



The influence of prey availability on behavioral decisions and reproductive success of a central-place forager during lactation

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ABSTRACT

Marine central-place foragers are increasingly faced with altered prey landscapes, necessitating predictions of the impact of such changes on behavior, reproductive success, and population dynamics. We used state-dependent behavioral life history theory implemented via Stochastic Dynamic Programming (SDP) to explore the influence of changes in prey distribution and energy gain from foraging on the behavior and reproductive success of a central place forager during lactation. Our work is motivated by northern fur seals (*Callorhinus ursinus*) because of the ongoing population decline of the Eastern Pacific stock and projected declines in biomass of walleye pollock (*Gadus chalcogrammus*), a key fur seal prey species in the eastern Bering Sea. We also explored how changes in female and pup metabolic rates, body size, and lactation duration affected model output to provide insight into traits that might experience selective pressure in response to reductions in prey availability. Simulated females adopted a central-place foraging strategy after an initial extended period spent on land (4.7–8.3 days). Trip durations increased as the high energy prey patch moved farther from land or when the energy gain from foraging decreased. Increases in trip duration adversely affected pup growth rates and wean mass despite attempts to compensate by increasing land durations. Metabolic rate changes had the largest impacts on pup wean mass, with reductions in a pup's metabolic rate allowing females to successfully forage at distances of 600+ km from land for up to 15+ days. Our results indicate that without physiological adaptations, a rookery is unlikely to be viable if the primary foraging grounds are 400 km or farther from the rookery. To achieve pup growth rates characteristic of a population experiencing rapid growth, model results indicate the primary foraging grounds need to be <150 km from the rookery.

1. Introduction

The availability of prey resources is a key feature driving the spatial distribution, foraging patterns, and activity budgets of predators (Benoit-Bird et al., 2013; Boyd et al., 2015; Davoren, 2013; Fauchald et al., 2000). In marine environments, predators are increasingly faced with altered prey landscapes resulting from fishing pressures and climate change. These changes can affect demographic trends, which are ultimately determined by foraging and reproductive decisions of individuals (Baylis et al., 2015; Bost et al., 2015; Meyer-Gutbrod et al., 2015; Murray et al., 2021; Salvadeo et al., 2015; Sherley et al., 2018; Soto et al., 2004; Trivelpiece et al., 2011). Species such as seabirds and many pinnipeds may be particularly affected by such changes because

they have life histories that are constrained by the need to balance provisioning young at terrestrial sites with foraging at sea. That is, central-place foragers are both reliant on localized prey patches to support the considerable costs of reproduction and exhibit high breeding-site fidelity that further constrains their ability to withstand changes in prey availability (Pichegru et al., 2010).

Central-place foragers employ a variety of behavioral mechanisms to cope with variability in prey landscapes, such as increasing foraging effort, extending trip durations, and switching to alternate prey species or foraging areas (Costa, 2008; Gladics et al., 2015; Wilson et al., 2005). For example, common murre (*Uria aalge*) foraged further from the colony and delivered larger capelin (*Mallotus villosus*) to their chicks during a year of low capelin density (Burke and Montevecchi, 2009). In

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otariids (sea lions and fur seals), the duration of lactation of some species is flexible, such that females may extend lactation beyond the typical dependency period when food availability is reduced (Jeglinski et al., 2012; Maniscalco, 2014; Trillmich, 1986). There are limits to the extent these behavioral strategies can mitigate the effects of prey landscape changes on reproductive success because, even if predators can find enough food to meet their energy needs, they can only consume or carry a finite amount of prey and offspring have limited fasting capabilities (Cohen et al., 2014; Costa et al., 1989; Le Bot et al., 2019; Ronconi and Burger, 2008). Indeed, prey depletion near the colony (“Ashmole’s halo”) is one factor known to regulate population densities of colonially-breeding central-place foragers (Ashmole, 1963; Elliott et al., 2009; Kuhn et al., 2014a; Weber et al., 2021).

There are a variety of approaches that have been used to predict behavioral responses of marine central-place foragers in the face of different environmental conditions. Statistical correlative habitat models are one of the most common approaches, which identify associations with environmental and physical features to predict spatial distribution under future conditions (Elith and Leathwick, 2009). State-space models and machine learning have been used to predict behaviors using movement characteristics derived from telemetry data (Browning et al., 2018; Jonsen et al., 2013; Michelot et al., 2017), which can then be linked with other datasets to understand behavioral changes in the context of environmental conditions and their influence on reproductive success (Russell et al., 2015). Process-based or mechanistic models, where assumptions about behavior are rooted in ecological theory, provide an alternate approach that can help overcome some of the challenges of these statistical-driven methods (Cuddington et al., 2013), such as their reliance on existing spatial distribution data and the inherent assumption that current behavior reflects future behavior (Muhling et al., 2020; Palacios et al., 2014). In these models, behaviors are an emergent model property that arise from interactions between multiple processes, such as physiology and resource availability (Chudzinska et al., 2021; Fiechter et al., 2016; Satterthwaite and Mangel, 2012), as opposed to derived from empirically collected data in statistical approaches.

In this paper, we explore the behavioral decisions of a central-place foraging marine mammal during lactation using state dependent life history theory implemented by Stochastic Dynamic Programming (SDP), which can be used for solving problems of decision making (Clark and Mangel, 2000; Houston et al., 1988). The underlying assumption of SDP models is that an individual acts in such a way to maximize some future reward, which in ecological applications is typically some metric of Darwinian fitness such as expected lifetime reproductive success (Mangel, 2015). This modeling approach has been used to address basic biological questions, including the evolution of behavior (Higginson et al., 2016; Houston et al., 2006), and inform management strategies in a diversity of ecosystems (Bogich and Shea, 2008; Martin et al., 2010; McCarthy et al., 2001; Milner-Gulland, 1997). In the marine environment, SDP models have been used in a variety of generalized and species-specific applications, such as predictions of prey choice (Tinker et al., 2009), responses to environmental change and anthropogenic activities (Pirrotta et al., 2018; Reimer et al., 2019; Satterthwaite and Mangel, 2012; Wiedenmann et al., 2011), migration (Yoshioka et al., 2019) and reproductive strategies (Griffen, 2018; McHuron et al., 2018), and physiological dynamics (Noren et al., 2009; Noren and Mangel, 2004).

We developed a species-specific SDP model, using northern fur seals (*Callorhinus ursinus*) as the motivating species, to explore the optimal behavioral choices during lactation under different hypothetical prey availability and distribution scenarios, and the resulting impacts on reproductive success. We then explored how changes in behavioral (lactation duration), physiological (metabolic rates), and morphological (body size) traits affected behavioral choices and reproductive parameters, with the intent of understanding if any of these trait changes conferred a reproductive benefit under adverse prey scenarios. These

traits were selected because of existing inter- and intraspecific variation within the otariid lineage, suggesting the potential for selective pressures on these traits. Northern fur seals are both a data-rich species and one with a clear management need to predict how environmental changes and fisheries management scenarios will impact population dynamics. The Eastern Pacific stock that breeds in the Bering Sea has experienced a population decline since the late 1990s, driven mostly by declines at the largest breeding rookery on St. Paul Island, Alaska (Muto et al., 2022; Towell et al., 2006). The cause of this decline is unknown, but reduced food availability is one hypothesized factor given disparities in maternal foraging trip durations, pup growth rates, and population trends among the three islands that make up the Eastern Pacific stock (Kuhn et al., 2014b, 2014a; McHuron et al., 2019, McHuron et al., 2020). Recent and unprecedented environmental conditions have resulted in range shifts of walleye pollock (*Gadus chalcogrammus*) into the northern Bering Sea (Eisner et al., 2020), which are one of the key prey items of northern fur seals on St. Paul Island (McHuron et al., 2020; Zeppelin and Ream, 2006). This is in addition to concerns about overlap between fur seals and the commercial pollock fishery (McHuron et al., 2020) and forecasted declines in pollock biomass due to climate change (Holsman et al., 2020). In using an approach that balanced a hypothetical and real-world application, we were able to assess model performance in relation to real fur seal behavior while exploring hypothetical questions about future behavior that would be challenging to address using statistical approaches.

2. Methods

2.1. Model overview

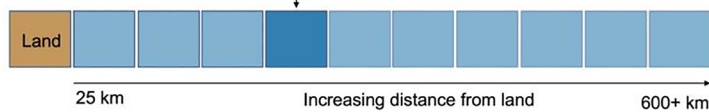
We focused on decisions faced by a lactating female northern fur seal who must provision (nurse) her pup on land but obtain resources for provisioning at sea. Specifically, we were interested in how behavioral decisions might change in response to changes in prey distribution and abundance, the resulting impacts on reproductive success, and how changes in body size, metabolic rates, and lactation duration might affect those outcomes. Emergent properties of the model included habitat type (land vs sea) and location at any given time, trip and land durations, and pup growth rates and wean masses.

