0.062	−0.214	−0.015
$\beta_{maternal\ age}$	−0.001	0.051	−0.083	0.078
$\beta_{litter\ mass}$	0.020	0.092	−0.128	0.164
$\beta_{days\ onshore\ \times\ litter\ size}$	−0.178	0.097	−0.332	−0.025
μ_{β_0}	2.342	0.057	2.254	2.433
σ_{β_0}	0.096	0.057	0.012	0.192
σ	0.187	0.036	0.136	0.249
Measurement error				
χ	0.934	0.008	0.920	0.945
τ	46.356	14.482	25.841	71.665

4.2. Energetic state mediates lactation performance

Although time onshore appeared to have the stronger effect on lactation, the dependence of both milk energy content and lactation probability on maternal energy density matched our expectations that females moderate investment in cubs based on their own energetic state. Maternal correlates of reproductive effort have been established in some fasting phocids, such as body mass in grey seals *Halichoerus grypus* (Mellish et al. 1999), harbour seals *Phoca vitulina* (Bowen et al. 2001), and southern elephant seals *Mirounga leonina* (Arnbom et al. 1997); and proportion of adipose tissue in northern elephant seals *M. angustirostris* (Crocker et al. 2001). However, milk production rates in fasting polar bears were previously found to be independent of body mass, albeit in a small number of individuals (Arnould & Ramsay 1994). Even though correlated with mass (Fig. S7), energy density represents the ratio of energy reserves to lean tissues (which incur

maintenance costs), and as such, may be a more suitable indicator of the fasting capacity of individual bears than total body mass (Molnár et al. 2011). By indicating how much energy is stored relative to how much is required for self-maintenance, energy density is potentially a crucial state variable in determining when females might reduce or terminate resource allocation to their young in favour of their own energetic needs. Reduction in offspring investment could occur as a direct physiological response to low body condition and food stress (Flint & Vernon 1998, Roche et al. 2007, Jonas & Woodside 2016), and/or via behavioural responses that precede physiological reductions in lactation output (e.g. rejection of cub suckling efforts) (Wade & Schneider 1992, Therrien et al. 2008).

Life-history theory suggests that older females may increase their investment in offspring to maximise fitness as they approach the end of their reproductive lifespan (Williams 1966, Clutton-Brock 1984, Roff 1992). However, there was no signal of increased lactation effort by older bears in our study. In general, polar bear litter size, litter mass, and reproductive effort increase with age/experience, before peaking and declining with senescence (Derocher & Stirling 1994, Folio et al. 2019). Body mass and body fat similarly tends to increase with age to an optimum at around 15 yr old in female polar bears, followed by a decline (Derocher et al. 1992, Atkinson & Ramsay 1995). Older bears, despite having more to gain in fitness terms, may be precluded from investing more in current reproduction by their reduced accumulation of body reserves prior to initiating fasting. Given that our sample included only 5 bears that were approaching the end of their reproductive lifespan (≥18 yr old), it is perhaps more likely that insufficient data on older individuals limited our ability to detect any increase in lactation effort with age. Additionally, we do not know the rate at which older females may have already lost cubs earlier in the season, potentially obscuring effects in our sampling period.

