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Cover: A female polar bear and her cubs stand on the sea ice by a fresh kill. Changes in the timing of spring ice melt are expected to reduce the caloric intake of polar bears, with implications for their reproductive rates (photo by Wayne Lynch, see Reimer *et al*., pp 3450–3461).

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PRIMARY RESEARCH ARTICLE

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Modeling optimal responses and fitness consequences in a changing Arctic

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Abstract

Animals must balance a series of costs and benefits while trying to maximize their fitness. For example, an individual may need to choose how much energy to allocate to reproduction versus growth, or how much time to spend on vigilance versus foraging. Their decisions depend on complex interactions between environmental conditions, behavioral plasticity, reproductive biology, and energetic demands. As animals respond to novel environmental conditions caused by climate change, the optimal decisions may shift. Stochastic dynamic programming provides a flexible modeling framework with which to explore these trade-offs, but this method has not yet been used to study possible changes in optimal trade-offs caused by climate change. We created a stochastic dynamic programming model capturing trade-off decisions required by an individual adult female polar bear (*Ursus maritimus*) as well as the fitness consequences of her decisions. We predicted optimal foraging decisions throughout her lifetime as well as the energetic thresholds below which it is optimal for her to abandon a reproductive attempt. To explore the effects of climate change, we shortened the spring feeding period by up to 3 weeks, which led to predictions of riskier foraging behavior and higher reproductive thresholds. The resulting changes in fitness may be interpreted as a best-case scenario, where bears adapt instantaneously and optimally to new environmental conditions. If the spring feeding period was reduced by 1 week, her expected fitness declined by 15%, and if reduced by 3 weeks, expected fitness declined by 68%. This demonstrates an effective way to explore a species' optimal response to a changing landscape of costs and benefits and highlights the fact that small annual effects can result in large cumulative changes in expected lifetime fitness.

KEYWORDS
climate change, energetic model, marine mammal, optimality theory, polar bear, state-dependent model, stochastic dynamic programming, *Ursus maritimus*

1 | INTRODUCTION

Natural selection acts across several interacting processes, including survival, mate-finding, foraging, and reproduction. Individuals must balance a series of trade-offs, whether through behavioral means or physiological adaptations. For example, an individual may need to choose between two possible foraging patches, taking into account the food available as well as the risk of predation in each patch (Holbrook & Schmitt, 1988; Ludwig & Rowe, 1990). Similarly, trade-offs between the quantity and viability of offspring determine optimal clutch size (Lack, 1947; Mangel, Rosenheim, & Adler, 1995). Natural selection favours individuals with higher fitness (here defined as an individual's expected lifetime reproductive success) resulting from life history strategies that successfully balance these competing factors. Environmental shifts caused by climate change may alter which strategies are successful, however, as the costs and benefits that an individual encounters change. Studying these shifting optimal responses requires simultaneous consideration of multiple interacting factors, accounting for an individual's need to balance survival with reproduction, often over multiple years and reproductive attempts.

Optimality theory aims to identify an individual's optimal decision in light of a set of benefits, costs, and constraints. Optimal decisions need not be the same for every individual at each time; each individual may be in one of several relevant states (e.g., their energetic state, reproductive state, or age) that may affect the decisions available to the individual, outcomes that are possible, as well as which decision is optimal. While these optimal adaptations may not be perfectly achieved, framing questions in this way provides insight into the competing forces faced by an individual (Parker & Smith, 1990).

Polar bears (*Ursus maritimus*) of different sexes and in different reproductive states vary in their choice of foraging habitat during the spring feeding period (Pilfold, Derocher, & Richardson, 2014; Stirling, Andriashek, & Calvert, 1993). Sea ice habitat used by polar bears in the southern Beaufort Sea can be broadly grouped into two types: active ice and fast ice (also known as landfast ice; Stirling et al., 1993). Active ice, including pack ice and the floe edge, is high-quality polar bear foraging habitat with abundant prey, namely ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*; Stirling et al., 1993). Near shore, fast ice provides lower quality foraging habitat, with the main available prey being naive but small ringed seal pups and, to a lesser extent, their mothers (Smith & Stirling, 1975). Male polar bears of all ages and females who are not accompanied by dependent offspring are found primarily in the active ice (Stirling et al., 1993). Female polar bears accompanied by dependent offspring (especially females with cubs of the year, COYs), however, are found more often in the fast ice (Stirling et al., 1993). This use of lower quality foraging habitat is thought to result from a risk avoidance strategy (Pilfold et al., 2014); cubs may be at risk of infanticide and cannibalism by adult males (Amstrup, Stirling, Smith, Perham, & Thiemann, 2006; Derocher & Wiig, 1999) or hypothermia due to the swimming that may be necessary in more active ice (Blix & Lentfer, 1979; Monnett & Gleason, 2006). Stirling et al. (1993) found that females with COYs in the southern Beaufort Sea were nearly twice as likely to be in fast ice as predicted.

In addition to the foraging decisions made on daily timescales, female polar bears also make facultative reproductive decisions. Female polar bears mate in the spring, but delay implantation until the autumn (Lønø, 1970; Ramsay & Stirling, 1988). If her energy reserves are too low at this time, a female polar bear may abort the pregnancy rather than continuing to deplete her reserves (Atkinson & Ramsay, 1995; Derocher, Stirling, & Andriashek, 1992). Similarly, if her energy reserves are sufficiently depleted while she still has dependent cubs, the quality of her milk will decline and eventually cease entirely, which may result in cub mortality (Derocher, Andriashek, & Arnould, 1993; Molnár, Klanjscek, Derocher, Obbard, & Lewis, 2009). The level of energy reserves at which it may be optimal for her to stop investing in her current reproductive attempt is unknown, and we address this knowledge gap here.

In recent decades, the ice-free period has increased approximately 10–20 days per decade across the southern Beaufort Sea (Parkinson, 2014). For polar bears, this results in a shorter feeding period over which they must attempt to acquire the necessary reserves to survive the longer summer fasting period (Pongracz & Derocher, 2017). These changing ice conditions have already been linked with smaller body size, reduced recruitment, and population declines in the Beaufort Sea (Hunter et al., 2010; Regehr, Hunter, Caswell, Amstrup, & Stirling, 2010; Rode, Amstrup, & Regehr, 2010).

What is known about polar bears' preferred foraging habitat has been studied within a framework of selection (i.e., habitat use vs. relative availability) (Durner et al., 2009, 2017; Stirling et al., 1993) or species distribution models (Pilfold et al., 2014). We took a different approach, using optimality theory to explore how much additional risk of cub mortality in the active ice would result in predictions of optimal habitat use similar to observed patterns of spatial segregation. We created a model to predict an individual's optimal foraging habitat (fast ice or active ice) based on their energetic and reproductive state. This model also allowed us to estimate the energetic thresholds below which it would be optimal for a female polar bear to abort her pregnancy or cease lactation. We then explored the implications of changes in the timing of spring sea ice breakup for polar bear foraging and reproductive decisions and, ultimately, individual fitness.

We desired a modeling framework that would allow for a high degree of flexibility in the stochastic nature of the model components as well as the feedback between the controls and the state. For this, the discrete nature and flexibility of stochastic dynamic programming (SDP) offers a convenient framework (Clark & Mangel, 2000; Houston & McNamara, 1999). SDP models, also known as dynamic state variable models, are individual-based models used to determine optimal decisions, given a known objective and constraints (Clark & Mangel, 2000). These models have been used for a variety of purposes, such as determining the optimal overwintering habitat of elk (*Cervus canadensis*) (Noonburg, Newman, Lewis, Crabtree, & Potapov, 2007), the conditions under which a predator with distinct predation strategies is predicted to switch between strategies (Dukas & Clark, 1995), and the effects of acoustic and other anthropogenic disturbances on marine mammals (McHuron, Costa, Schwarz, & Mangel, 2017; Schwarz, McHuron, Mangel, Wells, & Costa, 2016). These models have not yet, however, been used to study optimal responses to climate change.

We created an SDP model for an individual female polar bear over her entire adult lifetime, from sexual maturity until death (for other examples of SDP models spanning adulthood, see Marrow et al., 1996; McHuron, Schwarz, Costa, & Mangel, 2018). SDP allows integration of the bear's need to balance trade-offs between energy gain, reproduction, and cub survival (Clark & Mangel, 2000). The classical SDP patch choice model optimizes the patch choice of an individual over a short time frame; the individual must choose between different environments that each have different probabilistic costs and benefits. Our model is an extension of this, maximizing the individual's recruited offspring over her entire lifetime and including a variable reproductive state which is, itself, subject to optimization.

Model outputs are (a) her expected future fitness throughout her lifetime, and (b) a set of optimal decisions, dependent on energetic and reproductive state. The optimal decisions fall into two main categories: (i) during each spring, the daily optimal foraging patch (active ice or fast ice), and (ii) at the end of each spring, the decision, when relevant, whether to abort or continue a pregnancy, or whether to continue or cease milk production. We use this model to answer three questions: (a) How much added risk of cub mortality in the active ice would result in predictions of optimal habitat use similar to those observed? (b) What is the energetic threshold below which it is optimal for a female to abort her pregnancy or cease lactation? (c) What changes in foraging habitat selection and reproductive behavior do we predict if the spring feeding period is shortened, and the summer fasting period similarly lengthened, and what would be the resultant changes in her fitness?

2 | MATERIALS AND METHODS

We considered two possible spring foraging habitats, with an individual female making a daily decision to forage in either active or fast ice. The bear must choose where to forage based on the probability of finding and catching prey, the expected energetic returns of that prey, and the risk of cub mortality in each patch for females with cubs. We assumed that the female is able to switch between the two habitats daily and that her decision of where to forage is independent of which habitat she chose for the previous day.

Parameter values and functional forms are in Table 1, and Figure 1 provides a schematic of the events in 1 year. Our model included two state variables: $x(t,n)$, the energy reserves (MJ) of the bear, and $\eta(t,n)$, the bear's reproductive state, both at time t in the nth year of her adult life. We assumed death from starvation when her energy reserves fall to the critical level x_{crit} and an upper bound x_{max} on her reserves, so $x_{crit} \le x \le x_{max}$. Female polar bears may take one of four reproductive states, $\eta \in \{1,2,3,4\}$, corresponding to single, pregnant, with a litter of one or more COYs, and with a litter of one or more yearlings. Polar bears in the Beaufort Sea give birth to a litter of 1–3 cubs which remain with their mother until they are weaned. Weaning typically occurs in the spring of their second year, so a female may successfully wean a litter every 3 years at most (Ramsay & Stirling, 1988).