The key components of an SDP model include a time horizon with discrete time steps, one or more state variables, a terminal fitness function (if the time horizon is finite), a set of decisions or actions (here discrete behavioral choices), and a fitness function that describes the expected future reward for an optimally behaving individual. The value of this fitness function is determined by the dynamic programming equations, via iteration backwards in time. Together, these components allow for the determination of optimal time- and state-dependent behavioral decisions, referred to here as the backward iteration since the dynamic programming equations are solved backwards in time. The optimal behavioral decision is simply the one that maximizes the expected reproductive success across all behavioral choices. Monte Carlo simulations forward in time are then used to simulate populations where individuals move through the environment using the decisions derived from the backward iteration (see Clark and Mangel, 2000; Houston et al., 1988; Mangel, 2015 for further details). Essentially, the backward iteration determines how a fur seal should behave for each combination of state variables and the forward simulation explores the sequence of decisions a fur seal makes during lactation.

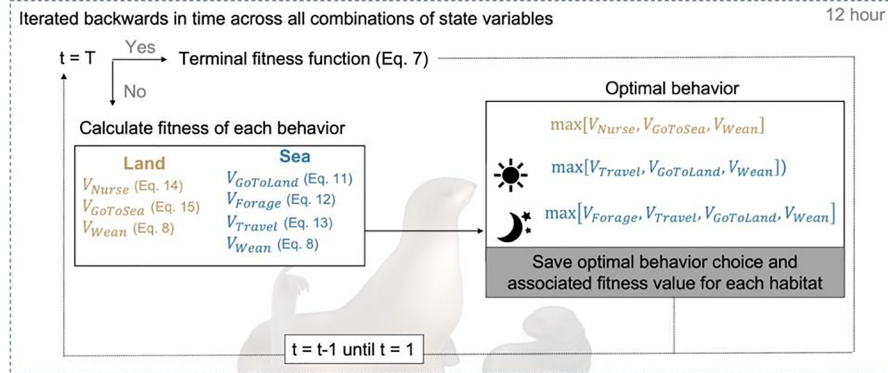
In this model, there are two habitats for a female fur seal: land or sea. We characterized land by a single location, and sea by ten discrete locations (Fig. 1). At sea, we determined whether a female is predicted to forage, travel within her current location or to a new location, go back to land, or wean her pup. On land, we determined whether a female is predicted to nurse her pup, go to sea, or wean her pup. The behavioral choices depended on two intrinsic state variables (female fat mass, pup mass), and one extrinsic state variable that was only applicable when a

1. Baseline model scenarios

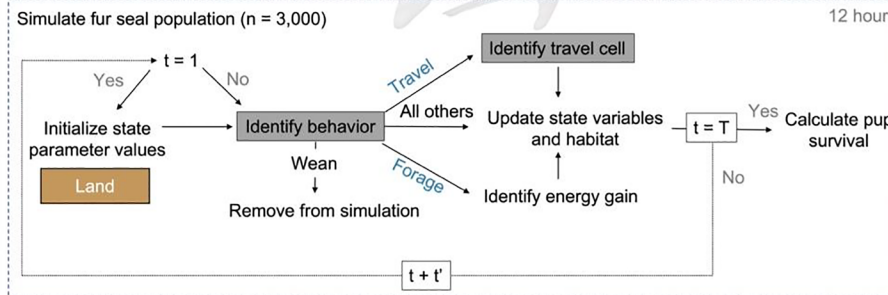
One high energy prey patch – specific location varied among scenarios



2. Backward iteration



3. Forward simulation



female was at sea (location, referred to as cell). There is a single backward iteration, where the two habitats are linked by the behavioral choices of going to land or to sea. The following sections provide further detail on each of the key model components, including the specific values and bounds of state variables and the state dynamics, which describe the underlying bioenergetics of how female fat mass and pup mass vary with behavior. A simplified schematic of the model is shown in Fig. 1.

2.2. Model scenarios

We ran a total of 30 different model scenarios to explore how behavioral choices of lactating females might change in response to prey distribution and abundance. In each scenario, there was one cell at sea that had abundant prey (the ‘high’ energy cell), while the other nine cells had less abundant prey (the ‘low’ energy cells), meaning a female received less energy from foraging in low energy cells compared with the high energy cell. Scenarios differed in the specific location of the high energy cell; since cells varied in how far they were from land, it allowed us to assess how optimal behavior should change as a prey patch moves farther away from land, where a female’s pup was located. We used three different values to characterize the amount of energy available in the high energy cell, referred to as the ‘high’, ‘average’, and ‘low’ energy gain scenarios. Since we ran all possible combinations of models, this resulted in 30 scenarios (10 prey location scenarios and 3 energy gain scenarios) for the baseline model, each with their own backward iteration. The values of some parameters, namely pup metabolic rate and milk intake, are different during the perinatal duration (the time spent on land immediately following birth) compared with other times

Fig. 1. Conceptual diagram of the stochastic dynamic programming model and different baseline model scenarios, parameterized for an adult female northern fur seal during lactation. Model scenarios (1) differed in the location of the high energy cell and the amount of energy gained from foraging in it, with the high energy cell located in only one of 10 potential locations for each scenario. In the backward iteration (2), the optimal behavior is the one that maximizes future reproductive success, with different optimal behaviors depending on whether a female is on land or at sea. Optimal behaviors were then used in an individual-based forward simulation (3); at the first time step a female is on land and give birth but thereafter her behaviors are dictated by the results of the backward iteration given her current habitat (land vs sea), values of the state variables, and model time. Fur seal image reprinted from *Marine Mammals of the World*, 2nd edition, T.A. Jefferson, M.A. Webber, and R.L. Pitman, Pinnipeds, page 360, 2015, with permission from Elsevier.

during lactation. Because of this, we also ran the baseline model using values specific to the perinatal duration.

We developed four alternate models (referred to as ‘trait changes’) to explore how behavioral, physiological, and morphological variation that currently exist within the otariid lineage affected behavioral decisions and reproductive success. These changes included an extension to the time horizon to increase lactation duration, an increase in body size, and reductions in either a female’s or a pup’s metabolic rate (Table 1). We did not include a reduction in body size since female northern fur seals are already among the smallest otariid females. We modeled changes as the endpoint of evolutionary change so that a separate backward iteration determined optimal behaviors under that adapted state. We ran each trait change model using all 30 scenarios of prey location and energy gain. These four models were meant to provide insight into whether there might be selective potential on any of these traits that might help northern fur seals adapt to adverse foraging conditions, such as reduced prey or prey being located further from land. Since each scenario was limited to a single change, results are conditioned on all other factors of their biology remaining the same.

2.3. Time horizon

We ran the baseline model from parturition to weaning at a 12-hour interval for a total of 283 time steps. The specific date of parturition was assumed to be July 13 (Gentry, 1998). We assumed that within a day, one 12-hour time step corresponded to ‘night’ (even time steps) and one to ‘day’ (odd time steps). This time horizon was approximately two weeks longer than the average lactation duration of northern fur seals (Goebel, 2002; McHuron et al., 2020). Under the trait change scenario

Table 1

Parameter values used in the baseline stochastic dynamic programming model and the four trait change models (LD = lactation duration, BS = body size, FM = female metabolism, PM = pup metabolism). Values for the trait change models are only shown if they differed from the baseline model. Point estimates are used in the backward iteration. For variables with standard deviations, values for each simulated individual in the forward simulation were drawn from a normal distribution, with limits indicated by minimum and maximum values. Detailed descriptions of each parameter and sources can be found in the text.

| Parameter | Notation | Baseline value | SD (min – max) | Trait change value |
|---|----------------|---------------------------|-----------------|-----------------------|
| Maximum lactation duration | T | 283 | | 610 - LD |
| <i>Female</i> | | | | |
| Mass (kg) | x_F | 36.0 | | 45.0 - BS |
| Critical fat mass (kg) | $x_{F_{crit}}$ | 1.8 | | 2.25 - BS |
| Maximum fat mass (kg) | $x_{F_{max}}$ | 7.5 | | 9.0 - BS |
| Metabolic rate (W kg ⁻¹) | | | | 60 % of baseline - FM |
| Sea | FMR_{Sea} | 6.64, 7.14 (summer, fall) | 0.82 (5.5–8.8) | |
| Land | FMR_{Land} | $FMR_{Sea}/1.8$ | | |
| Metabolic multiplier ^a (summer → fall) | – | 0.072 | 0.1 (-0.1–0.45) | |
| Transit speed (km hr ⁻¹) | – | 5.0 | | |
| Mortality at sea per time step | ρ | 0.0001405 | | |
| Energy gain from foraging (MJ) | E_{Prey} | | | |
| Low energy cells | | 40.0 | | |
| High energy cell (Low, Avg, High) | | 43.7, 58.3, 72.9 | | 54.7, 72.9, 91.1 - BS |
| Metabolizable energy | – | 0.82 | | |
| <i>Pup</i> | | | | |
| Mass at birth (kg) ^a | x_p | 5.5 | 0.63 | |
| Critical mass (kg) | $x_{P_{crit}}$ | 4.0 | | |
| Maximum mass (kg) | $x_{P_{max}}$ | 25.0 | | |
| Metabolic rate (MJ kg ⁻¹) | FMR | | | 60 % of baseline - PM |
| Perinatal | | 0.83 | 0.057 | |
| Pre molt | | 0.795 | 0.066 | |
| Molt | | 0.916 | | |
| Post molt | | 0.689 | | |
| Metabolic multiplier ^a | – | | | |
| pre molt → molt | | 1.152 | | |
| pre molt → postmolt | | 0.867 | | |
| Milk intake (MJ/day) | E_{Milk} | | | |
| Perinatal | | 9.95 | | |
| All other times | | See Fig. A1 | | |

^a Only used in the forward simulation.

for lactation duration, we increased the time horizon to 610 time steps. This value corresponds to a lactation duration typical of temperate otariids (Schulz and Bowen, 2004).