4.3. Offspring age and lactation

Lactation effort was further modulated by cub age class. For a given energy density, females with COY were more likely to sustain lactation and to produce milk of higher energy content than those with yearlings. Moreover, females with COY that were of higher maternal energy density also provided more energy-rich milk, whereas the milk energy from
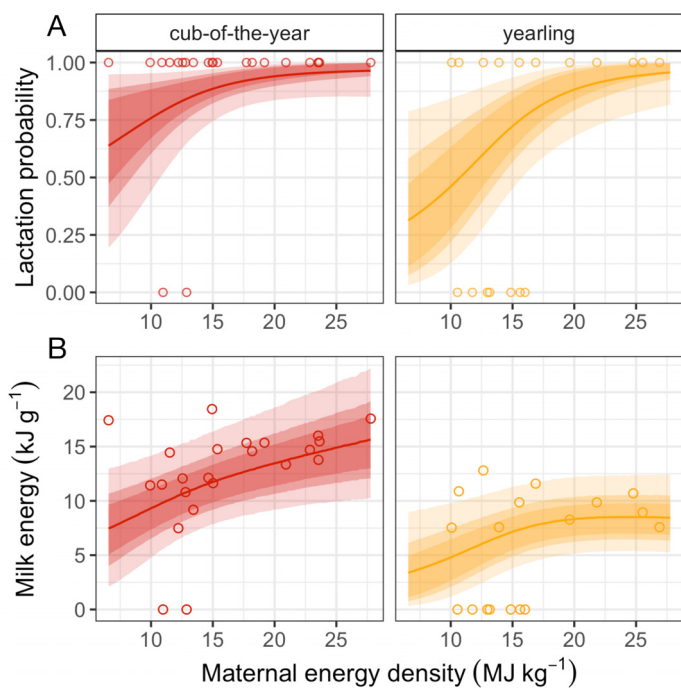
Fig. 3. (A) Lactation probability and (B) predicted gross milk energy of female polar bears as a function of maternal energy density and the age class of accompanying offspring. Lines in (A) and (B) show the mean of the posterior distribution and shaded areas show the prediction intervals from the second Bayesian hurdle model (Model 2), where (A) shows the zero process and (B) incorporates both the zero and continuous process (light, medium, dark shading = 89, 67, 50 % prediction intervals). Remaining variables were held at their mean values for predictions

Table 4. As in Table 3, but for Model 2 (with maternal energy density but not days onshore; see Table 2). See Eqs. 1 and 3 for parameter descriptions

Parameter	Mean	SD	Lower 89 %	Upper 89 %
Lactation probability				
$\psi_{\text{cub age class}}$	1.047	0.909	−0.419	2.473
$\psi_{\text{energy density}}$	−1.174	0.594	−2.168	−0.274
$\psi_{\text{litter size}}$	0.059	0.861	−1.307	1.445
$\psi_{\text{energy density} \times \text{cub age}}$	−0.003	0.610	−0.945	0.992
$\psi_{\text{maternal age}}$	−0.054	0.590	−0.975	0.897
$\psi_{\text{litter mass}}$	−0.436	0.818	−1.746	0.864
μ_{ψ_0}	−1.962	0.734	−3.225	−0.915
σ_{ψ_0}	2.039	1.409	0.269	4.468
Gross milk energy				
$\beta_{\text{cub age class}}$	−0.330	0.202	−0.650	−0.007
$\beta_{\text{energy density}}$	0.018	0.042	−0.050	0.085
$\beta_{\text{litter size}}$	−0.085	0.133	−0.295	0.130
$\beta_{\text{maternal age}}$	−0.021	0.056	−0.111	0.068
$\beta_{\text{litter mass}}$	0.025	0.097	−0.131	0.177
$\beta_{\text{energy density} \times \text{cub age}}$	−0.130	0.085	−0.266	0.003
μ_{β_0}	2.415	0.059	2.322	2.508
σ_{β_0}	0.107	0.058	0.016	0.203
σ	0.193	0.037	0.140	0.256
Measurement error				
χ	0.934	0.008	0.920	0.945
τ	46.350	14.541	25.852	71.711

Table 5. As in Table 3, but for Model 3 (describing storage energy loss [MJ] of female polar bears captured twice in the same season while fasting onshore in Western Hudson Bay; see Table 2). See Eqs. 5 and 6 for parameter descriptions

Parameter	Mean	SD	Lower 89 %	Upper 89 %
Storage energy loss				
$\beta_{s, \Delta \text{milk energy}}$	−0.314	0.188	−0.609	−0.016
$\beta_{s, \text{capture interval}}$	0.409	0.224	0.056	0.762
$\beta_{s, \text{initial energy density}}$	0.478	0.224	0.123	0.829
σ_s	0.624	0.166	0.421	0.917
Measurement error				
χ	0.942	0.008	0.930	0.953
τ	89.885	39.130	37.934	159.444