The time interval of our SDP routine was 1 day, resulting in the optimal decisions and resultant fitness for each day of each spring. The first day of spring, t_{spring}, coincides with the beginning of ringed seal pupping, signifying the beginning of a period of hyperphagia for polar bears (Ramsay & Stirling, 1988; Stirling & McEwan, 1975). During the spring, single females may also mate. Females are available to mate for the first time at the start of their sixth spring in the southern Beaufort Sea (approximately age 5.5, model year $n = 1$) (Lentfer, Hensel, Gilbert, & Sorensen, 1980; Stirling, Pearson, & Bunnell, 1976). We assumed both spring feeding and mating stop when the sea ice breaks up over the continental shelf in early summer, approximately on day $t_{breakup}$. We designated the days between t_{spring} and $t_{breakup}$ as spring, and the SDP model was used for each day in this period.

We assumed a maximum encounter of one prey item per day and that handling time and prey consumption also occur within this 1 day window. Prey are encountered and captured with a daily probability λ_i, depending on patch $i \in$ {fast ice, active ice}, with $\lambda_{fast\ ice} < \lambda_{active\ ice}$. On successfully catching prey, the bear's energetic state increases by $Y_i(t)$, the expected energetic gain from a seal in patch i on day t. The fast ice has lower expected daily energetic gain than the active ice (Figure S1).

At $t_{breakup}$, the bear's energetic fate for the remainder of the year is largely determined, as they fast during the summer and the subsequent autumn and winter months have reduced hunting success. While terrestrial feeding (Rode, Reist, Peacock, & Stirling, 2010) and feeding on whale carrion (Bentzen et al., 2007) have been observed, we assumed significant energy gains from these sources would be anomalous for an individual and thus not relevant for determining optimal strategies, so we did not consider these energy sources here. The summer ice-free period lasts for $\tau_{icefree}$ days (from $t_{breakup}$ to $t_{freezeup}$). During this time, the majority of bears remain on the sea ice as it retreats northward, though some spend summer on land (Atwood et al., 2016; Pongracz & Derocher, 2017).

After $t_{freezeup}$, nonpregnant bears resume hunting. Pregnant females den either on land or on the sea ice (Amstrup & Gardner, 1994; Lentfer, 1975), giving birth inside their dens around January 1 (Stirling et al., 1993). They remain in their dens for approximately τ_{den} days (from $t_{freezeup}$ onward). We assumed that a female polar bear experiences reproductive senescence each year with probability p_s(age), with the highest probability of senescence occurring in her early 20s (Ramsay & Stirling, 1988; Stirling, McDonald, Richardson, & Regehr, 2011). After this point, we assumed that she is unable to produce a new litter or successfully nurse an existing litter of COYs. If she had yearlings at this time, however, her remaining energetic investment is minimal, and hence, we assumed that they are successfully weaned.

We linked years together by mapping the bear's expected change in state from the end of one spring to the start of the next, using a method known as sequential coupling (Clark & Mangel, 2000; Mangel & Clark, 1988). Consider a bear at the end of spring, $t_{breakup}$, in her nth adult year, in reproductive state η, with energy reserves x. Her energetic state at the start of the following spring is a function of her state at the end of the current spring, $x(t_{spring}, n+1) = w_\eta(x(t_{breakup}, n))$. If the bear is pregnant ($\eta = 2$) at $t_{breakup}$, she has the facultative choice to either continue the pregnancy or to abort it. If the bear has a litter of COYs ($\eta = 3$), she will either continue to lactate or will cease lactation, resulting in litter loss. In these two cases of litter loss, w_η is modified to be w_η^{loss}. If she has a litter of yearlings ($\eta = 4$), she will continue to lactate if her energetic condition allows for it. However, even if she ceases lactation, her yearling cubs remain with her, eating from her kills and learning skills that aid survival.

TABLE 1 Summary table of parameters used in the stochastic dynamic programming model for an adult female polar bear. Parameters in light gray cells vary between active and fast ice. For additional details, see S1 (Supplementary Material)

Parameter	Values	Description	Sources and notes
Energetic state constraints			
x_{crit}	0 MJ	Critical energy reserves	Molnár et al. (2009)
x_{max}	8,822 MJ	Maximum possible energy reserves	calculated; S1
Time parameters			
T	24 years	Maximum years as a reproductively mature adult	From age 5–28
t_{spring}	April 1	Start of spring feeding period	Smith (1987)
$t_{breakup}$	July 17	Breakup	Stroeve and Meier (2018)
$t_{freezeup}$	October 8	Freezeup	Stroeve and Meier (2018)
$\tau_{icefree}$	83 days	Number of days between breakup and freezeup	Stroeve and Meier (2018)
General parameters			
$\lambda_{fast\ ice}$	1/3.5	Daily probability of obtaining prey	Stirling and Øritsland (1995)
$\lambda_{active\ ice}$	1/2.5	Daily probability of obtaining prey	Stirling and Øritsland (1995)
$Y_i(t)$	Range from 148 to 355 MJ	Expected energetic gains from single prey	Calculated; S1
a	$0.0002 \times \text{mass(kg)}^{2.41}$	Daily adult female energy expenditure (MJ)	Pagano et al. (2018)
σ	$0.996^{\left(365^{-1}\right)}$	Daily probability of female survival	Amstrup and Durner (1995)
$\hat{\sigma}$	$\sigma^{(\text{\# of "overwinter days"})}$	Overwinter probability of female survival	Amstrup and Durner (1995)
$p_s(\text{age})$	$\int_{\text{age}}^{\text{age}+1} e^{-(x/23)^{23}} \left(\frac{x}{23}\right)^{22} dx$	Probability of becoming senescent at a given age	Modified from Schwartz et al. (2003)
Single (η = 1) parameters			
$\epsilon(t)$	0.05	Daily probability of encountering a mate	Molnár, Derocher, Lewis, and Taylor (2008)
τ_{mate}	17 days	Length of pairing during mating	Molnár et al. (2008)
Pregnancy (η = 2) parameters			
τ_{den}	134 days	Number of days in maternity den	Amstrup and Gardner (1994)
Cubs of the year (COY) litter (η = 3) parameters			
$\sigma_0^{fast\ ice}$	$0.651^{\left(365^{-1}\right)}$	Daily probability of COY litter survival	Amstrup and Durner (1995)
$\sigma_0^{active\ ice}$	Unknown	Daily probability of COY litter survival	Estimated; (2)
$g_3(x,t)$	$0.24 \times \text{mass}^{0.75}$	Daily lactation costs, yearling litter	Gittleman and Oftedal (1987)
Yearling litter (η = 4) parameters			
$\sigma_1^{fast\ ice}$	$0.86^{\left(365^{-1}\right)}$	Daily probability of yearling litter survival	Amstrup and Durner (1995)
$\sigma_1^{active\ ice}$	Unknown	Daily probability of yearling litter survival	Estimated; (1)
$g_4(x,t)$	$0.1 \times \text{mass}^{0.75}$	Daily lactation costs, yearling litter	Arnould and Ramsay (1994)
k	1.15	Expected size of recruited litter	Hunter et al. (2010)

We deterministically modeled these changes in storage energy from the end of one spring to the start of the next, henceforth referred to as "overwinter," which includes the summer ice-free period, autumn, and winter. During the summer ice-free period, we assumed that a female bear's daily energy expenditure for personal maintenance is approximately her resting metabolic rate (RMR), regardless of reproductive state (Robbins, Lopez-Alfaro, Rode, Tøien, & Nelson, 2012). We assumed that her energy storage decreases daily by the sum of her RMR and any additional lactation requirements. Once the ice freezes in the autumn, nonpregnant

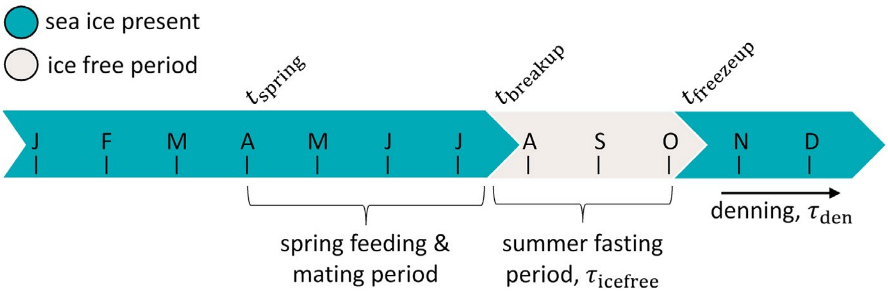

FIGURE 1 Annual ice conditions and key foraging and reproductive events for an adult female polar bear. Our stochastic dynamic programming model predicts a bear's daily optimal choice of foraging habitat in the spring (from t_{spring} to $t_{breakup}$), and her optimal reproductive strategy over the summer and subsequent winter (from $t_{breakup}$ until t_{spring} the following year) [Colour figure can be viewed at wileyonlinelibrary.com]

bears resume hunting, but with limited success (Stirling & Øritsland, 1995). We assumed that the energy stores of bears who resume hunting do not continue to decline, finding adequate food to maintain their condition until the start of the next spring. Pregnant bears enter a den and continue to decrease their energy stores daily according to their denning metabolic rate (DMR). In all cases, if the female's reserves are insufficient at the end of spring, $t_{breakup}$, then $w_\eta(\cdot) = x_{crit}$ and the female dies during the overwinter period. Overwintering energetic and reproductive state dynamics are described in full detail in S2 (Supplementary Material).

2.1 | Additional risk in the active ice

Estimates of the magnitude of the additional risk for cubs in the active ice do not exist. We here explore, within the constraints and assumptions of our SDP model, how much additional risk of cub mortality could lead to the spatial segregation observed in the southern Beaufort Sea. We chose to focus our attention on the higher probability of mortality experienced by a litter of COYS. We assumed that the daily probability of mortality for a litter of yearlings in the active ice is only slightly higher (we chose 10%) than in the fast ice, so the probability of litter survival is

$$\sigma_1^{\text{active ice}} = 1 - 1.1\underbrace{(1 - \sigma_1^{\text{fast ice}})}_{\text{mortality}}. \tag{1}$$

We then explored how changing the mortality scaling factor affects the proportion of time a female with COYs spends in the active ice, where

$$\sigma_0^{\text{active ice}} = 1 - (\text{scaling factor})\underbrace{(1 - \sigma_0^{\text{fast ice}})}_{\text{mortality}}. \tag{2}$$

Using estimates of polar bear habitat selection (figure 8 in Stirling et al., 1993), we assumed that the main ice types considered in that study (fast ice, pack ice, and the floe edge) were equally available to a given female polar bear. We then normalized the selection coefficients so that they summed to 1 and used this as a rough estimate of the time spent in each ice type, resulting in an estimate of 37% of time spent in the active ice for females with a litter of COYs.