2.4. State variables

Female fat mass $X_F(t)$ at time t with particular value denoted by x_F , was the metric used to describe a female’s energy reserves. It was bounded by a lower ($x_{F_{crit}}$) and upper ($x_{F_{max}}$) limit, where mortality was assumed to occur when fat mass fell below $x_{F_{crit}}$. We assumed values of 5 % of body mass and 20 % of body mass for $x_{F_{crit}}$ and $x_{F_{max}}$, respectively.

Upper limits were informed by fat mass estimates from northern fur seals soon after parturition (Springer et al., 2008). Behavioral choices were assessed at intervals of 0.5 kg.

Pup mass $X_P(t)$ at time t with particular value denoted by x_P , was the metric used to describe a pup’s energy reserves. It was bounded by a lower ($x_{P_{crit}}$) and upper ($x_{P_{max}}$) limit, where mortality was assumed to occur when pup mass fell below $x_{P_{crit}}$. We assumed values of 4 kg and 25 kg for $x_{P_{crit}}$ and $x_{P_{max}}$, respectively. These values were below the birth mass of female pups ($x_{P_{crit}}$; Boltnev et al., 1998) and higher than the estimated mass of weaning of male pups ($x_{P_{max}}$; Goebel, 2002). We assessed behavioral choices at intervals of 1.0 kg.

Instead of having a single cell that represented sea, we included multiple cells to facilitate the real-world application of this model for predicting the spatial distribution of fur seals in nature. Location (cell) $C(t)$ at time t with particular value denoted by c was one of 10 discrete cells that differed in their distance from land. Each cell was 48×48 km, with distances between the cell midpoint and land that ranged from 25 km to 619 km. The size of the cell was chosen so that it was feasible for a fur seal to transit the entire length of a cell in a single time step.

2.5. Determining the physiological parameters

The parameters that influenced calculations of how female fat mass or pup mass changed from one time step to the next for each behavior were body size, metabolic rates, pup milk intake (only when nursing), prey energy intake (only when foraging), metabolizable energy (the proportion of ingested energy available after fecal and urinary energy losses), and the composition of new tissue growth (or tissue catabolism). Northern fur seal physiology has been well studied compared with other marine mammal species, and in almost all cases we were able to use empirically derived data from fur seals at two Eastern Pacific stock islands, St. Paul and St. George, to parameterize the model. We chose parameter values based on an 8-year-old female and female pups; focusing on a single female age and pup sex reduced computational time. The choice of pup sex was arbitrary, but we include mention of it because some parameter values differ between male and female pups. A summary of all parameter values under the baseline and trait change models can be found in Table 1.

2.5.1. Body size

Body size was relevant to the physiological dynamics since it affected critical and maximum fat mass levels, total metabolic costs, and energy gain from foraging. For lactating females, we used a body mass of 36 kg (Scheffer and Wilke, 1953). In the body size trait change model, this value was increased to 45 kg.

2.5.2. Metabolic rates

Estimates of field metabolic rates (FMR) were derived from doubly labeled water studies conducted in 1995 and 1996 on lactating females (McHuron et al., 2019) and pups at different developmental stages (Donohue et al., 2002). For lactating females, we used different metabolic rates for land and sea, and between summer and fall (Table 1). For pups, we used different metabolic rates for the pre-molt, molt, and post-molt period. Pups are born with their natal coat that they being to molt approximately 1.5–2.0 months after birth, which appears to influence their thermoregulatory costs (Donohue et al., 2002). For the perinatal duration model, we used pup metabolic rates derived from Antarctic fur seals (*Arctocephalus gazella*), a fur seal species that is similar in body size and lactation duration to northern fur seals (McDonald et al., 2012).

2.5.3. Pup milk intake

The amount of milk consumed by a pup for each time step spent suckling was primarily derived from data presented in Donohue et al. (2002), where milk intake was measured in pups that were approximately 15–100 days of age using doubly labeled water. We recalculated daily pup milk intake so that it reflected actual daily milk intake as

opposed to the typical representation of daily milk intake that is integrated across the entire maternal cycle (trip and land duration). We modeled daily milk intake as a function of body mass (Fig. A1), assuming a non-linear relationship since studies on other fur seal species have found a non-linear relationship (Arnould et al., 1996; Arnould and Hindell, 2002). For the perinatal duration model, we assumed that 4–8 kg pups (the likely range of pup mass during this time) consumed 9.95 MJ day⁻¹ (Costa and Gentry, 1986).

2.5.4. Energy gain

For lactating females, energy gain from foraging (E_{Prey}) depended on location, with one of the ten cells having high energy gain and the rest low energy gain. Specific values were chosen so that cells with low energy gain ($E_{Prey} = 40$ MJ for all scenarios) were sufficient for a female's own metabolic needs but could not support the entire cost of lactation. In the high energy cell, E_{Prey} was set at a maximum value assuming that a female could not physically consume more than 30 % percent of her body mass per day (10.8 kg in the baseline, 13.5 kg in the trait change model for body size). Thus, E_{Prey} in the high energy cell varied depending on the value chosen for prey energy density (Table 1). We used a value of 5.4 MJ kg⁻¹ for the average energy gain scenario, since this is the average prey energy density of the diet of Pribilof Island fur seals (McHuron et al., 2020). The high and low energy gain scenario values were assumed to be 25 % higher or lower than this average value (Table 1).

2.5.5. Metabolizable energy

For lactating females, we used a value of 0.82, which was the average value from the bioenergetic model in McHuron et al. (2020). For pups, the metabolizable efficiency of milk was assumed to be 0.95; this has not been directly measured in marine mammals but is presumably high (Ortiz et al., 1984).

2.5.6. Tissue composition

For lactating females, we assumed that any excess energy was stored as fat, and that a negative energy balance was met through fat catabolism, using a conversion of 39.3 MJ kg⁻¹. While this is an oversimplification of natural energy dynamics because females also produce some milk while at sea (Arnould and Boyd, 1995) and may utilize protein when fasting (Rosen, 2021), the dynamics of these decisions are largely unknown. In pups, new tissue synthesis was assumed to be 54.0 % fat and 46.0 % protein (approximated from data in Donohue et al. (2002), energy density of 18.0 MJ kg⁻¹ for protein), whereas tissue catabolism was assumed to be 95.0 % fat and 5.0 % protein (Arnould et al., 2001b), ignoring any contribution of water to mass changes.

2.6. State dynamics

Given that the female forages in cell c at time t , the fat mass dynamics were

$$X_{F_{Forage}}(t+1) = \min \left[X_F(t) + \frac{0.82 \cdot E_{Prey}(c) - FMR_{Sea}(t)}{39.3}, X_{F_{Max}} \right] \quad (1)$$

where E_{Prey} is the energy (in MJ) gained from foraging in cell c , and $FMR_{Sea}(t)$ is her metabolic cost at time t (Table 1).

The fat mass dynamics of a female that chose to go to land, travel, or go to sea were

$$X_{F_{GoToLand,Travel,GoToSea}}(t+t') = X_F(t) - \frac{FMR_{Sea}(t)}{39.3} \quad (2)$$

where t' is the number of time steps it takes a female to travel from cell c (or land) to her intended destination; $t' = 1$ except when going to land where t' was estimated based on the distance of cell c to land and the average transit rate of northern fur seals when traveling (Table 1). In

nature, females may forage along the inbound and output portion of their trip (McClintock and Michelot, 2018), but for simplicity we assumed directed travel with no foraging from the current cell back to land. To account for this, we assumed that the future expected fat mass of a female was equivalent to that of traveling a single time step.

When nursing, a female's fat mass dynamics were

$$X_{F_{Nurse}}(t+1) = X_F(t) - \left(\frac{FMR_{Land}(t) - \frac{E_{Milk}}{2}}{39.3} \right) \quad (3)$$

where $FMR_{Land}(t)$ is a female's metabolic costs on land and E_{Milk} is the daily milk energy consumption by a pup given its mass at time t . Since the model time step was 12 h, E_{Milk} was divided in half.