females with yearlings plateaued for females in better condition. This partial decoupling of milk energy from maternal energetic status in females with yearlings highlights that there is a potential limit to the investment that mothers of older offspring will make when fasting. Indeed, given that most yearlings in this subpopulation will have parted from their mother by the following breeding season in late spring/early summer (Stirling et al. 1999), females may already be shifting to prioritizing resource allocation towards future reproduction efforts (McNamara & Houston 1996), a pattern that broadly agrees with weaning curves in black bears *Ursus americanus* and grizzly bears *U. arctos* (Farley & Robbins 1995). Interestingly, no difference in gross milk energy has been observed in females with older cubs while bears are foraging on the sea ice (Derocher et al. 1993), underscoring that any decline in lactation performance with offspring age may depend on whether females fuel reproductive investment using incoming environmental energy or are reliant on their own body reserves. Even after accounting for

differences in age and number of offspring, as well as differences in fasting time and female body condition/age, considerable intraspecific variation remained in lactation, suggesting that additional environmental, intrinsic, and/or genetic factors may further determine milk production in polar bears.

4.4. Implications for population dynamics

Reduction of female investment in lactation during the fasting period may have considerable implica-
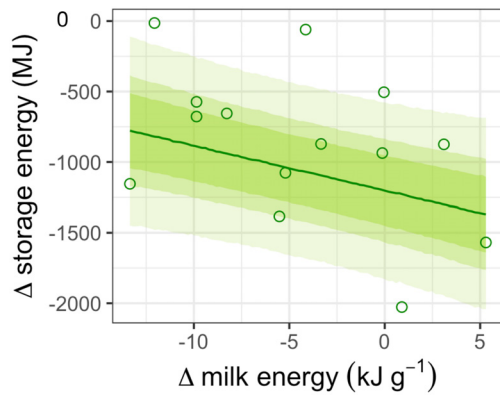
Fig. 4. Total storage energy loss and change in milk energy content of female polar bears that were recaptured during a single onshore fasting season in Western Hudson Bay. Solid line shows the mean of the posterior distribution, and shaded areas show the prediction intervals from the Bayesian model (light, medium, dark shading = 89, 67, 50% prediction intervals). Remaining variables were held at their mean values for predictions

Table 6. Mean, SD, and 89% credible intervals of the posterior distribution for the parameters of the models describing change in body mass (kg), storage energy (MJ), and straight-line body length (cm) of polar bears cubs captured twice in the same season while onshore in Western Hudson Bay (Models 4–6; see Table 2). See Eqs. 7–9 for parameter descriptions.

| Parameter	Mean	SD	Lower 89%	Upper 89%
Body mass				
$\beta_{c,\,\Delta\text{ milk energy}}$	−0.106	0.135	−0.318	0.105
$\beta_{c,\text{ capture interval}}$	0.416	0.136	0.201	0.628
$\beta_{c,\text{ initial mass}}$	0.826	0.134	0.612	1.035
σ_c	0.539	0.114	0.392	0.743
Storage energy				
$\beta_{c,\,\Delta\text{ milk energy}}$	−0.212	0.247	−0.600	0.173
$\beta_{c,\text{ capture interval}}$	0.029	0.238	0.351	0.403
$\beta_{c,\text{ initial storage energy}}$	0.591	0.253	0.183	0.985
σ_c	0.868	0.212	0.603	1.246
Straight-line body length				
$\beta_{c,\,\Delta\text{ milk energy}}$	0.831	0.160	0.583	1.094
$\beta_{c,\text{ capture interval}}$	0.316	0.081	0.194	0.452
$\beta_{c,\text{ initial length}}$	0.709	0.146	0.481	0.946
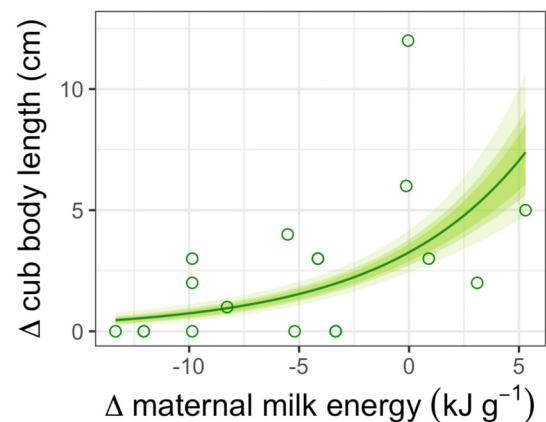
Fig. 5. Offspring growth (difference in straight-line body length) in response to the change in maternal milk energy content between captures during the onshore fasting period in Western Hudson Bay. Solid line shows the mean of the posterior distribution, and shaded areas show the prediction intervals from the Bayesian model (light, medium, dark shading = 89, 67, 50% prediction intervals). Remaining variables were held at their mean values for predictions