We performed 1,000 Monte Carlo simulations to determine the mortality scaling factor that resulted in ~37% of time spent in the active ice for a modeled female bear. In each simulation, the scaling factor of Equation 2 was chosen randomly from all real numbers in the interval 2–5, inclusive. We then fit an exponential curve to a plot of the proportion of days in the spring a female with a litter of COYs spent in the active ice, against the scaling factor. We determined the scaling factor that resulted in approximately 37% of time spent in the active ice, and used that value as our estimate of additional risk for females with cubs.

This value of 37% assumes that all ice types are equally available to a bear, with no variation in space or time. In reality, we would expect the availability of each ice type to vary both regionally and through time, so to explore model sensitivity to this value, we also considered values ranging from 20% to 50%.

2.2 | Fitness functions

We formalized the above into state-dependent fitness functions, $F_\eta(x,t,n)$, describing the expected number of offspring recruited to the population resulting from the optimal decisions taken at time t in the nth year of a female's adult life, for a bear in reproductive class η with energetic state x. The expected number of offspring is considered from time t in year n to the end of the individual's reproductive years (similar to the R_0 of life history theory). We considered offspring recruited if they survive to the beginning of their third spring (age 2.5 years), when they are weaned (Ramsay & Stirling, 1988).

The optimal decision at each time is that which results in the maximum expected reproductive success as compared against all other possible decisions. For each day during spring, we calculated the value of the fitness function in each of the two ice types, and the optimal patch was the one with the higher fitness function. At the end of each spring, we calculated the fitness function for any relevant reproductive decisions over the remainder of the year (i.e., whether to continue or abort a pregnancy, to continue or cease lactation), and the optimal decision was that with the higher fitness function.

A terminal fitness function describes the bear's expected future fitness at the terminal time, here chosen to be the last day of the spring feeding period in the bear's final year at age 28, by which time we assumed that the bear would have experienced reproductive senescence and thus have no future fitness gains (i.e., the terminal fitness function is 0 for all bears).

Regardless of reproductive state, we assumed the order of stochastic events each day to be the following: (a) individual survival (with daily probability σ), (b) change in reproductive state (pregnancy, litter loss/survival), (c) foraging success or failure. Following these events, we updated the bear's energetic and reproductive states accordingly, including daily metabolic costs. This order is similar over winter, but without including probabilistic daily foraging success. The bears die if x falls to x_{crit} at any point.

2.3 | Fitness of a single bear (η = 1)

On any day in spring, a single female may be paired with a male with daily probability $\epsilon(t)$. We assumed that the density of males and the probability of mating remain constant throughout a female's life. This mating process takes, on average, τ_{mate} days. While mating, we assumed that she devotes negligible energy to hunting (Stirling, Spencer, & Andriashek, 2016) and loses energy reserves daily according to a, her daily personal maintenance costs (MJ). Note that a depends on her mass (Table 1), which changes slightly each day as she depletes her reserves during mating; this has been implemented in the model code, but our notation here describes her change in state with the term $-a\tau_{mate}$ for ease of interpretation. Her fitness function throughout spring is

$$F_1(x,t,n)=\max_i\left\{\underbrace{\sigma}_{\text{survive}}\left(\underbrace{\epsilon(t)F_2(x-a\tau_{mate},t+\tau_{mate},n)}_{\text{mate}}+\underbrace{(1-\epsilon(t))}_{\text{do not mate}}\left[\underbrace{\lambda_iF_1(x-a+Y_i,t+1,n)}_{\text{find food}}+\underbrace{(1-\lambda_i)F_1(x-a,t+1,n)}_{\text{do not find food}}\right]\right)\right\}, \quad (3)$$

for $t \in [t_{spring}, t_{breakup})$, where $i \in$ {active ice, fast ice} and where $[t_{spring}, t_{breakup})$ denotes all days from t_{spring} (inclusive) up to but not including $t_{breakup}$.

Over winter, her reproductive state remains the same and her energetic state changes according to $w_1(x)$. She survives the winter with probability $\hat{\sigma}$ (S2, Supplementary Material), so her overwinter fitness function is

$$F_1(x,t_{breakup},n)=\begin{cases}\underbrace{\hat{\sigma}}_{\text{survive}}\;F_1(w_1(x),t_{spring},n+1), & n<T\\ 0, & n=T\end{cases}. \quad (4)$$

2.4 | Fitness of a pregnant bear (η = 2)

We assumed that aborting a litter is confined to the autumn; once a female is pregnant, she remains pregnant for the remainder of the spring, so

$$F_2(x,t,n)=\max_i\left\{\underbrace{\sigma}_{\text{survive}}\left[\underbrace{\lambda_iF_2(x-a+Y_i,t+1,n)}_{\text{find food}}+\underbrace{(1-\lambda_i)F_2(x-a,t+1,n)}_{\text{do not find food}}\right]\right\}, \quad (5)$$

where $t \in [t_{spring}, t_{breakup})$. Over summer, she fasts, and after the ice reforms over the continental shelf in the autumn, she goes into her maternity den for τ_{den} days to give birth. We assumed that she makes a facultative decision before going into her den, either to abort the pregnancy or continue it, based on her energy stores and future expected fitness. If the pregnancy is terminated, her reproductive status changes accordingly and she does not enter a maternity den, thus avoiding further depletion of her energy reserves. The resulting overwinter fitness function is

$$F_2(x,t_{breakup},n)=\begin{cases}\underbrace{\hat{\sigma}}_{\text{survive}}\max\left\{\underbrace{F_3(w_2(x),t_{spring},n+1)}_{\text{continue pregnancy}},\underbrace{F_1(w_2^{loss}(x),t_{spring},n+1)}_{\text{abort pregnancy}}\right\}, & n<T\\ 0, & n=T\end{cases}. \quad (6)$$

2.5 | Fitness of a bear accompanied by cubs of the year (η = 3)

The female loses her litter from nonstarvation causes with probability σ_0^i, after which she returns to being single. Females who lose their litter in the spring are able to become pregnant again that same spring (Ramsay & Stirling, 1986). We assumed that she may become pregnant again beginning the next day.

If she does not lose her litter, she first devotes energy a (MJ) to her own maintenance needs and then allocates energy to lactation (King & Murphy, 1985) according to the function $g_3(x - a, t)$. If she has insufficient energy for lactation (i.e., $g_3(\cdot) = 0$), we assumed that she loses the litter. Her fitness function throughout the spring is

$$F_3(x,t,n)=\max_i\left\{\underbrace{\sigma}_{\text{survive}}\left(\underbrace{\sigma_0^i}_{\text{litter survives}}\left[\underbrace{\lambda_iF_3(x-a-g_3(x-a,t)+Y_i,t+1,n)}_{\text{find food}}+\underbrace{(1-\lambda_i)F_3(x-a-g_3(x-a,t),t+1,n)}_{\text{do not find food}}\right]+\underbrace{(1-\sigma_0^i)}_{\text{lose litter}}\times\left[\underbrace{\lambda_iF_1(x-a+Y_i,t+1,n)}_{\text{find food}}+\underbrace{(1-\lambda_i)F_1(x-a,t+1,n)}_{\text{do not find food}}\right]\right)\right\}, \quad (7)$$

where $t \in [t_{spring}, t_{breakup})$. Over winter, the litter either becomes a year older (so in the subsequent spring, she has a yearling litter) or she ceases lactation and they die. As the cubs are still reliant on milk throughout this year, we assumed that the litter dies if she dies. Her overwinter fitness function is

$$F_3(x,t_{breakup},n)=\begin{cases}\underbrace{\hat{\sigma}}_{\text{survive}}\max\left\{\underbrace{F_4(w_3(x),t_{spring},n+1)}_{\text{continue lactation}},\underbrace{F_1(w_3^{loss}(x),t_{spring},n+1)}_{\text{cease lactation}}\right\}, & n<T\\ 0, & n=T\end{cases}. \quad (8)$$

2.6 | Fitness of a bear accompanied by yearlings ($\eta = 4$)

We assumed that yearlings still gain significant energy intake from milk in spring, so if the female's reserves are too low (i.e., $g_4(\cdot) = 0$) and she ceases lactation, she loses the litter. Her fitness function throughout spring is

$$F_4(x,t,n)=\max_i\left\{\underbrace{\sigma}_{\text{survive}}\left(\underbrace{\sigma_1^i}_{\text{litter survives}}\left[\underbrace{\lambda_i F_4(x-a-g_4(x-a,t)+Y_i,t+1,n)}_{\text{find food}}\right.\right.\right.$$
$$\left.+\underbrace{(1-\lambda_i)F_4(x-a-g_4(x-a,t),t+1,n)}_{\text{do not find food}}\right]+\underbrace{(1-\sigma_1^i)}_{\text{lose litter}}\left[\underbrace{\lambda_i F_1(x-a+Y_i,t+1,n)}_{\text{find food}}\right.$$
$$\left.\left.\left.+\underbrace{(1-\lambda_i)F_1(x-a,t+1,n)}_{\text{do not find food}}\right]\right)\right\}, \quad (9)$$

where $t \in [t_{\text{spring}}, t_{\text{breakup}})$. If she has insufficient resources to provide milk for her yearling litter after their second spring, we assumed that the litter remains with her, continuing to share her kills and learn additional survival skills (Stirling & McEwan, 1975). Due to the lack of data on the survival of unaccompanied yearlings in the Beaufort Sea following their second spring, we assumed that yearling survival is unchanged in the event that the female dies (Derocher & Stirling, 1996; Ramsay & Stirling, 1988). On recruitment, her lifetime fitness increases by k, the expected litter size of a recruited litter, so

$$F_4(x,t_{\text{breakup}},n)=\begin{cases} k+\underbrace{\hat{\sigma}}_{\text{survive}}F_1(w_4(x),t_{\text{spring}},n+1), & n<T \\ 0, & n=T \end{cases}. \quad (10)$$

2.7 | Model analysis

We solved the SDP model using the standard method of backward iteration (Clark & Mangel, 2000). In doing so, we obtained the optimal foraging habitat for a bear in each energetic and reproductive state for each day in spring. We also calculated the optimal reproductive decisions from one spring to the next for pregnant females and females with a litter of COYs in each energetic state. We obtained estimates of fitness under the assumption that she follows these optimal decisions throughout her lifetime.