The mass dynamics of a pup whose mother was foraging, traveling, or going to sea were

$$X_{P_{Forage,Travel,GoToSea}}(t+1) = X_P(t) - 1.5 \left(\frac{0.95 \cdot FMR(t)}{39.3} + \frac{0.05 \cdot FMR(t)}{18.0} \right) \quad (4)$$

where $FMR(t)$ is the pup's metabolic costs at time t , and 0.95 and 0.05 are the proportion of mass loss that comes from fat and protein stores, respectively. We included a multiplier (1.5) on mass loss because initial model runs indicated that pup mass loss while fasting was lower than empirical measurements from Antarctic fur seals (Arnould et al., 1996), a species that has similar metabolic and milk intake parameters as northern fur seals (Donohue et al., 2002; McDonald et al., 2012). Pup mass dynamics were nearly identical when the female was returning to land, except that t' accounted for the possibility of multiple time steps for the female to reach land

$$X_{P_{GoToLand}}(t+t') = X_P(t) - 1.5 \left(\frac{0.95 \cdot FMR(t) \cdot t'}{39.3} + \frac{0.05 \cdot FMR(t) \cdot t'}{18.0} \right) \quad (5)$$

When the female was nursing, the pups mass dynamics were calculated as

$$X_{P_{Nurse}}(t+1) = X_P(t) + \frac{0.54 \cdot 0.95 \cdot \frac{E_{Milk}}{2} - FMR(t)}{39.3} + \frac{0.46 \cdot 0.95 \cdot \frac{E_{Milk}}{2} - FMR(t)}{18.0} \quad (6)$$

where 0.95 is the metabolizable efficiency of milk and 0.54 and 0.46 are the proportion of surplus energy allocated to fat and protein mass gain, respectively.

2.7. Fitness function and end condition

We denote the fitness function by $F_{Sea}(x_F, x_P, c, t)$ or $F_{Land}(x_F, x_P, t)$ and define it to be the expected total probability that a female and her pup will survive to return to the breeding grounds given that female fat mass $X_F(t) = x_F$, pup mass $X_P(t) = x_P$, and current cell $C(t) = c$, where the expectation is taken over the stochastic events of survival and food distribution. Since we focus this model on a single age instead of modeling decisions across the entire lifespan of a female, fitness includes her own survival since we assume that some reproduction will occur in the future. There is a fitness function for each habitat type since a female can either be on land or at sea, and there are different behavioral choices associated with each habitat.

If $\phi_F(x_F)$ denotes the probability that a female who weans her pup with fat mass x_F returns to land in the following year, $\phi_P(x_P)$ denotes the probability that a pup with mass x_P at the time of weaning survives to age two, and T denotes the maximum possible length of lactation

$$F_{Wean}(x_F, x_P, T) = \phi_F(x_F) + \phi_P(x_P) \equiv \Phi(x_F, x_P) \quad (7)$$

In the absence of empirical data on the functional form of this relationship, we assumed that female survival increased linearly from 0 between the critical fat mass and 50 % of the maximum fat mass, which

corresponds to 10 % of total body mass since 20 % was the upper limit. At fat mass levels >50 % of the maximum fat mass, we fixed survival at 0.95, the age-specific survival of an 8-year old female (Lander, 1981; Fig. A2). This inflection point was based on data indicating that in October and November, fat composition of lactating females was approximately 10 % (Banks et al., 2006; Springer et al., 2008). We ran a sensitivity analysis on the specific location of this value using a second fitness function where the value for the inflection point was lowered to 41.6 % of the maximum fat mass (8.3 % of total body mass). The designation of pup survival to age two is just a reflection of data availability and does not affect the model output. Once they disperse, most pups do not return to land until the age of two; thus, this is the first age at which survival is typically estimated (Lander, 1979).

The pup fitness function varied with pup age because the diving ability of pups improves as they age (Baker and Donohue, 2000). Thus, even if a pup was weaned at an early age, we assumed it was unlikely to leave land until 100 days of age and would need energy reserves to reach this age. The mass needed to support metabolic costs up until this time was therefore subtracted from the wean mass and the resulting mass was used to calculate the probability of survival.

$$V_{Wean}(x_F, x_P, t) = \phi_F(x_F) + \phi_P(x_P - \Delta x_P(t)) \quad (8)$$

where $\Delta x_P(t)$ was the reduction in body mass depending on the age of the pup, as described above. If the pup was 100 days or older $\Delta x_P(t)$ was zero.

2.8. Stochastic dynamic programming equations

The dynamic programming equations are then

and

$$F_{Sea}(x_F, x_P, c, t) = \underset{\text{day}}{\max} \left[\underset{\text{night}}{\max} [V_{Forage}(x_F, x_P, c, t), V_{Travel}(x_F, x_P, c, t), V_{GoToLand}(x_F, x_P, c, t), V_{Wean}(x_F, x_P, t)] \right] \quad (9)$$

$$F_{Land}(x_F, x_P, t) = \max[V_{Nurse}(x_F, x_P, t), V_{GoToSea}(x_F, x_P, c, t), V_{Wean}(x_F, x_P, t)] \quad (10)$$

where the terms on the right-hand side are the fitness values associated with each behavioral choice, described in further detail below. Because much of the dive activity of northern fur seals occurs at night (Kuhn et al., 2014a), we only allowed a female to forage during the night (even time steps of the model). Doing so allowed us to use maximum daily consumption estimates to limit energy gain while avoiding the inclusion of an additional state variable associated with stomach fullness. The optimal behavior is the one that maximizes fitness. The values of F_{Land} and F_{Sea} are linked by the behaviors of going to sea or going to land. An alternate way to structure the model that would give the same result is to consider land as one of the unique values of the location state variable c , which would result in a single F per time step that would be the maximum across all land and sea behaviors. In theory this structure would be simpler than the one we chose, but in practice it is more challenging to implement given that the state variables, state dynamics, and behavioral choices are somewhat different between land and sea.

The fitness value of traveling from cell c to land is

$$V_{GoToLand}(x_F, x_P, c, t) = e^{-\rho t} F_{Land}(x'_F, x'_P, t + t') \quad (11)$$

where ρ is the per time step probability of mortality ($e^{-\rho}$ is thus the per time step probability of survival), t' is the number of time steps between

cell c and land, and x'_F and x'_P are the new states associated with going back to land (Eqs. (2) and (5)).

The fitness value of foraging within cell c is

$$V_{Forage}(x_F, x_P, c, t) = e^{-\rho} F_{Sea}(x'_F, x'_P, c, t + 1) \quad (12)$$

where x'_F and x'_P are the new states associated with foraging in cell c (Eqs. (1) and (4)).

The fitness value of traveling from cell c to c' is

$$V_{Travel}(x_F, x_P, c, t) = \max_{c' \text{ in } \eta(c)} [e^{-\rho} F_{Sea}(x'_F, x'_P, c', t + 1)] \quad (13)$$

where $\eta(c)$ denotes cell c and all the cells adjacent to it, and x'_F and x'_P are the new states given movement between cell c and c' (Eqs. (2) and (4)). We allowed a female to travel within her existing cell, in addition to adjacent cells, since foraging was only a behavioral option at night. Without the option to travel within the current cell, it would not have been possible for a female to continually forage within a single cell because she would be forced to travel out of that cell during the day and thus at the next night time step would be in a different cell.

The fitness value of nursing is

$$V_{Nurse}(x_F, x_P, t) = F_{Land}(x'_F, x'_P, t + 1) \quad (14)$$

where x'_F and x'_P are the new states after nursing for a single time step (Eqs. (3) and (6)).

The fitness value of going to sea is calculated in the same way as the fitness value of traveling so that

$$V_{GoToSea}(x_F, x_P, t) = \max_{c' \text{ in } \eta(c)} [e^{-\rho} F_{Sea}(x'_F, x'_P, c', t + 1)] \quad (15)$$

where $\eta(c)$ is the cell with land and all cells adjacent to it and x'_F and x'_P

are the new states associated with traveling (Eqs. (2) and (4)). Because we assumed a linear foraging environment, there was only one cell a female could enter from land; however, this equation shows how to modify the model when multiple cells can be accessed from land.

If at any time x'_F fell below the critical mass, a female died and her fitness was based solely on her pup's mass at that time (assuming $x'_P \geq x_{PCrit}$). Similarly, if at any time x'_P fell below the critical level (assuming $x'_F \geq x_{FCrit}$) then the expected fitness was based solely on the female's mass at that time. We ranked ties in fitness among behavioral states as $V_{Wean} > V_{GoToLand} > V_{Forage} > V_{Travel}$ when at sea or $V_{Wean} > V_{GoToSea} > V_{Nurse}$ when on land, using the assumptions that when there is no fitness benefit, land should be preferred over sea and that the most energetically beneficial behavior should be preferred within each habitat. When determining the optimal cell to travel to, ties in fitness were given to the first occurrence of that value.

We solved Eqs. (9)–(15) backwards starting at $t = T$; doing so allowed us to determine the optimal time- and state-dependent behaviors for when a lactating female is on land and at sea. We ran a separate backward iteration for each of the 30 prey scenarios under the baseline and trait change models, as well as a separate backward iteration for land decisions using pup metabolic rates and milk intake rates from the perinatal duration. We also ran a separate backward iteration on a single prey energy gain scenario using the altered fitness function to assess the sensitivity of the results to changes in the inflection point of this function.

