

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

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1 **Abstract**

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

23

24

25 **Keywords:** northern fur seal, *Callorhinus ursinus*, stochastic dynamic programming, life history

26 theory, bioenergetics

27 **1. Introduction**

28 The availability of prey resources is a key feature driving the spatial distribution, foraging
29 patterns, and activity budgets of predators (Benoit-Bird et al., 2013; Boyd et al., 2015; Davoren,
30 2013; Fauchald et al., 2000). In marine environments, predators are increasingly faced with
31 altered prey landscapes resulting from fishing pressures and climate change. These changes can
32 affect demographic trends, which are ultimately determined by foraging and reproductive
33 decisions of individuals (Baylis et al., 2015; Bost et al., 2015; Meyer-Gutbrod et al., 2015;
34 Murray et al., 2021; Salvadeo et al., 2015; Sherley et al., 2018; Soto et al., 2004; Trivelpiece et
35 al., 2011). Species such as seabirds and many pinnipeds may be particularly affected by such
36 changes because they have life histories that are constrained by the need to balance provisioning
37 young at terrestrial sites with foraging at sea. That is, central-place foragers are both reliant on
38 localized prey patches to support the considerable costs of reproduction and exhibit high
39 breeding-site fidelity that further constrains their ability to withstand changes in prey availability
40 (Pichegru et al., 2010).

41
42 Central-place foragers employ a variety of behavioral mechanisms to cope with variability in
43 prey landscapes, such as increasing foraging effort, extending trip durations, and switching to
44 alternate prey species or foraging areas (Costa, 2008; Gladics et al., 2015; Wilson et al., 2005).
45 For example, common murre (*Uria aalge*) foraged further from the colony and delivered larger
46 capelin (*Mallotus villosus*) to their chicks during a year of low capelin density (Burke and
47 Montevecchi, 2009). In otariids (sea lions and fur seals), the duration of lactation of some species
48 is flexible, such that females may extend lactation beyond the typical dependency period when
49 food availability is reduced (Jeglinski et al., 2012; Maniscalco, 2014; Trillmich, 1986). There are

50 limits to the extent these behavioral strategies can mitigate the effects of prey landscape changes
51 on reproductive success because, even if predators can find enough food to meet their energy
52 needs, they can only consume or carry a finite amount of prey and offspring have limited fasting
53 capabilities (Cohen et al., 2014; Costa et al., 1989; Le Bot et al., 2019; Ronconi and Burger,
54 2008). Indeed, prey depletion near the colony (“Ashmole’s halo”) is one factor known to regulate
55 population densities of colonially-breeding central-place foragers (Ashmole, 1963; Elliott et al.,
56 2009; Kuhn et al., 2014a; Weber et al., 2021).

57

58 There are a variety of approaches that have been used to predict behavioral responses of marine
59 central-place foragers in the face of different environmental conditions. Statistical correlative
60 habitat models are one of the most common approaches, which identify associations with
61 environmental and physical features to predict spatial distribution under future conditions (Elith
62 and Leathwick, 2009). State-space models and machine learning have been used to predict
63 behaviors using movement characteristics derived from telemetry data (Browning et al., 2018;
64 Jonsen et al., 2013; Michelot et al., 2017), which can then be linked with other datasets to
65 understand behavioral changes in the context of environmental conditions and their influence on
66 reproductive success (Russell et al., 2015). Process-based or mechanistic models, where
67 assumptions about behavior are rooted in ecological theory, provide an alternate approach that
68 can help overcome some of the challenges of these statistical-driven methods (Cuddington et al.,
69 2013), such as their reliance on existing spatial distribution data and the inherent assumption that
70 current behavior reflects future behavior (Muhling et al., 2020; Palacios et al., 2014). In these
71 models, behaviors are an emergent model property that arise from interactions between multiple
72 processes, such as physiology and resource availability (Chudzinska et al., 2021; Fiechter et al.,

73 2016; Satterthwaite and Mangel, 2012), as opposed to derived from empirically collected data in
74 statistical approaches.

75

76 In this paper, we explore the behavioral decisions of a central-place foraging marine mammal
77 during lactation using state dependent life history theory implemented by Stochastic Dynamic
78 Programming (SDP), which can be used for solving problems of decision making (Clark and
79 Mangel, 2000; Houston et al., 1988). The underlying assumption of SDP models is that an
80 individual acts in such a way to maximize some future reward, which in ecological applications
81 is typically some metric of Darwinian fitness such as expected lifetime reproductive success
82 (Mangel, 2015). This modeling approach has been used to address basic biological questions,
83 including the evolution of behavior (Higginson et al., 2016; Houston et al., 2006), and inform
84 management strategies in a diversity of ecosystems (Bogich and Shea, 2008; Martin et al., 2010;
85 McCarthy et al., 2001; Milner-Gulland, 1997). In the marine environment, SDP models have
86 been used in a variety of generalized and species-specific applications, such as predictions of
87 prey choice (Tinker et al., 2009), responses to environmental change and anthropogenic activities
88 (Pirota et al., 2018; Reimer et al., 2019; Satterthwaite and Mangel, 2012; Wiedenmann et al.,
89 2011), migration (Yoshioka et al., 2019) and reproductive strategies (Griffen, 2018; McHuron et
90 al., 2018), and physiological dynamics (Noren et al., 2009; Noren and Mangel, 2004).