In addition to these standard model outputs, we ran Monte Carlo simulations for a bear behaving optimally (Figure S2). Each simulation had an initial condition randomly drawn from the distribution of energetic states calculated from data on bears captured in the Canadian Beaufort Sea in the spring from 1974 to 2010 (for details, see Bromaghin et al., 2015). We calculated mass from the measurements of length and axillary girth (Thiemann, Lunn, Richardson, & Andriashek, 2011), which was then converted into estimates of storage energy (equation 11 in Molnár et al., 2009). We used data on 44 female bears, 5–7 years old, captured before April 15 (i.e., near the start of spring). Each simulation began with a bear available for their first pairing, so $\eta(t_{\text{spring}}, 1) = 1$.

Spring (from t_{spring} to t_{breakup}) in our base model was 108 days. To explore the effect of a shorter spring feeding period, we considered dates of t_{breakup} up to 3 weeks earlier. We assumed that reductions in the length of spring resulted directly in a longer summer ice-free period, for example, if t_{breakup} was 2 weeks earlier, then τ_{icefree} was 2 weeks longer. All computations were performed using Matlab 2018b, and all code has been uploaded to a GitHub repository where it is freely available (https://doi.org/10.5281/zenodo.2401363).

3 | RESULTS

3.1 | Additional mortality risk for cubs in the active ice

A 3.5-fold increase in the daily probability of mortality for a litter of COYs (i.e., a scaling factor of 3.5 in Equation 2 resulted in a female spending approximately 37% of her time in the active ice (Figure S3). We thus used a value of $\sigma_0^{\text{active ice}} = 0.9959$ in our SDP model (Equation 2).

3.2 | Optimal foraging patch selection

Regardless of energetic state, the optimal foraging habitat for a single or pregnant bear is nearly exclusively the active ice (Figure 2). The optimal foraging habitat of a bear accompanied by dependent offspring (COYs or yearlings) is the fast ice early in the spring, and then either the active ice or fast ice, depending on her energetic state near the end of the spring (Figure 2). Provided she behaves optimally, a bear will, on average, approximately quadruple her energy reserves over the spring (Figure S4). If the spring feeding period was shortened by 1, 2, or 3 weeks, we predict that the median amount of time an optimally behaving female with COYs or yearlings would spend in the active ice would increase substantially (Figure 3).

3.3 | Optimal reproductive strategy over winter

In our model, a female will abort her pregnancy or cease lactation for her litter of COYs over winter when her reserves at the end of spring are low (Figure 4). If t_{breakup} is decreased by 3 weeks, these thresholds increase by 20%–30% (Figure 5a). The threshold for ceasing lactation with a litter of COYs was more sensitive to changes in t_{breakup} than the threshold for aborting a pregnancy (Figure 5a). For reductions in the length of spring, the changes in the optimal foraging habitats combined with the changes in optimal reproductive strategies translated into declines in the bear's expected fitness (Figure 5b). Lifetime reproductive output declined by 15% if t_{breakup} was reduced by 1 week, and by 68% when reduced by 3 weeks.

When we explored the sensitivity of the model to the percentage of time a female spends in the active ice (taken to be 37%

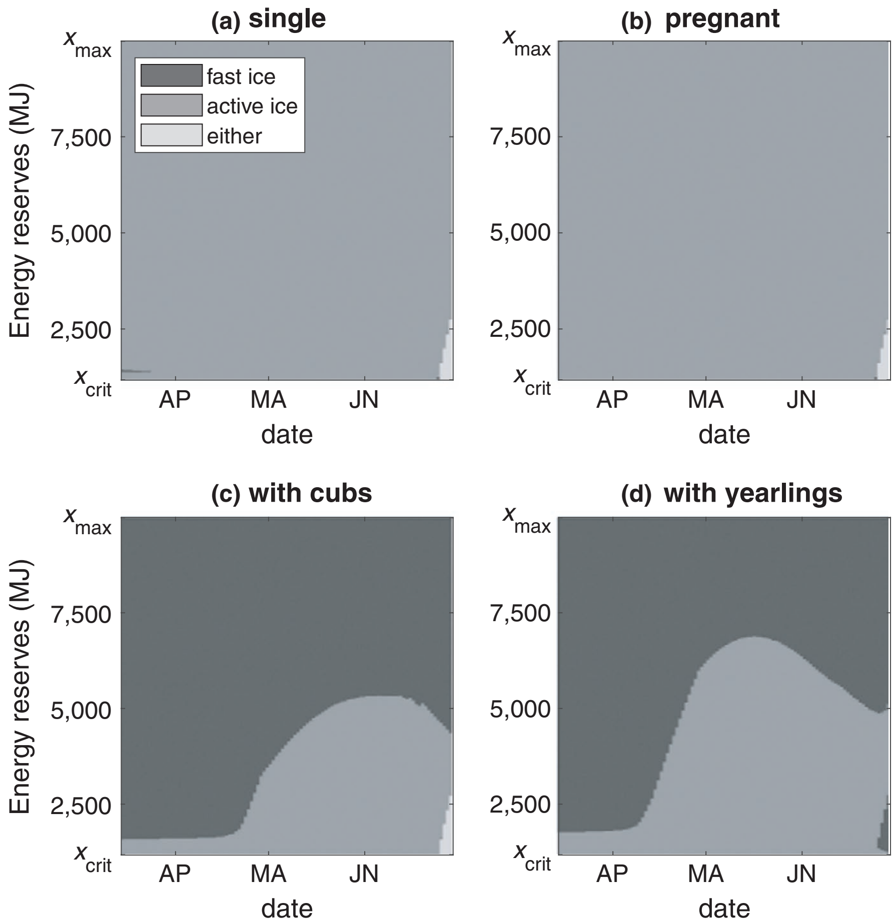

FIGURE 2 Optimal foraging decisions for a 10-year-old adult female polar bear (n = 6) in each reproductive state, each energetic state, and for each day throughout the spring (AP, MA, and JN refer to April, May, and June, respectively). Similar optimal foraging decisions for all ages are available in Figures S5–S8

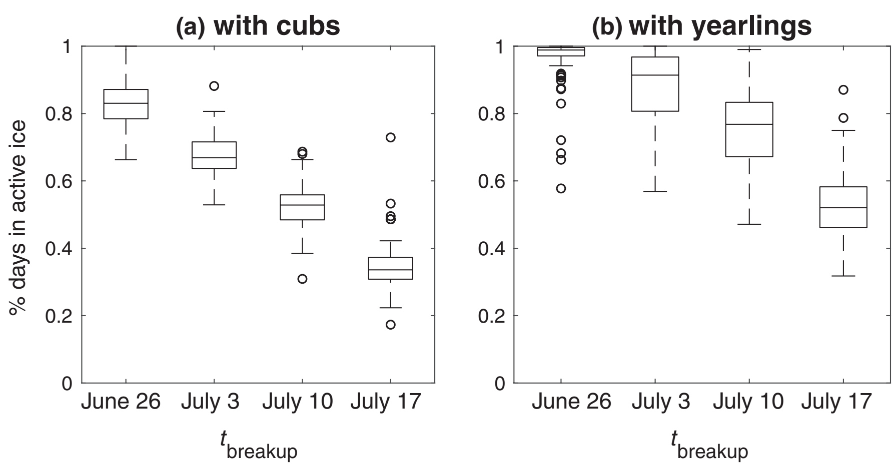

FIGURE 3 The percentage of spring days that an optimally behaving female with dependent offspring (either cubs of the year or yearlings) spends in the active ice (instead of the fast ice), as the length of spring varies from 87 ($t_{breakup}$ = June 26) to 108 days ($t_{breakup}$ = July 17). One hundred simulations were performed for each length of spring

above), varying it from 20% to 50%, we found that error propagation throughout the model was insubstantial. These variations resulted in small changes in expected lifetime fitness and in the general fitness response to changes in the length of spring (Figure S9).

4 | DISCUSSION

We have constructed a sophisticated behavioral model, coupled to life history theory for female polar bears. This model was used to study optimal trade-offs in hunting habitat and reproductive strategy, and the changes in these optimal trade-offs resulting from climate change. We used this model to answer three questions.

The first question was how much additional risk of cub mortality in the active ice would result in levels of spatial segregation in our SDP model similar to what is observed in the southern Beaufort Sea. We found that a 3.5-fold increase in the daily probability of mortality for a litter of COYs resulted in a female spending approximately 37% of her time in the active ice. While the resultant daily difference in

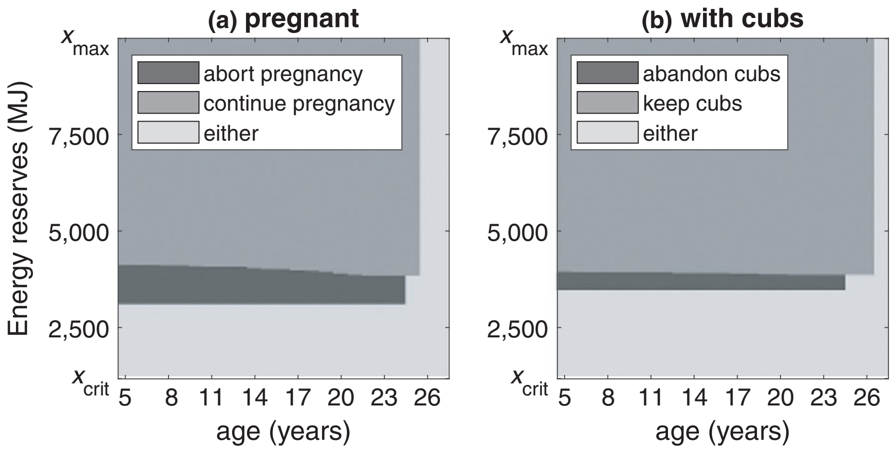

FIGURE 4 Optimal overwinter reproductive strategies for both a pregnant female (a) and a female with a litter of cubs of the year (b) at the end of each spring, for each energetic state

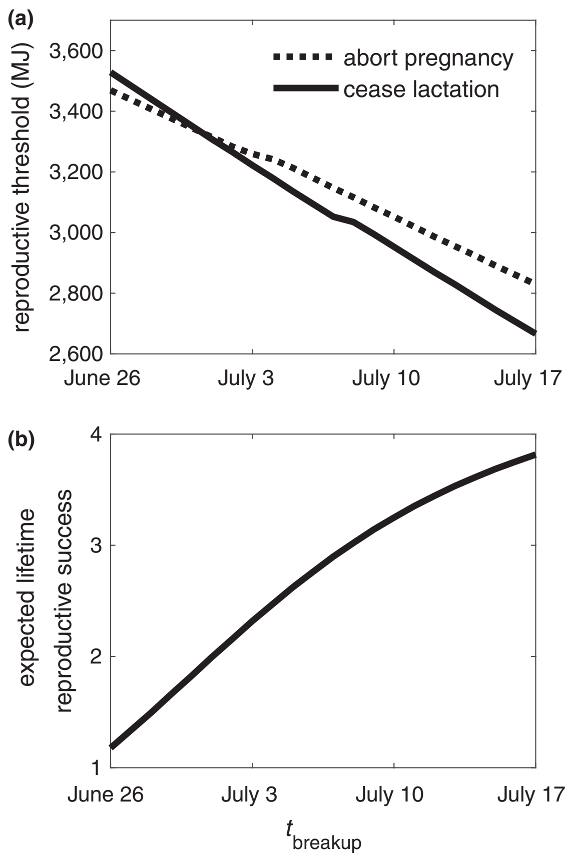

FIGURE 5 (a) Changes in the reproductive energetic thresholds as $t_{breakup}$ is varied. Below these thresholds, it is optimal for a female to either abort her pregnancy or cease lactation for her litter of cubs of the year. Results are shown for a 10-year-old female. (b) Concurrent changes in a female's lifetime fitness (i.e., the expected number of offspring recruited over a female's lifetime) corresponding to early breakup dates. Note that a value of 2 would correspond approximately with population replacement, assuming a 50:50 sex ratio (Stirling & Øritsland, 1995)

survival may seem insignificant ($\sigma_0^{\text{fast ice}} = 0.9988$ vs. $\sigma_0^{\text{active ice}} = 0.9959$), the difference in survival probability in each patch over the entire 108-day spring is large; $(\sigma_0^{\text{fast ice}})^{108} \approx 0.88$ as compared with $(\sigma_0^{\text{active ice}})^{108} \approx 0.64$.