2.9. Forward simulation

We used the optimal behavioral decisions identified in each backward iteration to quantify the distribution of behaviors and resulting reproductive parameters in a fur seal population. We initiated simulations at birth with all females on land; the initial condition of each female was set at the maximum fat mass. We drew pup mass at birth (Boltnev and York, 2001), and female and pup metabolic rates from normal distributions based on empirical data to incorporate known individual and/or temporal variation in these parameters into the simulations (Table 1). In contrast to the backward iteration where we used mean values for different seasons (females) or developmental stages (pups), we used multipliers on the initial metabolic rates that were randomly drawn from these normal distributions (Table 1). The purpose for doing this was to ensure that all individuals followed the seasonal or developmental pattern. Using mean values for metabolic rates in the backward iteration but distributions in the forward simulation assumes that decision rules are the same regardless of a female's metabolic rate, an assumption that should be met given that the energy available in the low energy cells would still be too little to meet a female's total energy needs (metabolism + lactation) even with the lowest possible metabolic rate. Between the time a female gave birth and went to sea on her first foraging trip, we used the behavioral decisions derived using the perinatal parameters; after that point we switched to the output from backward iterations using non-perinatal parameters. Females that weaned their pup were removed from future time steps in the simulation.

We ran a forward simulation for each combination of prey energy gain (3 scenarios), location of the high energy cell (10 scenarios), and trait changes (4 changes), using decisions from the appropriate backward iteration for the scenario combination. A forward simulation was also run for all 10 location scenarios using the average prey energy gain scenario for the fitness function sensitivity analysis. We ran 50 replicates for each unique combination of scenarios. In each replicate, we simulated 3,000 fur seals, which is roughly the number of 8-year-old females in the population from the East complex on St. Paul Island in 2018 (McHuron et al., 2020). We calculated summary statistics (mean \pm SD) for each replicate, including trip and shore durations, pup growth rates, lactation duration, and pup wean mass, all of which were emergent properties of the model. We averaged these values across all replicates in each of the scenario combinations.

Our approach assumes that female behavior is perfectly matched to the environment, since we used the same prey scenario in the backward iteration and forward simulation. That is, there are no mismatches between what females expect to encounter and what they do encounter. In the real world, this is unlikely to be the case, particularly early in lactation when female fur seals first arrive in the Bering Sea and must learn about the distribution and abundance of prey in that year. Prey distribution and abundance is also dynamic, and there may also be mismatches between expectation and reality throughout lactation. While behavior/environment mismatches and subsequent learning can be incorporated into SDP models (Hilborn and Mangel, 1997; Mangel and Clark, 1988), it increases the complexity of the model and was outside the scope of this paper. Since we ran each prey scenario as a separate forward simulation, results are meant to represent distinct populations with different expectations for prey distribution and abundance, and do not necessarily represent optimal trip and land durations of females within a population that may be switching among different prey patches.

2.10. Evaluating the model

We used empirical data collected from fur seals on all three of the Eastern Pacific stock islands (St. Paul, St. George, and Bogoslof) to confront the model output (*sensu* Hilborn and Mangel, 1997) with data on the natural behavior of fur seals. At St. Paul Island, fur seals have

experienced lower pup growth rates and a population decline since the late 1990s, whereas at Bogoslof Island fur seals have experienced greater pup growth rates and rapid population growth since the colony was established in the 1980s (Kuhn et al., 2014a; Muto et al., 2022; Towell et al., 2006). Foraging trip durations are considerably longer on St. Paul and St. George Islands compared to Bogoslof Island because fur seals at Bogoslof Island travel shorter distances to reach prey patches (Kuhn et al., 2014a).

Empirical data came from a variety of sources, including visual observations of marked individuals (MML unpubl. data), satellite- or VHF-tagged females (e.g., Kuhn et al., 2014b), and longitudinal pup growth rate measurements (Donohue et al., 2002; Goebel, 2002). We compared general patterns in overall behavior and examined how the relationships between 1) trip duration and maximum straight-line distance from land, 2) trip and land durations, and 3) pup growth rates and trip durations differed between the model output and empirical data. While valuable for model evaluation, it should be noted that these datasets are not exact comparisons with the model since we focused on a single female age with a fixed starting mass and explored multiple different scenarios for a simplified foraging environment.

3. Results

3.1. Cell use

Females spent the greatest proportion of time foraging in the high energy cell in almost all prey scenarios in the baseline model. This value was 100 % when the high energy cell was the one closest to land; however, females increasingly foraged in low energy cells as the distance of the high energy cell from land increased (Fig. 2). Across all scenarios, there was little to no change in the percentage of time spent foraging in the high energy cell among months. For example, in the average prey energy gain scenario, maximum absolute differences between July and November ranged from 0 % to 9.9 %, with an overall mean of 3.8 % across all prey location scenarios.

3.2. Land and trip durations

During the perinatal period, simulated females spent an extended amount of time on land with their pup before departing on their first foraging trip (Fig. 3). The average perinatal duration across all 30 prey scenarios in the baseline model was 6.6 days. After this period, simulated fur seals adopted a central place foraging strategy, alternating between time spent on land nursing their pup and foraging at sea (Fig. 3). Across all prey scenarios, trip durations averaged 2.9 – 11.2 days with 1.2 – 3.1-day nursing visits onshore. For comparison, trip durations of satellite-tagged fur seals from the empirical dataset ranged from 0.2 to 12.7 days at sea, with 95 % of shore durations \leq 3.1 days. Foraging trip durations were generally shortest in July, with trip durations in other months that were on average 32 % higher across all prey scenarios. Trip durations of simulated fur seals increased as the distance of the high energy cell from land increased (Fig. 4A), with corresponding increases in land durations (Fig. 5B). Decreased prey energy gain in the high energy cell resulted in increased trip durations for a given distance between land and the high energy cell (Fig. 4A).

Qualitative comparisons between simulated fur seals and empirical data revealed that the model captured the general patterns in trip and land durations of northern fur seals, particularly with respect to how differences in travel distances to foraging grounds affected behavioral patterns (Fig. 3). There was a similar relationship between trip duration and the maximum distance traveled from land between the model output and empirical data, although the model overestimated trip durations for a given distance compared with actual fur seal behavior (Fig. 5A). There was close overlap between the model and empirical data for the relationship between land and trip durations (Fig. 5B).

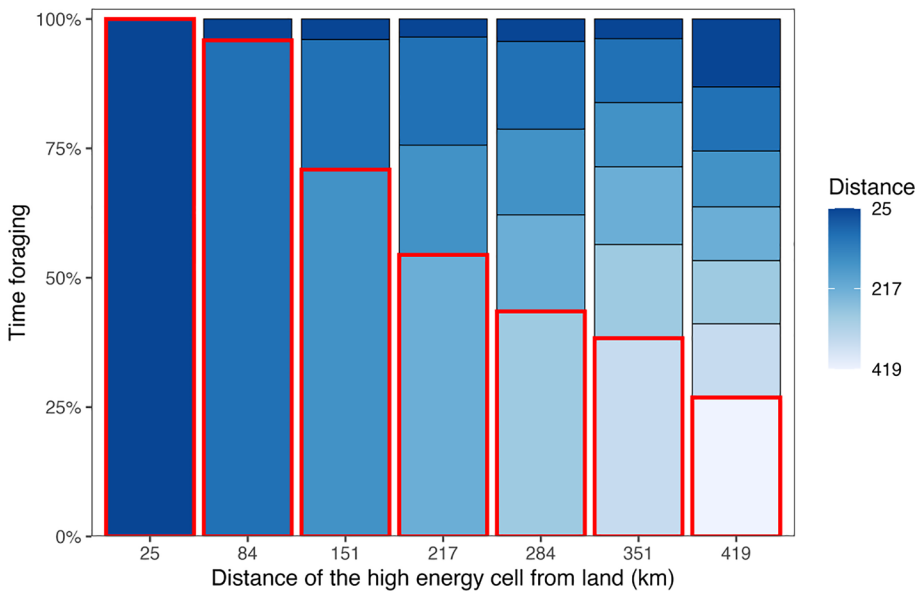


Fig. 2. An example of the allocation of foraging time among cells when the distance of the high energy cell from land ranged from 25 to 400+ km. Results are shown for the average prey energy gain scenario and were averaged across all 3,000 females in a single replicate. Three of the ten prey location scenarios are not shown since there was no foraging at these distances because pups were weaned before the first foraging trip. Colors represent different cells, with darker colors representing cells closer to land. For each distance, the amount of foraging time spent in the high energy cell is outlined in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