tions for the survival of both a female and her offspring. For the female, short-term benefits in energy savings are clear. For example, previous bioenergetic models of fasting thresholds, i.e. time until starvation based on energetic requirements, estimated that a female with COY in Western Hudson Bay could fast for approximately 111 d longer if lactation ceased immediately upon fasting rather than lactating throughout (Molnár et al. 2020). The consequences of reduced lactation for cubs are less certain. In the short term, a reduction in maternal milk provisioning may limit cub growth, as observed here and in grey seals (Iverson et al. 1993). Subsequently, and depending on offspring age and their body condition, cubs may remain with the female sharing her seal kills, or be weaned and become independent, or succumb to starvation or other sources of mortality (e.g. cannibalism, drowning). Though previously common, independent 1 yr olds are now extremely rare in Western Hudson Bay (Derocher & Stirling 1995, Stirling et al. 1999), suggesting that most COY of non-lactating females either die or remain with their mother for an additional year. Declining cub survival rates in years of poor sea ice and longer periods fasting onshore point towards cub mortality becoming increasingly likely if females stop lactating (Derocher & Stirling 1996, Regehr et al. 2007). For yearlings, which are closer to weaning and hence less reliant on milk, reductions in lactation may be buffered in the short term if the cub has accumulated sufficient energy stores of its own to survive the fasting period. Nonetheless, any declines in cub growth or body condition may carry over and potentially

affect subsequent survival post-weaning (Derocher & Stirling 1996, Dahle et al. 2006). Moreover, structural size in juvenile bears has been linked to subsequent size as adults (Atkinson et al. 1996, Richardson 2014), meaning reduced milk quality and knock-on effects on cub growth may play a role in a shift towards smaller adult body sizes. A decline in body size has been observed in Western Hudson Bay adult females (Derocher & Stirling 1995, Atkinson et al. 1996,

Sciullo et al. 2016) and also in the Southern Beaufort Sea subpopulation, where many bears have been forced onshore or onto suboptimal sea-ice habitat for prolonged periods (Rode et al. 2010).

Earlier sea-ice melt and later freeze-up dates have extended the fasting period for Western Hudson Bay polar bears to ~3–4 wk longer than pre–1980 (Lunn et al. 2016, Molnár et al. 2020). Associated declines in body condition indicate that bears are becoming increasingly energetically stressed (Stirling et al. 1999), and lactation performance is likely already compromised as a result (Molnár et al. 2020). However, to our knowledge, research to evaluate the milk energy content of lactating polar bears on land has not occurred in almost 3 decades. Contemporary measurements of milk energy content and lactation performance, and comparisons with other subpopulations, would offer important insight into whether the mechanisms and functional dependencies identified in our study have changed, and how these may differ between subpopulations. Sea-ice loss from climate warming is projected to continue (IPCC 2019), while prey productivity and/or distribution may also be affected by changing environmental conditions. To quantify the exact consequences for demographics, the fate of offspring once a female reduces or terminates lactation effort is an area for further exploration, particularly given that rapid Arctic warming will increasingly force individuals to undertake longer periods without access to primary prey.

LITERATURE CITED

Arnbom T, Fedak MA, Boyd IL (1997) Factors affecting maternal expenditure in southern elephant seals during lactation. Ecology 78:471–483

Arnould JPY, Ramsay MA (1994) Milk production and milk consumption in polar bears during the ice-free period in western Hudson Bay. Can J Zool 72:1365–1370

Atkinson SN (1996) Ecophysiological studies of body composition, body size, and reproduction in polar bears. PhD thesis, University of Saskatchewan, Saskatoon

Atkinson SN, Ramsay MA (1995) The effects of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). Funct Ecol 9:559–567

Atkinson SN, Stirling I, Ramsay MA (1996) Growth in early life and relative body size among adult polar bears (*Ursus maritimus*). J Zool 239:225–234

Bowen WD, Iverson SJ, Boness DJ, Oftedal OT (2001) Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. Funct Ecol 15:325–334