As the energetic threshold below which a female aborts a pregnancy or ceases lactation was unknown, we did not define these quantities in the SDP model a priori, choosing instead to make this emergent behavior the second question we addressed. As expected, there was a set of energetic states in which it was optimal for a female to either abort her pregnancy or cease lactation, resulting in litter loss. In these states, the immediate loss of offspring was outweighed by an increase in the number of future possible offspring resulting from the female retaining her energetic reserves.

Our third question explored the optimal behavior for a female polar bear who has perfect knowledge of her changed environment with a shorter spring feeding period and longer summer as well as the ability to adapt immediately. While polar bears surely do not have perfect information, these results provide a best-case scenario and allowed us to estimate an upper bound on her fitness under these changed conditions. Even if a female bear can instantaneously change the type of ice in which she is foraging, as well as her reproductive behavior, our model still predicted substantial decreases in fitness, and it is reasonable to assume that realized fitness declines would be even greater.

For context, the spring ice breakup has occurred approximately 9 days earlier per decade in the southern Beaufort Sea since the 1980s (Parkinson, 2014; Stern & Laidre, 2016). Based on this trend, a polar bear cub born now will experience average spring ice breakup more than 3 weeks earlier than in the 1980s, so we may already expect to observe shifts in foraging and reproductive behavior, with accompanying fitness declines.

We have only modeled a reduction in the length of spring feeding period and corresponding increase in the length of the summer fasting period. This is a simplification of the effects of climate change, as the risk factors of different ice habitats would also likely change along with this changing ice phenology. For example, polar bear populations are expected to decline in the coming decades (Hunter et al., 2010), and several populations—including that of the southern Beaufort Sea—are already declining (Bromaghin et al., 2015; Lunn et al., 2016). This reduced density of bears may result in lower encounter rates and so a reduced risk of infanticide. Conversely, bears that are encountered may be more desperate and more prone to hunger-motivated cannibalism. Ringed seal abundance is also expected to decline, with projected concurrent shifts in ringed seal population age structure (Ferguson et al., 2017; Kelly et al., 2010; Reimer, Caswell, Derocher, & Lewis, 2019), changing the availability of energetic rewards in all ice types.

SDP models often result in emergent features which seem intuitive once they appear but one may not have thought of otherwise (Mangel, 2015; McHuron et al., 2018). The light gray in the lower right hand corner of all but the bottom right plot in Figure 2 implies that it does not matter in which ice type the female forages. This is because her reserves are depleted to a level so low that she cannot survive the overwinter period, regardless of where she hunts in those final days. If she has a litter of yearlings (bottom right plot), however, this same region suggests that it is optimal for her to be in the fast ice. She will still die over winter, however, because our model allows yearling cubs to survive even if she dies, provided they make it to the end of their second spring, her fitness is higher if she makes a desperate final attempt in the active ice to acquire enough energy to continue lactating until $t_{breakup}$.

When a pregnant female's reserves at the end of spring are too low, it does not matter whether she continues her pregnancy or not, or whether she continues lactation or not, as indicated by the horizontal light gray areas in Figure 4. In these cases, she does not have enough reserves to survive either way, so she will lose her potential litter and any future litters regardless. The vertical light gray bars in both plots of Figure 4 result from the probabilities of reproductive senescence we have imposed, since after senescence, we assumed that new litters will not be recruited and so her fitness is independent of her reproductive status.

Previous research on polar bear energetics and behavioral ecology allowed for meaningful parametrization of many of the key parameters of our model. However, notable uncertainty exists for several parameters. Perhaps most notably, we assumed that a female with cubs spends 37% of her time in the active ice, but this will likely vary both spatially and with time, both seasonally and interannually. Our model results showed robustness to changes in this parameter, however, with only small changes in expected lifetime fitness and a similar magnitude of change resulting from a shorter spring.

Furthermore, the occurrence and timing of reproductive senescence for polar bears is also poorly understood. While the implications of our chosen distribution for the age of senescence may not be large at the population level, as few females survive past this age, the possibility for one additional litter may be large for an individual's lifetime reproductive success. Reproductive senescence in female polar bears is thought to effectively result from a decline in body condition with age (Derocher & Stirling, 1994). However, as we have not included this level of detail in our model (i.e., including a change in female's hunting ability and knowledge over time), we have imposed senescence in this way.

Our work leads to several new hypotheses, for which the data are already available to explore. Data on polar bear body condition, as well as the location, date, and reproductive status of each bear, were collected for population monitoring. The results of our model suggest exploring if females with cubs in poor body condition are more often found in the active ice than females in better condition. Furthermore, our results suggest that a female with cubs may spend more time in the active ice as breakup occurs earlier. A shift of female hunting habitat choice may already be apparent over the past several decades as ice breakup has shifted to occur earlier (Parkinson, 2014; Stern & Laidre, 2016).

SDP models allow us to explore both what types of selective forces may have led to observed traits as well as explore bounds for how individuals may adapt to new conditions. Models such as this one allow us to consider interactions between several important concepts, including changing ecological conditions, behavioral plasticity, reproductive biology, and optimal foraging. This can lead to new hypotheses, as well as sharpening our intuition about the trade-offs faced by individuals in complex ecological landscapes.

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SUPPORTING INFORMATION

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

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Supplementary materials for “Modelling optimal responses and fitness consequences in a changing Arctic”

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S1 Parametrization and functional forms

We parametrized our model and chose functional forms to reflect the ecology of the southern Beaufort Sea population of polar bears.

S1.1 Energetic state constraints

x_{crit}

We assumed that if a bear's energy reserves are reduced to $x_{\text{crit}} = 0$ MJ, the bear dies of starvation [Molnár et al., 2009].

x_{max}

We assumed a maximum mass of four times a bear's structural mass [Molnár et al., 2009]. Structural mass was calculated as in Eq. (S2.1), with $x(t) = 0$. The storage energy of a bear with this maximum mass was estimated using equations (11) and (12) in Molnár et al. (2009) . For a bear of length L= 1.96m, $x_{\text{max}} = 8822$ MJ.

S1.2 Time parameters

T

We assumed a female is first available to mate in the spring at age 5. As females generally stop reproducing in their late 20s, we have taken a maximum age of 28, since she will not have any fitness gains after this age. Thus the number of years we consider is $T = 24$.

t_{spring}

Ringed seal pupping begins in early April, reaching its peak mid-April [McLaren, 1958; Smith, 1987], so we assumed polar bears may start experiencing net energetic gains at approximately $t_{\text{spring}} =$ April 1 (ordinal day 91).

t_{breakup}

We assumed net energetic gains decline sharply around the time of sea ice breakup, defined as the first day on which the average sea ice concentration over the Southern Beaufort Sea subpopulation area declined below 50% [Etkin, 1991; Stirling, 2005; Ferguson et al., 2017]. Sea ice data was obtained from the National Snow and Ice Data Center [Stroeve and Meier, 2018]. Satellite imagery was available from 1979 until the present, but in an attempt to capture the scenario before significant climate change impacts, we calculated the average breakup date using only the 1980s, resulting in $t_{\text{breakup}} =$ July 17 (ordinal day 198).

τ_{icefree}

As above, we calculated freezeup as the first day in autumn that the mean sea ice concentration rose above 50%. The mean day of freezeup in the 1980s was t_{freezeup} = October 8 (ordinal day 281). The number of days between breakup and freezeup was $\tau_{\text{icefree}} = 83$.

S1.3 General parameters

λ_i

The daily probability of finding and catching prey is thought to depend on patch choice between active ice and fast ice, with active ice believed to have a higher density of prey that are more vulnerable to predation. Stirling and Øritsland (1995) estimated that bears caught a seal approximately every 3 days in the spring. We used $\lambda_{\text{fast ice}} = 1/3.5$ and $\lambda_{\text{active ice}} = 1/2.5$.

$Y_i(t)$

When a polar bear catches a prey item, the expected energetic value depends on the type and size of seals available in patch i at time t. The expected value of prey for a given ice habitat (i = fast ice or active ice) was calculated as

$$Y_i(t) = \sum_{\text{species}} \left[\Pr(\text{species}) \left(\sum_{\text{seal class}} \Pr(\text{seal class}|\text{species}) \times (\text{energetic value}|\text{seal class, species}) \right) \right], \quad \text{(S1.1)}$$

where 'species' ranged through ringed and bearded seals and 'seal class' ranged through pups and juveniles/adults. Each of the probabilities was conditional on patch, i, and date, t. The $\Pr(\text{species})$ depended on habitat. Estimates were made using data on seals killed by polar bears in the Beaufort Sea (data from [Pilfold et al., 2012]). In the fast ice, where bearded seals are uncommon, $\Pr(\text{ringed seals}) = 0.97$ and $\Pr(\text{bearded seals}) = 0.03$. In the active ice, these values changed to be 0.84 and 0.16, respectively.

The $\Pr(\text{seal class}|\text{species})$ also depended on habitat. In the fast ice, pups made up 52% of the observed ringed seal kills, while juveniles/adults made up 48%. In the active ice, ringed seal pup kills were observed with higher frequency, and these values changed to 72% and 28%, respectively. Of the few bearded seal kills observed, all were juveniles/adults in the fast ice, while 27% were pups and 73% were juveniles/adults in the active ice.