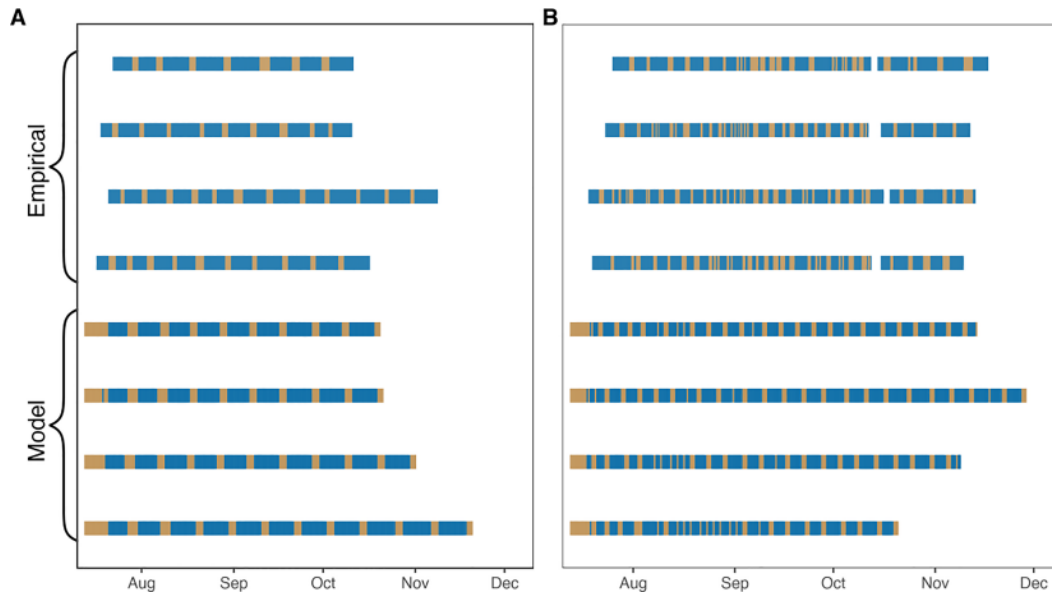


Fig. 3. Examples of time-location budgets for four simulated fur seals (model) and four instrumented lactating females from St. Paul Island (empirical, A) and Bogoslof Island (B), highlighting the similarity in behavior between model output and empirical data (within a plot) and the effect of environmental differences on behavior (between plots). Colors represent time spent on land (tan) or at sea (blue). Model comparisons with St. Paul Island were derived from the average prey energy gain scenario where the location of the high energy cell was 151 km away from land, whereas comparisons with Bogoslof Island were derived from the high prey energy gain scenario where the high energy cell was 25 km away from land. These comparisons were selected to best match the foraging distance of instrumented lactating females and approximated prey energy density consumed at each island. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Pup growth and lactation duration

Pup growth rates decreased as trip durations increased except when the high energy cell was <100 km from land (Fig. 6A). Mean values ranged from 0.008 to 0.15 kg day⁻¹ (high prey energy gain), 0.005 – 0.10 kg day⁻¹ (average), and 0.03 – 0.01 kg day⁻¹ (low). In comparison, pup growth rates from the empirical dataset ranged from 0.017 to 0.14 kg day⁻¹. Pup mass at weaning followed a similar pattern, with average masses that ranged from 6.5 kg to 21.6 kg (Fig. 6B). There were no corresponding data on wean mass from the empirical dataset. Changes in prey energy gain affected the maximum distance the high energy cell could be from land while still supporting a lactation duration

that was considerably longer than the perinatal duration (Fig. 7A), with access to more energy dense prey allowing females to achieve higher pup growth and wean mass for a given distance from land (Fig. 6A and 6B).

Mean lactation durations across all prey scenarios ranged from 6.6 to 131.5 days (out of a maximum allowed of 141.5 days; Fig. 7A). There was a strong bimodality in lactation durations; most pups were either weaned within 10 days of birth or supported for at least 110 days. This may have been because we used the same prey environment for the backward iteration and forward simulation, so that optimal decisions were based on a perfectly matched environment in the forward simulation, and that each environment was static within a prey scenario.

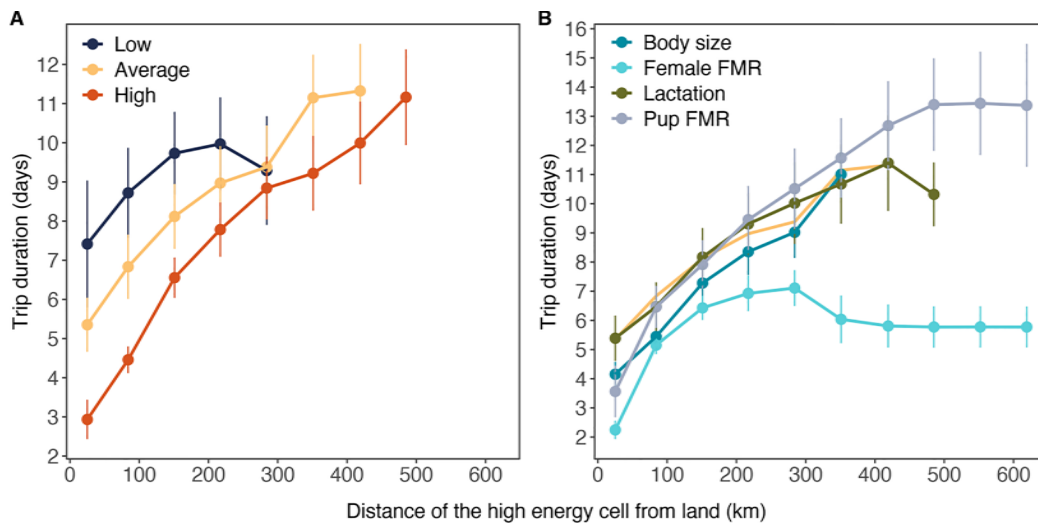


Fig. 4. The effects of changes in the distance of the high energy cell from land on trip duration, colored by the different prey energy gain scenarios (A) or trait changes (B). In B, only results from the average prey energy gain scenario are shown, with the results from the baseline model in orange for comparison. Each point represents the mean value across 50 replicates. Error bars represent the average within replicate SD. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

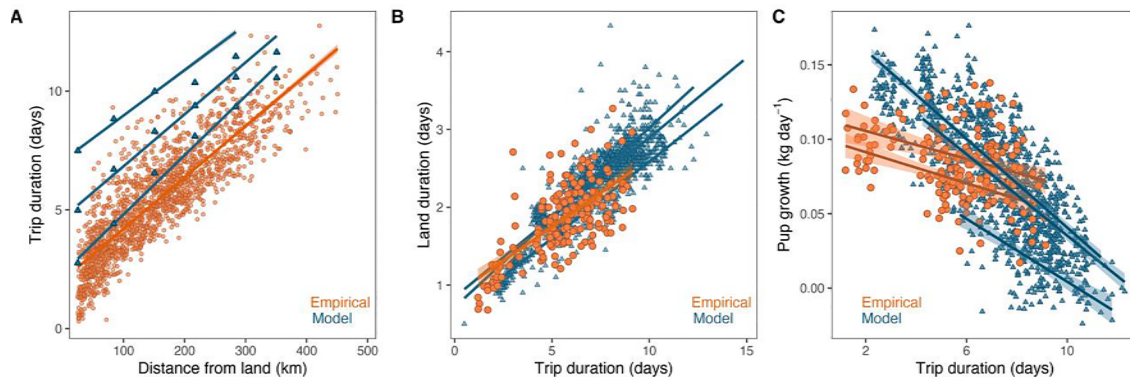


Fig. 5. Comparisons between model output and empirical data for the relationships between trip duration and distance from land (A), land and trip duration (B), and pup growth rate and trip duration (C). Individual regression lines are presented for each prey energy gain scenario (high, average, low). In A, points are averages for each prey scenario from a single replicate (model) or values for individual foraging trips of instrumented females (empirical). Model results represent the distance of the high energy cell from land, while empirical results are the maximum straight-line distance from land on each foraging trip. In B, each point represents the average trip and land duration for individual females. In C, points are paired mean trip durations and pup growth rates from individual females. In all plots, differences in size and transparency of points are solely for visual purposes. In B and C, a subset of model points are shown for ease of visualization.