Bunnell F, Tait D (1981) Population dynamics of bears—implications for management. In Fowler CW, Smith TD (eds) Dynamics of large mammal populations. Wiley, New York, NY, p 75–98

Clutton-Brock TH (1984) Reproductive effort and terminal investment in iteroparous animals. Am Nat 123:212–229

Crocker DE, Williams JD, Costa DP, Le Boeuf BJ (2001) Maternal traits and reproductive effort in northern elephant seals. Ecology 82:3541–3555

Dahle B, Zedrosser A, Swenson JE (2006) Correlates with body size and mass in yearling brown bears (*Ursus arctos*). J Zool 269:273–283

Derocher AE, Stirling I (1994) Age-specific reproductive performance of female polar bears (*Ursus maritimus*). J Zool 234:527–536

Derocher AE, Stirling I (1995) Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. Can J Zool 73:1657–1665

Derocher AE, Stirling I (1996) Aspects of survival in juvenile polar bears. Can J Zool 74:1246–1252

Derocher AE, Stirling I, Andriashek D (1992) Pregnancy rates and serum progesterone levels of polar bears in western Hudson Bay. Can J Zool 70:561–566

Derocher AE, Andriashek D, Arnould JPY (1993) Aspects of milk composition and lactation in polar bears. Can J Zool 71:561–567

Farley SD, Robbins CT (1994) Development of two methods to estimate body composition of bears. Can J Zool 72:220–226

Farley SD, Robbins CT (1995) Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 73:2216–2222

Festa-Bianchet M, Côté SD, Hamel S, Pelletier F (2019) Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. J Anim Ecol 88:1118–1133

Flint DJ, Vernon RG (1998) Effects of food restriction on the responses of the mammary gland and adipose tissue to prolactin and growth hormone in the lactating rat. J Endocrinol 156:299–305

Folio DM, Aars J, Gimenez O, Derocher AE, Wiig Ø, Cubaynes S (2019) How many cubs can a mum nurse? Maternal age and size influence litter size in polar bears. Biol Lett 15:20190070

Gabry J, Mahr T (2022) 'Bayesplot: plotting for Bayesian models.' R package. https://mc-stan.org/bayesplot/

Gabry J, Simpson D, Vehtari A, Betancourt M, Gelman A (2019) Visualization in Bayesian workflow. J R Stat Soc Ser A Stat Soc 182:389–402

Gaillard JM, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294–3306

Galicia MP, Thiemann GW, Dyck MG (2020) Correlates of seasonal change in the body condition of an Arctic top predator. Glob Change Biol 26:840–850

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2013) Bayesian data analysis, 3rd edn. CRC Press, New York, NY

Hamel S, Gaillard JM, Yoccoz NG, Loison A, Bonenfant C, Descamps S (2010) Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecol Lett 13:915–935

Hobbs TN, Hooten MB (2015) Bayesian models: a statistical primer for ecologists. Princeton University Press, Princeton, NJ

Hurley W (1989) Mammary gland function during involution. J Dairy Sci 72:1637–1646

IPCC (2019) IPCC Special Report on the ocean and cryosphere in a changing climate. In: Pörtner HO, Roberts DC, Masson-Delmotte V, Zhai P and others (eds.), 1st ed. https://www.ipcc.ch/srocc/

Iverson SJ, Bowen WD, Boness DJ, Oftedal OT (1993) The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). Physiol Zool 66:61–88

Jonas W, Woodside B (2016) Physiological mechanisms, behavioral and psychological factors influencing the transfer of milk from mothers to their young. Horm Behav 77:167–181

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78: 57–66

Kooijman SALM (2010) Dynamic energy budget theory for metabolic organisation. Cambridge University Press, Cambridge

Lunn NJ, Servanty S, Regehr EV, Converse SJ, Richardson E, Stirling I (2016) Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay. Ecol Appl 26:1302–1320

McElreath R (2020) Statistical rethinking. A Bayesian course with examples in R and Stan., 2nd edn. CRC Press, Boca Raton, FL

McNamara JM, Houston AI (1996) State-dependent life histories. Nature 380:215–221

Mellish JAE, Iverson SJ, Bowen WD (1999) Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. Physiol Biochem Zool 72:677–690