We used previous estimates for the energetic values of ringed seals. Gross energy estimates for ringed seal pups were 41.9 MJ through April, 209.3 from May 1–15, and 418.7 MJs for the remainder of the spring [Stirling and Øritsland, 1995]. Subadult and adult ringed seals have a gross energy content of approximately 628 MJs [Stirling and Øritsland, 1995]. However, a polar bear is thought to only be able to eat a maximum 20% of its mass in one meal [Best, 1977]. Thus for a female polar bear who may average 200kg, we assumed she may consume a maximum of 40kg per day. An adult ringed seal weighs an average of 57 kg [Lydersen and Gjertz, 1987]. If the female can only eat 40 kg, she consumes approximately 70% ($= 40/57$) of the available mass. We thus assumed maximum energetic intake in one day to be 439.6 MJs ($= 0.7 * 628$).

In the absence of information on the energetic value of bearded seal pups, we multiplied the ringed seal pup energetic values by a scaling factor to obtain estimates for the calories obtained from bearded seal pups. To obtain this scaling factor, we divided the average mass of bearded seal pups (62kg [Derocher et al., 2002]) by the average mass of ringed seals pups (11kg [Derocher et al., 2002]) to obtain a bearded seal pup scaling factor of 5.64. We then multiplied the energetic values of ringed seal pups by this scaling factor to obtain estimates for the energetic value of bearded seal pups. Our estimate for a neonate bearded seal pups was thus 236 MJs for its first two weeks of life, after which time we assumed it provided the maximum value of 439.6 MJs. Bearded seals pup later than ringed seals, with their pupping beginning approximately May 1 [Lentfer, 1988; Watanabe et al., 2009]. To account for the change in availability of bearded seal pups, we kept all probabilities as described above, but kept the energetic value of bearded seal pups to be 0 MJs before May 1 in an attempt to incorporate reduced prey availability before bearded seal pupping.

We then multiplied all estimates by 0.92, the proportion of energy available for bears to metabolize after consumption [Best, 1977]. We assumed a linear relationship of pup calories between the three time periods of April 1, May 1, and May 15. Inserting all of these values into (S1.1) provided our estimates of the expected energetic value of a prey item, conditional on the ice foraging habitat (Fig. S1).

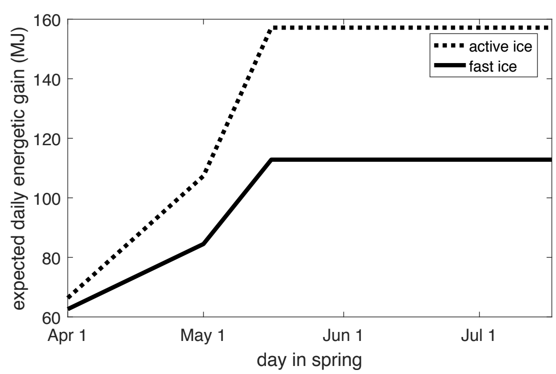

Figure S1: Expected daily energetic value of a prey item; the daily probability of a successful hunt multiplied by the expected energetic gain ($\lambda_i \times Y_i(t)$), dependent on foraging habitat $i \in \{\text{active ice}, \text{fast ice}\}$ at time t in spring.

a

We used the equation of Pagano et al. (2018) to estimate a female bear's daily field metabolic rate (FMR) during the spring (MJ/day),

$$\text{FMR} = 0.0002 \times \text{mass}^{2.41},$$

where mass (kg) was calculated as in Eq. (S2.1).

σ

We used 0.996 as our estimate of an adult female bear's annual survival probability in the Beaufort Sea [Amstrup and Durner, 1995]. We assumed daily survival to be constant throughout the year, so daily survival was calculated as the 365$^{\text{th}}$ root of annual survival,

$$\sigma = 0.996^{365^{-1}}.$$

$\widehat{\sigma}$

The number of days not considered as part of spring was

$$\#\text{ of `overwinter' days} = 365 - (t_{\text{breakup}} - t_{\text{spring}}),$$

which, for our estimated parameter values, was 258 days. The probability of overwinter survival $\widehat{\sigma}$ was calculated from the daily survival probabilities, multiplied by the number of days included in the 'overwinter' period, so $\widehat{\sigma} = \sigma^{258} \approx 0.9972$. Note that we updated this value each time we considered an earlier breakup and corresponding longer 'overwinter' period.

$p_s(\textbf{age})$

Functional reproductive senescence has been suggested to occur during a female's early 20s [Ramsay and Stirling, 1988; Derocher and Stirling, 1994; Regehr et al., 2007; Stirling et al., 2011]. While polar bears are physiologically able to reproduce into their 30s in captivity [Latinen, 1987], they may have trouble accumulating sufficient fat stores to do so in the wild after their prime years [Derocher and Stirling, 1994].

We used the generalized extreme value distribution to describe the probability of senescence occurring at a given age, as was used to successfully model grizzly bear (*Ursus arctos*) senescence [Schwartz et al., 2003]. We used a value of 1 for the shape parameter, as found for grizzly bears [Schwartz et al., 2003], but shifted the distribution to have a mode at age 23, resulting in the probability density function

$$f(x) = e^{-(x/23)^{23}} \left(\frac{x}{23}\right)^{22},$$

where x is the bear's age, to the day, converted into decimal years. To get the probability of senescence over an entire year, we integrated, so

$$p_s(\text{age}) = \int_{\text{age}}^{\text{age+1}} e^{-(x/23)^{23}} \left(\frac{x}{23}\right)^{22} dx.$$

As we assumed a bear must become senescent, we use a conditional probability to capture the probability of becoming senescent at a given age, given that she is not yet senescent by her current age, i.e.,

$$p_s(\text{age}) = \frac{\int_{\text{age}}^{\text{age+1}} e^{-(x/23)^{23}} \left(\frac{x}{23}\right)^{22} dx}{\int_{\text{age}}^{\infty} e^{-(x/23)^{23}} \left(\frac{x}{23}\right)^{22} dx}.$$

This resulted in a left-skewed probability density function, where the probability of becoming senescent between ages 20 and 25 is 0.96 (specifically, the probabilities of becoming senescent before age 20 or after age 25 are 0.039 and 0.001, respectively).

S1.4 Single ($\eta = 1$) parameters

$\epsilon(t)$

The probability of a single bear mating is high, here taken to be 0.99 over the entire spring [Molnar et al., 2008]. We assumed that the daily probability of finding a mate is independent of age, and does not vary over the mating period. Mating must start τ_{mate} days before breakup, in order for there to be sufficient time for the pair to mate successfully, so the number of days where a female is available to mate is

$$\text{mating days} = (t_{\text{breakup}} - \tau_{\text{mate}}) - t_{\text{spring}}.$$

This resulted in the daily probability of finding a mate,

$$\begin{aligned}\epsilon(t) &= 1 - \text{probability of not finding a mate}\\ &= 1 - (1 - 0.99)^{1/(\text{mating days})}\end{aligned}$$

for $t = 1, \ldots, (\text{mating days})$. For our values of t_{spring}, t_{breakup}, and τ_{mate}, this resulted in a daily estimate of $\epsilon(t) \approx 0.05$. If the depletion of the female's reserves following mating would cause her to die, we assumed she does not mate.

τ_{mate}

Mating takes approximately 17 days [Molnar et al., 2008], with other estimates around this value: 16 days [Derocher et al., 2010], 18 days [Wiig et al., 1992], and 13 days [Stirling et al., 2016].

S1.5 Pregnancy ($\eta = 2$) parameters

τ_{den}

We assumed den entry and emergence occur approximately on November 17 and March 31, respectively [Amstrup and Gardner, 1994], so $\tau_{\text{den}} = 134$.

S1.6 Cubs of the year litter ($\eta = 3$) parameters

$\sigma_0^{\text{fast ice}}$

Using the annual survival probability of 0.651 of a COY litter from Amstrup and Durner (1995) , we took the daily probability of survival to be the 365th root of this value. We assumed this value pertains to females with COYs who spend their time mainly in the fast ice, so $\sigma_0^{\text{fast ice}} = 0.651^{365^{-1}}$.

$g_3(x, t)$, $g_4(x, t)$

For a female with a litter of dependent COYs or yearlings ($\eta = 3, 4$), the female has some energetic threshold below which lactation ceases [Robbins et al., 2012]. If the female is well above x_{crit}, she invests a target amount, m_η, daily, and if she is unable to invest m_η without falling to x_{crit}, she ceases lactation. The energetic costs of lactation were,

$$g_\eta(x(t)) = \begin{cases} m_\eta, & x > x_{\text{crit}} + m_\eta \\ 0, & \text{else} \end{cases}, \quad \eta = 3, 4.$$

The litter is lost if a female's reserves are too low to produce milk (i.e., $g_\eta(x(t)) = 0$). We assumed $m_3 = 0.24 \times \text{mass}^{0.75}$, the milk production of black bears (*Ursus americanus*) during mid-lactation [Gittleman and Oftedal, 1987; Arnould and Ramsay, 1994], and $m_4 = 0.1 \times \text{mass}^{0.75}$, as it falls between the values of 0.17 and 0.05 $\times\text{mass}^{0.75}$ describing milk production over a litter's first and second summers, respectively [Arnould and Ramsay, 1994].

S1.7 Yearling litter ($\eta = 4$) parameters

$\sigma_1^{\text{fast ice}}$

We used an annual survival probability 0.86 for a yearling litter [Amstrup and Durner, 1995], again taking the daily probability of survival to be the 365th root of this value. We again assumed this value pertains to females who spend their time mainly in the fast ice, so $\sigma_0^{\text{fast ice}} = 0.86^{365^{-1}}$.

k

We used the expected litter size of a recruited litter, averaged over the values for 2001–2003, in Hunter et al. (2010), resulting in $k = 1.15$ offspring expected in each recruited litter. Ramsay and Stirling (1986) found a similar mean yearling litter size of 1.1 cubs.

S2 Details of over-winter functions, $w_\eta(x)$

We assumed a resting metabolic rate, RMR, calculated based on the bear's mass each day through the summer icefree period. Mass (kg) was estimated from storage energy, $x(t)$ (MJ), and body length, L (m), using Eq. 18C in Molnár et al. (2009) :

$$\text{mass} = \frac{x(t) + 390.53 \times \mathrm{L}^3}{26.14}. \tag{S2.1}$$

We assumed an average adult female body length of L$= 1.96$m [Derocher and Stirling, 1998]. The allometric regression for RMR in vertebrate-eating carnivores [McNab, 1988], RMR $= 0.392 \times$ mass$^{0.813}$, has been suggested as appropriate for polar bears [Pagano et al., 2018]. For a fixed body length, we highlight the reliance on her energy reserves by writing RMR$(x(t))$ below.