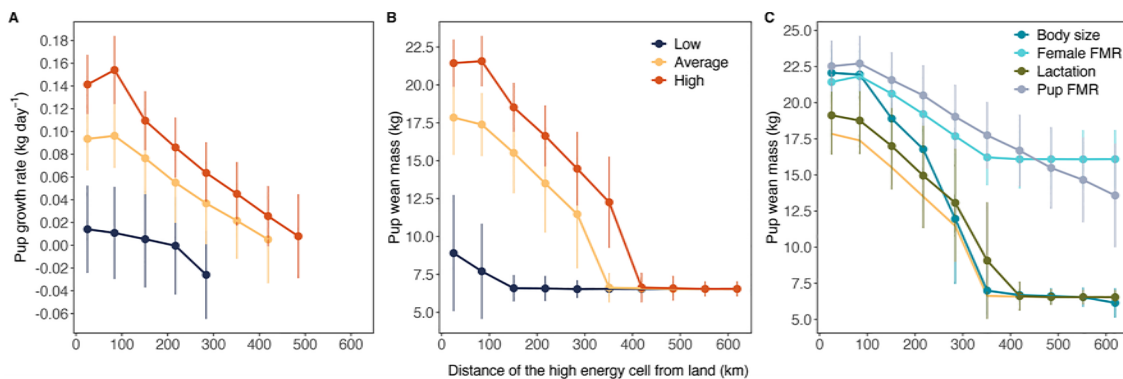


Fig. 6. The effects of changes in the distance of the high energy cell from land on pup growth rate (A) and pup wean mass (B, C), colored by the different prey energy gain scenarios (A, B) or trait changes (C). Only results from the average prey energy gain scenario are shown in C, with the results from the baseline model in orange for comparison. Each point represents the mean value across 50 replicates. Error bars represent the average within replicate SD. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

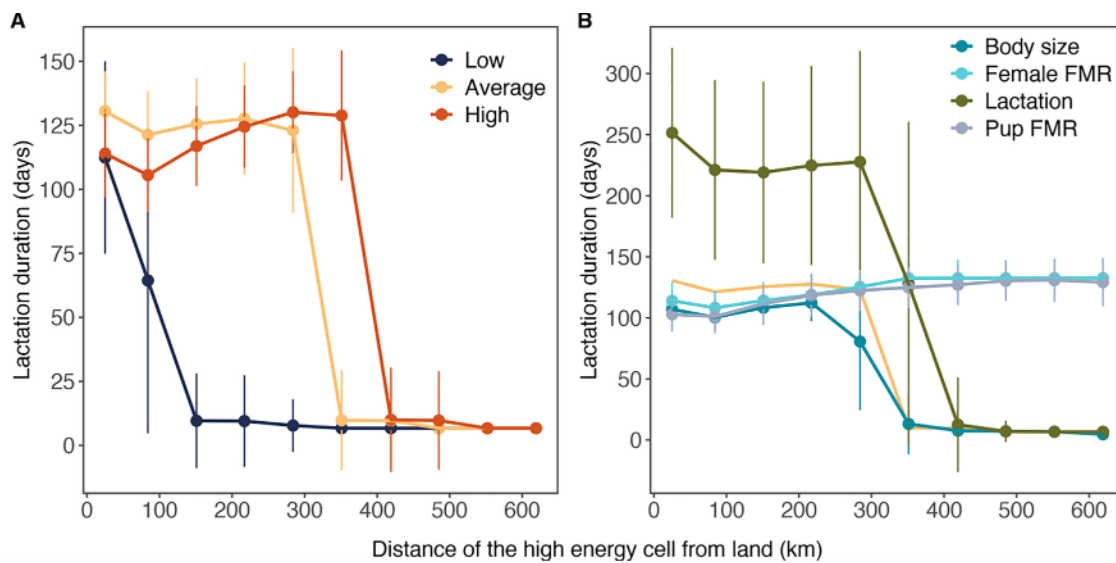


Fig. 7. The effects of changes in the distance of the high energy cell from land on lactation duration, colored by the different prey energy gain scenarios (A) or trait changes (B). In B, only results from the average prey energy gain scenario are shown, with the results from the baseline model in orange for comparison. Each point represents the mean value across 50 replicates. Error bars represent the average within replicate SD. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Thus, under suboptimal prey scenarios where the probability of pup survival was virtually zero, simulated females ‘knew’ there was no fitness benefit of continuing lactation beyond the perinatal duration. Scenario means of female fat mass at the time of weaning were 3.5 – 4.1 kg (9.8 – 11.4 % of total body mass), with slightly lower values for scenarios where the average age at weaning was at least 110 days vs 10 days or less (overall mean of 10.2 % vs 11.4 %).

3.4. Sensitivity to fitness function

Lowering the fat mass at which female survival plateaued at 0.95 by 20 % resulted in small changes to the absolute values of behavioral and reproductive parameters. Across prey location scenarios, it generally increased pup growth rate, wean mass, and land durations, and decreased trip and lactation durations (Fig. A3A). For example, pup growth rates increased by 0.0035–0.0082 kg day⁻¹ across all prey location scenarios between the baseline and the altered fitness function output, which resulted in pups that were on average 0.02 – 0.63 kg heavier at weaning. Relative changes in trip and land durations, pup wean mass, and lactation durations were all <5 %, while relative changes in pup growth rates primarily ranged from 6.5 to 16.2 % (Fig. A3A). Altering the fitness function did not change the patterns of how each variable changed in response to increased distance of the high energy cell from land (Fig. A3B).

3.5. Trait change models

There were only two trait changes that allowed for successful reproduction when the distance of the high energy cell exceeded 350 km (Fig. 6C and 7B). Reduced pup metabolic rates allowed females to forage at distances just over 600 km from land for up to 15 + days while maintaining average pup growth rates and wean masses of 0.05–0.6 kg day⁻¹ and 13.0–14.9 kg, respectively, across all three prey scenarios (Fig. 4B). In contrast, reductions in a female’s metabolic rate allowed her to use low energy cells closer to land, particularly as the distance of the high energy cell from land increased (Fig. 4B). For example, under the average prey energy gain scenario where the high energy cell was 284 km from the rookery, females with a reduced metabolic rate spent an average of 11.9 % foraging in the high energy cell compared with 43.6 % in the baseline model.

The remaining traits had little influence on the ability of a female to successfully reproduce when the high energy cell exceeded 350 km from land. That is, even if traits could evolve, they would not improve reproductive success under our prey scenarios. When the amount of time available for lactation increased, females altered their behavior so that land and trip durations were on average 7.7 % shorter and 13.1 % longer, respectively, compared with the baseline model. This resulted in reduced milk intake rates and pup growth rates, but since pups were being nursed for a longer duration, pup wean masses remained largely unchanged from the baseline model. An increase in body mass was beneficial when the high energy cell was relatively close to land, allowing females to wean pups at a higher mass compared with the baseline model (Fig. 6C). Pup wean masses were higher when foraging closer to land because larger females on average spent less time at sea than females in the baseline model (66–71 % vs 69–74 %). While total metabolic demands increased with body size, larger females could consume greater total amounts of prey per time step than smaller females, which allowed them to have shorter trip durations and thus spend more total time on land with their pups compared with females in the baseline model (Fig. 4B).

4. Discussion

In this paper, we explored how optimal behaviors of female northern fur seals, a central-place forager during lactation, changed under different prey scenarios and how beneficial hypothetical trait changes were in facilitating reproduction in the face of prey changes. Behavioral decisions, such as how long to spend at sea foraging and nursing a pup on land, were emergent model properties, allowing for independent comparisons with empirical data. Below we provide further discussion of model and empirical comparisons, focusing in particular on potential causes of discrepancies between the two, and the insights that can be gleaned about wild fur seals despite the hypothetical nature of the prey scenarios and trait change models. While the application of our model here was largely hypothetical, the structure could be relatively easily adapted to incorporate a more realistic foraging environment for northern fur seals or other otariid species that could then be used to predict spatial distribution and reproductive success under hindcasted and forecasted conditions. Since any predictions of spatial distribution would not be constrained by current fur seal behavior, our model

provides the framework towards understanding how fur seals may respond to novel environmental conditions in the Bering Sea.

4.1. Influences of prey availability on behavior and pup growth

Central-place foraging emerged from the model to balance tradeoffs associated with terrestrial reproduction and aquatic foraging. Following birth, simulated fur seals spent an extended amount of time on land with their pup before leaving on their first foraging trip. The average perinatal duration across all prey scenarios in the baseline model was 6.6 days (individual scenario means ranged from 4.7 to 8.3 days), which is slightly lower than but within the range of the 8.2 day average (range of 4.8–13.5 days) exhibited by wild northern fur seals (data from Merrill et al., 2021). Variation in the perinatal duration was largely influenced by a female's expectation of prey availability; durations were shortest when the high energy cell was closest to land, increased quickly to a peak, and then declined to 6.5 days for the remaining distances. This expectation may explain why model values were slightly lower than empirical data, since wild fur seals do not know exactly where prey will be and thus likely provide a buffer to their pup in the case of longer than expected trip durations. Foraging trip durations of simulated fur seals were shortest in July, presumably because pups required less energy and had limited fasting capabilities, with little change in cell use among months. Increases in foraging trip durations throughout lactation are common in northern fur seals (Merrill et al., 2021) and other otariids (Arnould and Hindell, 2001; Georges and Guinet, 2000; Higgins and Gass, 1993), and while our model indicates they occur in the absence of shifts in prey availability and distribution, it does not preclude the possibility that shifts in the prey landscape also contribute to these patterns in nature.

The duration of foraging trips is an influential factor on pup growth rates, weaning mass, and survival for otariids, at least when changes in trip duration are attributable to changes in prey availability and not simply a result of individual behavioral variation (Doidge and Croxall, 1989; Georges and Guinet, 2000; Lunn et al., 1993). Land durations may increase slightly with trip duration but are generally more consistent and not sufficient to compensate for the increased fasting time of the pup. In extreme cases, foraging trips may be so long that the pup starves before the mother returns from her foraging trip (Costa et al., 1989), which for northern fur seals appears to be about 10–12 days, at least early in lactation (Calambokidis and Gentry, 1985). Consistent with empirical observations, foraging trip durations of simulated fur seals increased in response to both changes in distribution (the location of the high energy cell) and availability (prey energy gain), which generally had a negative impact on pup growth rates and wean masses. Our observation that trip durations increased when prey energy gain was reduced, even when the distance of the high energy cell from land remained constant, supports suggestions by Boyd (1997) and Costa et al. (1989) that female fur seals may have a set energy target they attempt to reach before returning to their pup.