Miller EN, Lunn NJ, McGeachy D, Derocher AE (2022) Autumn migration phenology of polar bears (*Ursus maritimus*) in Hudson Bay, Canada. Polar Biol. 45: 1023–1034

Molnár PK, Klanjscek T, Derocher AE, Obbard ME, Lewis MA (2009) A body composition model to estimate mammalian energy stores and metabolic rates from body mass and body length, with application to polar bears. J Exp Biol 212:2313–2323

Molnár PK, Derocher AE, Klanjscek T, Lewis MA (2011) Predicting climate change impacts on polar bear litter size. Nat Commun 2:186

Molnár PK, Bitz CM, Holland MM, Kay JE, Penk SR, Amstrup SC (2020) Fasting season length sets temporal limits for global polar bear persistence. Nat Clim Chang 10:732–738

Oftedal OT (1993) The adaptation of milk secretion to the constraints of fasting in bears, seals, and baleen whales. J Dairy Sci 76:3234–3246

Oftedal OT (2000) Use of maternal reserves as a lactation strategy in large mammals. Proc Nutr Soc 59:99–106

Oftedal OT, Gittleman JL (1989) Patterns of energy output during reproduction in carnivores. In Gittleman JL (ed): Carnivore behavior, ecology, and evolution. Gittleman JL (ed) Springer US, Boston, MA, p 355–378

Pilfold NW, Hedman D, Stirling I, Derocher AE, Lunn NJ, Richardson E (2016) Mass loss rates of fasting polar bears. Physiol Biochem Zool 89:377–388

Pond CM, Mattacks CA, Colby RH, Ramsay MA (1992) The anatomy, chemical composition, and metabolism of adipose tissue in wild polar bears (*Ursus maritimus*). Can J Zool 70:326–341

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Ramsay MA, Stirling I (1988) Reproductive biology and ecology of female polar bears (*Ursus maritimus*). J Zool 214: 601–633

Regehr EV, Lunn NJ, Amstrup SC, Stirling I (2007) Effects of earlier sea ice breakup on survival and population size of polar bears in Western Hudson Bay. J Wildl Manag 71: 2673–2683

Richardson ES (2014) The mating system and life-history of the polar bear. PhD thesis, University of Alberta, Edmonton

Roche JR, Lee JM, Macdonald KA, Berry DP (2007) Relationships among body condition score, body weight, and milk production variables in pasture-based dairy cows. J Dairy Sci 90:3802–3815

Rode KD, Amstrup SC, Regehr EV (2010) Reduced body size and cub recruitment in polar bears associated with sea ice decline. Ecol Appl 20:768–782

Roff D (1992) The evolution of life histories: Theory and analysis. Chapman & Hall, New York, NY

Sciullo L, Thiemann GW, Lunn NJ (2016) Comparative assessment of metrics for monitoring the body condition of polar bears in western Hudson Bay. J Zool 300: 45–58

Smith TG (1980) Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Can J Zool 58: 2201–2209

Stan Development Team (2021) RStan: the R interface to Stan. R package. http://mc-stan.org/

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Stephens PA, Boyd IL, McNamara JM, Houston AI (2009) Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90:2057–2067

Stirling I, Derocher AE (2012) Effects of climate warming on polar bears: a review of the evidence. Glob Change Biol 18:2694–2706

Stirling I, Øritsland NA (1995) Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. Can J Fish Aquat Sci 52:2594–2612

Stirling I, Spencer C, Andriashek D (1989) Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. J Wildl Dis 25:159–168

Stirling I, Lunn NJ, Iacozza J (1999) Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climatic change. Arctic 52:294–306

Therrien JF, Côté SD, Festa-Bianchet M, Ouellet JP (2008) Maternal care in white-tailed deer: trade-off between maintenance and reproduction under food restriction. Anim Behav 75:235–243

Thometz NM, Kendall TL, Richter BP, Williams TM (2016) The high cost of reproduction in sea otters necessitates unique physiological adaptations. J Exp Biol 219: 2260–2264

Vehtari A, Gabry J, Magnusson M, Yao Y, Bürkner P, Paananen T, Gelman A (2022) Loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package. https://mc-stan.org/loo/

Wade GN, Schneider JE (1992) Metabolic fuels and reproduction in female mammals. Neurosci Biobehav Rev 16: 235–272

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's Principle. Am Nat 100: 687–690