For an individual who is pregnant ($\eta = 2$) and produces offspring by the following spring, it is necessary to differentiate between her resting and denning metabolic rates, as the metabolic rate of a female in a den is lower than her resting metabolic rate [Atkinson and Ramsay, 1995; Robbins et al., 2012]. Her denning metabolic rate was calculated as DMR $= 0.02 \times$ mass$^{1.09}$, which included the demands of both gestation and lactation in the den [Robbins et al., 2012].

For each day over summer, $t \in [t_{\text{breakup}}, t_{\text{breakup}} + \tau_{\text{icefree}}]$, we calculated the bear's energy demands, depending on her state $x(t)$. Her state was then reduced by this amount and this new state was used to calculate her energy expenditure over the next day. We describe each case explicitly now. For an individual who is single ($\eta = 1$) at the end of spring ($t = t_{\text{breakup}}$),

$$w_1(x) = \max\left\{ x_{\text{crit}},\, x - \left(\sum_{t=t_{\text{breakup}}}^{t_{\text{breakup}}+\tau_{\text{icefree}}} \text{RMR}(x(t)) \right) \right\}.$$

The overwinter change in state of a pregnant female ($\eta = 2$) is as follows,

$$w_2(x) = \max\left\{ x_{\text{crit}},\, x - \left(\sum_{t=t_{\text{breakup}}}^{t_{\text{breakup}}+\tau_{\text{icefree}}} \text{RMR}(x(t)) \right) - \left(\sum_{t=t_{\text{breakup}}+\tau_{\text{icefree}}}^{t_{\text{breakup}}+\tau_{\text{icefree}}+\tau_{\text{den}}} \text{DMR}(x(t)) \right) \right\}.$$

For an individual who is pregnant but aborts the pregnancy, we simplified by assuming litter loss occurs after summer but before denning, so

$$w_2^{\text{loss}}(x) = \max\left\{ x_{\text{crit}},\, x - \left(\sum_{t=t_{\text{breakup}}}^{t_{\text{breakup}}+\tau_{\text{icefree}}} \text{RMR}(x(t)) \right) \right\} = w_1(x).$$

If a female with a COY litter ($\eta = 3$) keeps her litter through to the following spring, her energetic costs over summer will include the daily costs of lactation, $m_{3.\text{summer}}$ (MJ), in addition to her own maintenance. We used $m_{3.\text{summer}} = 0.17 \times \text{mass}^{0.75}$ where mass is the bear's mass (kg) at $t = t_{\text{breakup}}$ to estimate her target daily summer milk production [Arnould and Ramsay, 1994]. Her state change from one spring to the next followed

$$w_3(x) = \max\left\{ x_{\text{crit}},\, x - \left(\sum_{t=t_{\text{breakup}}}^{t_{\text{breakup}}+\tau_{\text{icefree}}} (\text{RMR}(x(t)) + m_{3.\text{summer}}(x(t))) \right) \right\}.$$

If she loses the litter, we assumed litter loss occurs halfway through the summer icefree period, and so

$$w_3^{\text{loss}}(x) = \max\left\{ x_{\text{crit}},\, x - \left(\sum_{t=t_{\text{breakup}}}^{t_{\text{breakup}}+\tau_{\text{icefree}}/2} (\text{RMR}(x(t)) + m_{3.\text{summer}}(x(t))) \right) - \left(\sum_{t=t_{\text{breakup}}+\tau_{\text{icefree}}/2+1}^{t_{\text{breakup}}+\tau_{\text{icefree}}} (\text{RMR}(x(t))) \right) \right\}.$$

We assumed that a female with a yearling litter that survives to the end of their second spring ($\eta = 4$) keeps her litter through to the following spring. By this age, her main contribution to her litter is through prey she has killed and teaching her young to hunt. We assumed her milk production by this time is negligible, so her only energetic costs are due to her own maintenance,

$$w_4(x) = \max\left\{ x_{\text{crit}},\, x - \left(\sum_{t=t_{\text{breakup}}}^{t_{\text{breakup}}+\tau_{\text{icefree}}} \text{RMR}(x(t)) \right) \right\} = w_1(x).$$

S3 Supplementary figures

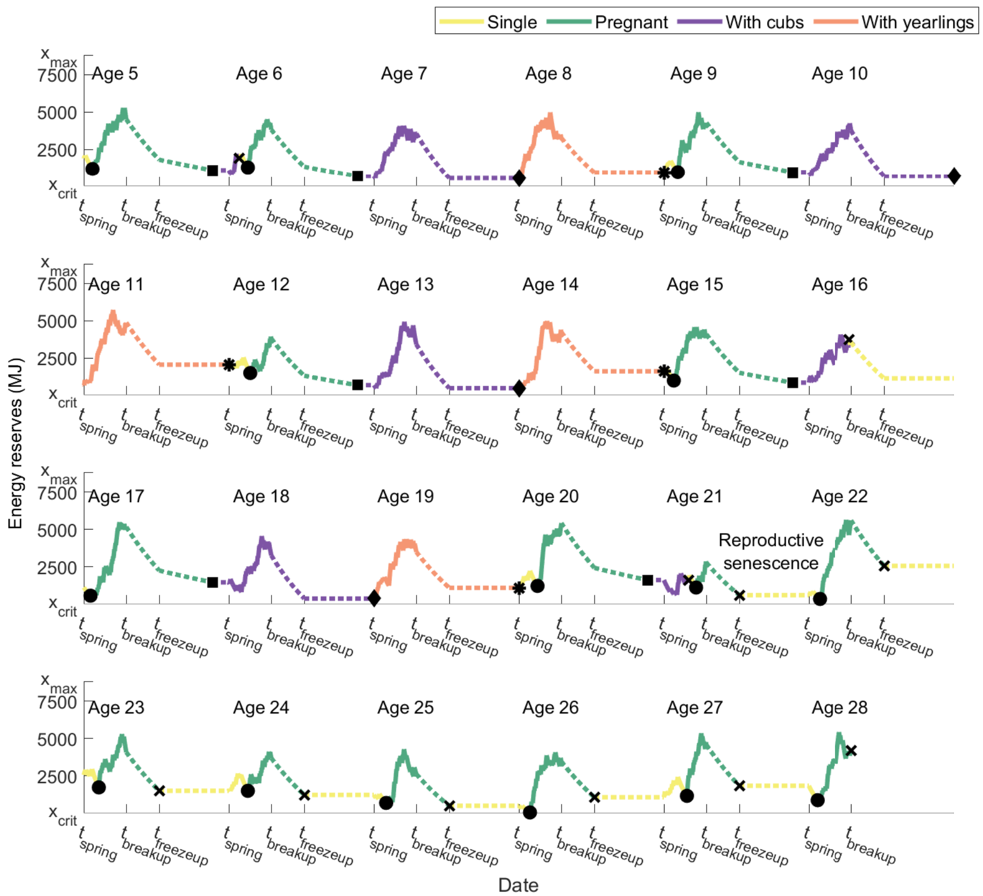

Figure S2: One Monte Carlo simulation of an adult female bear's reproductive and energetic state throughout her reproductive years, assuming optimal foraging habitat selection in spring (not shown here). Solid lines represent the output from the stochastic dynamic programming model. Dashed lines are the deterministic changes in state from the end of one spring to the beginning of the next. Key life history events are noted as follows: circles denote successful mating; squares denote the birth of a litter; diamonds denote the transition of a litter from cubs to yearlings; **x** denotes the loss of a pregnancy or litter; and * denotes litter recruitment.

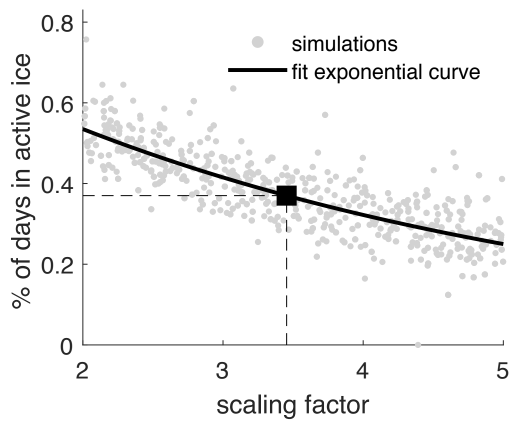

Figure S3: The proportion of spring days spent in the active ice by a female with a litter of cubs of the year, as simulated with 1000 Monte Carlo simulations from our stochastic dynamic programming model. In each simulation, the probability of mortality in the active ice is set to be the probability in the fast ice, multiplied by some scaling factor. We estimated the scaling factor that results in approximately 37% of the females' time being spent in the active ice.

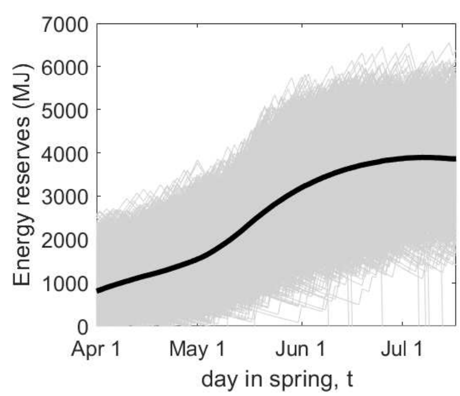

Figure S4: 10000 Monte Carlo simulations of a 10 year old bear's energy stores throughout spring. Each grey line denotes one Monte Carlo simulation. The black line is the mean across simulations.