Model predictions of pup growth rates in response to trip durations were more extreme than relationships derived from empirical data, with maximum mean pup growth rates (0.15 kg day^{-1}) that were higher than the mean of 0.11 kg day^{-1} that has been reported in female pups from Bogoslof Island where the population has experienced rapid growth (Banks et al., 2006; Springer et al., 2008). Since the model did well in predicting land durations as a function of trip duration (i.e., we did not overestimate milk energy delivery because of too much time spent on land), this discrepancy may be related to our simplification of milk delivery decisions that resulted in a constant value of milk energy transfer (relative to pup body mass) during nursing regardless of the female's fat reserves, behavior, and pup's metabolic needs or body condition. Milk energy delivery varies depending on female mass and trip and land durations (Arnould et al., 1996; Costa and Gentry, 1986; Georges et al., 2001), and is likely also influenced by pup suckling efficiency and the amount of time spent suckling in a given period. The majority of

suckling events are initiated and terminated by the pup (Macy, 1982; Ono et al., 1987) and it may be that pup body condition influences motivational state while the female is present (Arnould et al., 2001a). It also is possible that a female may be less receptive to nursing attempts when her pup is in good body condition and foraging trips are short, preferentially retaining fat reserves to mitigate potential future periods of poor foraging success. Pups also exhibit several behavioral strategies to cope with extended maternal trip durations, such as reductions in activity and attempts to suckle on other females (Lunn, 1992; Macy, 1982; Ono et al., 1987), which may reduce the severity of weight loss and temper declines in pup growth rates. The data we used to parameterize the milk energy delivery and pup metabolic rates in the model were collected over two decades ago (Donohue et al., 2002); additional data collection would help illuminate how these values may be changing in response to environmental conditions, which would refine our ability to parameterize pup growth dynamics and lactation costs. Indeed, one important role of models such as this one is to suggest those empirical data that are most valuable to collect.

Poor prey quality (i.e., 'junk-food') has been hypothesized by some as a contributing factor to the decline of two Alaskan otariids, northern fur seals and Steller sea lions (*Eumetopias jubatus*), as well as other marine central-place foragers (Gomez et al., 2016; Österblom et al., 2008; Trites, 2021; Wanless et al., 2005; Wolf and Mangel, 2008). Our model shows that prey energy density impacts the behavior and reproductive success of fur seals, with fur seals in the low prey energy gain scenario having the longest foraging trips and lowest pup growth rates for a given distance. Pup growth rates in this scenario were near zero, even when females traveled very short distances (25 km) to the foraging patch. These results highlight the dramatic impact that poor quality prey can have on reproductive success, but also show that the interaction between prey energy density and prey distribution is an important driver of changes in pup growth rates. For example, in the average prey energy gain scenario, which was parameterized based on recent fur seal diet and prey energy density estimates from the Pribilof Islands (McHuron et al., 2020), fur seals were able to achieve pup growth rates comparable to those from a population experiencing rapid growth (Banks et al., 2006) if the high energy cell was relatively close to land. Thus, the same prey item could likely result in rapid population growth in some scenarios and population declines in others, even if the energy density of that prey remains the same. High-quality prey did provide a buffer to changes in prey distribution, with simulated females maintaining pup growth rates exceeding 0.1 kg day^{-1} when the high energy cell moved to just over 200 km from land. While modeled as a change in prey energy density, these conclusions are broadly applicable to other situations that would influence the amount of energy gained while foraging, such as changes in prey abundance.

4.2. Influences of trait changes on behavior and pup growth

Trait changes that affected pup fasting ability or durations were the only viable way to support reproduction when the distance of the high energy cell from land resulted in trip durations that consistently exceeded 10 days. The two trait changes that accomplished this did so through different mechanisms: i) reduced female metabolic rates allowed females to maintain short foraging trips by exploiting lower quality prey patches close to land, whereas ii) reduced pup metabolic rates allowed females to extend foraging trip durations to reach distant prey patches. It seems unlikely that there would be strong selective pressure for reduced female metabolic rates to evolve solely in response to changes in prey distribution, as the positive effect on pup wean mass was contingent on the availability of other prey resources close to land. In addition, low adult metabolic rates appear to be largely confined to tropical species as an adaptation to environmental factors, such as low productivity and warm air temperatures (Careau et al., 2007; Costa and Trillmich, 1988; Villegas-Amtmann et al., 2017; Wiersma et al., 2007), so it is unclear if these are attainable in temperate or polar

environments. Reduced pup metabolic rates have been documented in subantarctic fur seals (*Arctocephalus tropicalis*), a species where maternal trip durations can last upwards of 3 weeks (Arnould et al., 2003; Verrier et al., 2009). These reductions occur because pups are able to decrease thermoregulation costs by reduced swimming activity, intense fat deposition, and a temperate climate (Arnould et al., 2003; Verrier et al., 2009). While our results indicate that, of those examined, reductions in pup metabolic rates may be the best mechanism for northern fur seals to adapt to long maternal trip durations, this can delay the development of diving capabilities (Arnould et al., 2003; Verrier et al., 2011). It is unclear how selective pressure to reduce thermoregulation costs would balance with the need to develop diving capabilities in a species like northern fur seals that has such a short lactation period, particularly when they need to forage independently very soon after weaning. It is likely that changes in milk energy density also play a role in a pup's fasting ability, as milk fat content increases with trip duration within and across otariid species (Georges et al., 2001; Ochoa-Acuna et al., 1999; Trillmich and Lechner, 1986). These changes were not investigated here because northern fur seals already have one of the highest milk fat content of otariids (Costa and Gentry, 1986).

Variability in otariid lactation durations, which range from four months to several years, has been attributed to environmental differences associated with latitude (Ofstedal et al., 1987; Schulz and Bowen, 2005; Trillmich, 1990). To optimize energy efficiency, lactation durations should be as short as possible since costs increase with longer durations because the female is supporting both growth and metabolic costs of her pup (Costa, 1993; Stephens et al., 2014). At roughly four months, northern fur seals have one of the shortest lactation durations of any otariid, a duration that is largely consistent despite the wide latitudinal range among breeding rookeries (34° N–57° N). When we extended the lactation duration to 10 months, simulated females altered their trip and land durations so that less energy was provided to the pup per unit time. Thus, pup growth rates were reduced but pups were weaned at similar masses as in the baseline model, regardless of the prey scenario. It was somewhat surprising that a longer lactation duration did not result in increased pup wean masses under the low energy gain scenario compared with the baseline model; however, it is important to consider that we did not alter any other lactation parameters, such as milk energy delivery per unit time. Instead, simulated females spent more time at sea and less time on land to achieve this reduction, and since these durations are so influential on pup growth, further model exploration as to how changes in multiple factors interact (e.g., milk energy delivery, female or pup body size) might provide better insight into the conditions under which a longer lactation period would be beneficial. What we can conclude is that under current rates of milk delivery, there is unlikely to be strong selective pressure for a longer lactation duration for northern fur seals, which may explain the consistency in lactation duration across their breeding range.

5. Conclusions

Our model provides insights that are applicable to northern fur seals and the current population decline despite the simplified and hypothetical aspects of the model. Results indicate that a rookery is unlikely to be viable if a female fur seal must consistently travel 400 km (straight line distance) or farther to reach the primary foraging grounds, unless there are physiological changes that affect the fasting capabilities of the pup. Whether or not a reduction in pup metabolic rate is a viable strategy remains unknown, since it is unclear how flexible this parameter is, particularly as reductions in activity rates could adversely affect other aspects of pup development. Regardless, our results indicate that further empirical studies of pup metabolic rates may be warranted. To obtain pup growth rates approaching those of a population experiencing rapid growth (Banks et al., 2006; Springer et al., 2008), our model indicates the potential foraging grounds need to be <150 km from the rookery assuming an average prey energy density of 5.4 MJ kg⁻¹. These

conclusions assume that a female is able to consume a maximum of 30 % of her body mass per day, which is within the range estimated from captive juveniles (Rosen et al., 2012) but may be slightly high given previous consumption estimates for free-ranging fur seals of ~26 % (Perez and Mooney, 1986). The ability of the model to reproduce behavior (and behavioral responses to prey) consistent with northern fur seals and other otariids indicate its utility in additional applications to this and other systems. Such applications include a model extension to encompass the lifetime of a female fur seal and the incorporation of empirically derived prey energy landscapes to predict the impact of a changing climate and commercial fishing pressures on behavior, reproductive success, and population dynamics of northern fur seals from the Eastern Pacific stock.

CRedit authorship contribution statement

Elizabeth A. McHuron: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Jeremy T. Sterling:** Conceptualization, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Marc Mangel:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtbi.2022.111392>.

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