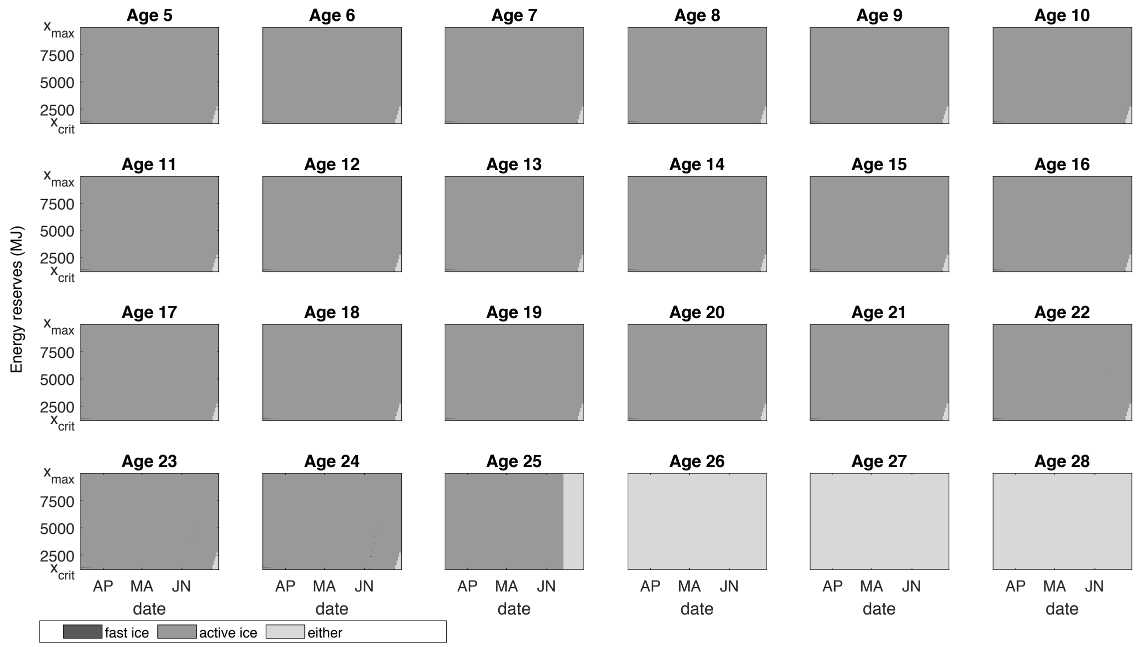

Figure S5: Optimal foraging decisions for a single bear at each age, in each reproductive state, in each energetic state, and for each day throughout the spring.

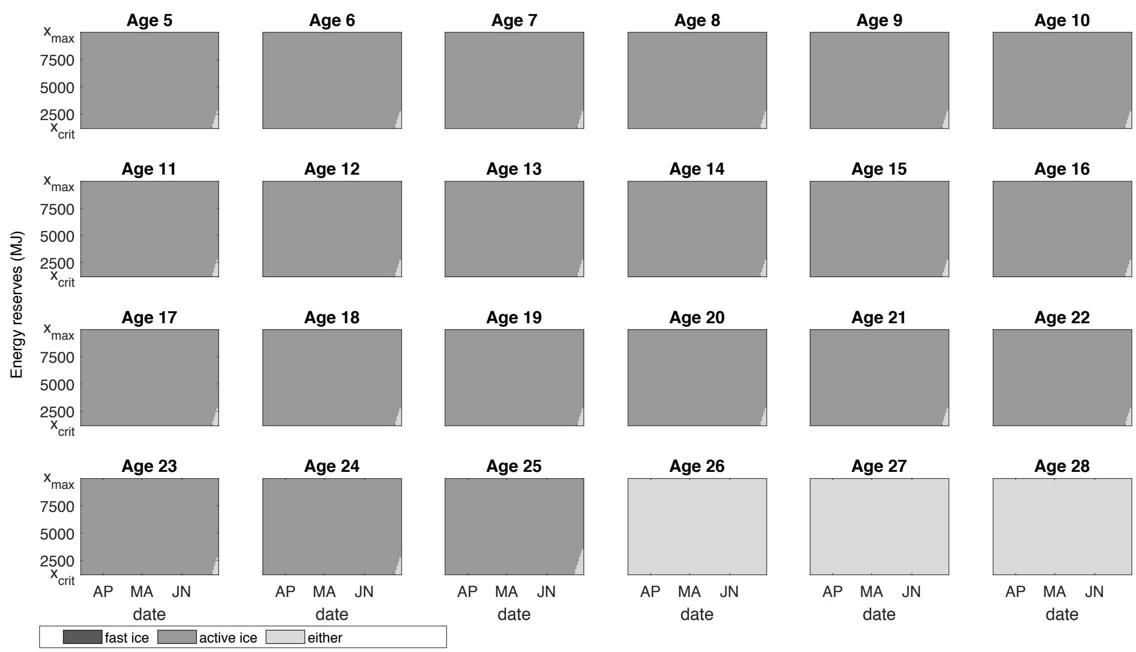

Figure S6: Optimal foraging decisions for a pregnant bear at each age, in each reproductive state, in each energetic state, and for each day throughout the spring.

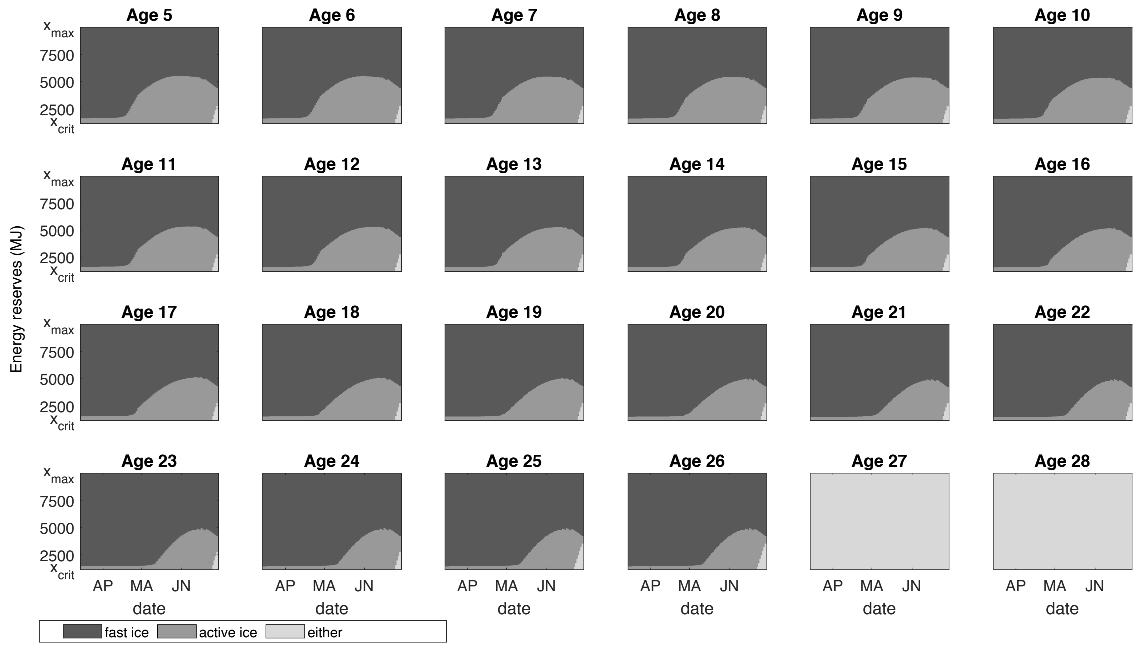

Figure S7: Optimal foraging decisions for a bear with a litter of COYs at each age, in each reproductive state, in each energetic state, and for each day throughout the spring.

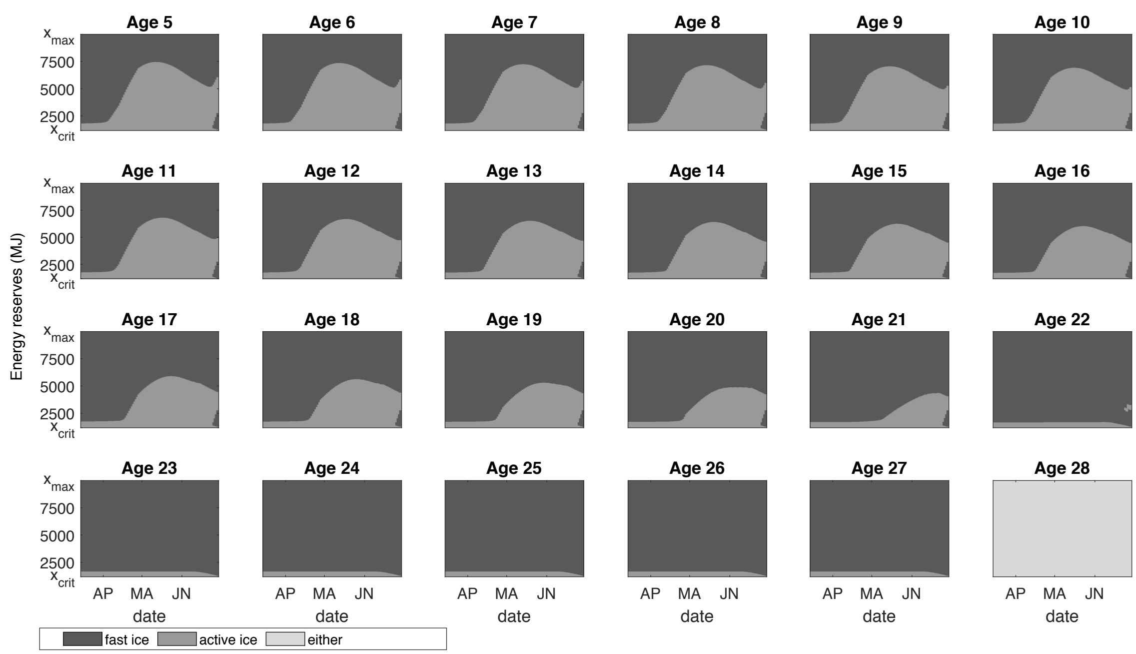

Figure S8: Optimal foraging decisions for a bear with a yearling litter at each age, in each reproductive state, in each energetic state, and for each day throughout the spring.

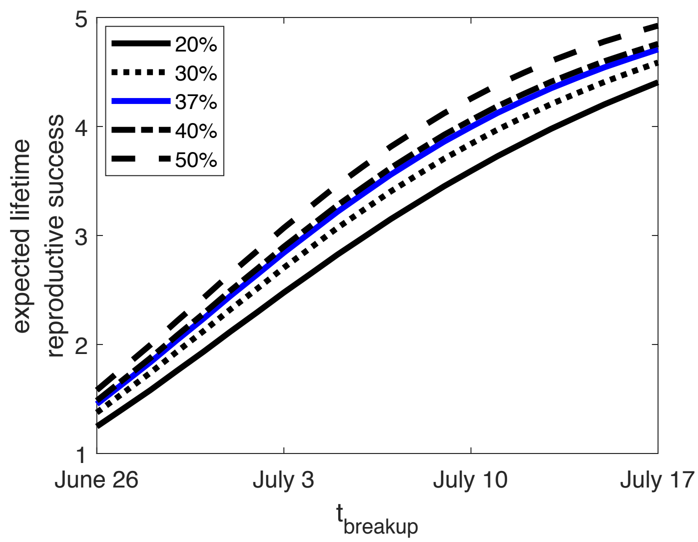

Figure S9: Changes in fitness and the fitness response to a shorter spring for varying assumed percentages of time spent in the active ice by a female with a litter of COYs. The blue line corresponds to the value of 37% used in the main body of the text, and is the same as the curve in Fig. 5b.

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