91

92 We developed a species-specific SDP model, using northern fur seals (*Callorhinus ursinus*) as
93 the motivating species, to explore the optimal behavioral choices during lactation under different
94 hypothetical prey availability and distribution scenarios, and the resulting impacts on
95 reproductive success. We then explored how changes in behavioral (lactation duration),

96 physiological (metabolic rates), and morphological (body size) traits affected behavioral choices
97 and reproductive parameters, with the intent of understanding if any of these trait changes
98 conferred a reproductive benefit under adverse prey scenarios. These traits were selected because
99 of existing inter- and intraspecific variation within the otariid lineage, suggesting the potential
100 for selective pressures on these traits. Northern fur seals are both a data-rich species and one with
101 a clear management need to predict how environmental changes and fisheries management
102 scenarios will impact population dynamics. The Eastern Pacific stock that breeds in the Bering
103 Sea has experienced a population decline since the late 1990s, driven mostly by declines at the
104 largest breeding rookery on St. Paul Island, Alaska (Muto et al., 2022; Towell et al., 2006). The
105 cause of this decline is unknown, but reduced food availability is one hypothesized factor given
106 disparities in maternal foraging trip durations, pup growth rates, and population trends among the
107 three islands that make up the Eastern Pacific stock (Kuhn et al., 2014b, 2014a; McHuron et al.,
108 2019, 2020). Recent and unprecedented environmental conditions have resulted in range shifts of
109 walleye pollock (*Gadus chalcogrammus*) into the northern Bering Sea (Eisner et al., 2020),
110 which are one of the key prey items of northern fur seals on St. Paul Island (McHuron et al.,
111 2020; Zeppelin and Ream, 2006). This is in addition to concerns about overlap between fur seals
112 and the commercial pollock fishery (McHuron et al., 2020) and forecasted declines in pollock
113 biomass due to climate change (Holsman et al., 2020). In using an approach that balanced a
114 hypothetical and real-world application, we were able to assess model performance in relation to
115 real fur seal behavior while exploring hypothetical questions about future behavior that would be
116 challenging to address using statistical approaches.

117

118 **2. Methods**

119 *2.1 Model overview*

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

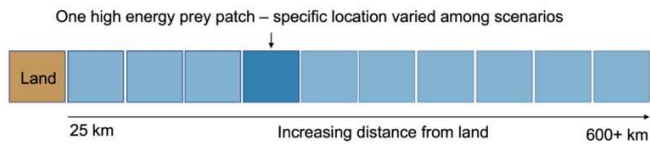
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128 The key components of an SDP model include a time horizon with discrete time steps, one or
129 more state variables, a terminal fitness function (if the time horizon is finite), a set of decisions
130 or actions (here discrete behavioral choices), and a fitness function that describes the expected
131 future reward for an optimally behaving individual. The value of this fitness function is
132 determined by the dynamic programming equations, via iteration backwards in time. Together,
133 these components allow for the determination of optimal time- and state-dependent behavioral
134 decisions, referred to here as the backward iteration since the dynamic programming equations
135 are solved backwards in time. The optimal behavioral decision is simply the one that maximizes
136 the expected reproductive success across all behavioral choices. Monte Carlo simulations
137 forward in time are then used to simulate populations where individuals move through the
138 environment using the decisions derived from the backward iteration (see Clark and Mangel,
139 2000; Houston et al., 1988; Mangel, 2015 for further details). Essentially, the backward iteration
140 determines how a fur seal should behave for each combination of state variables and the forward
141 simulation explores the sequence of decisions she makes during lactation.

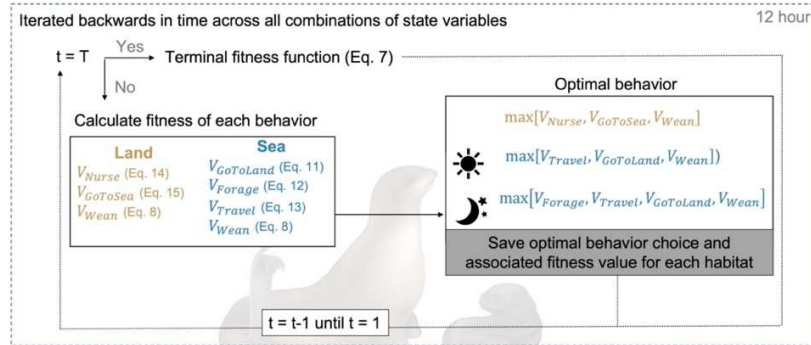
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143 In this model, there are two habitats for a female fur seal: land or sea. We characterized land by a
144 single location, and sea by ten discrete locations (Fig. 1). At sea, we determined whether a
145 female is predicted to forage, travel within her current location or to a new location, go back to
146 land, or wean her pup. On land, we determined whether a female is predicted to nurse her pup,
147 go to sea, or wean her pup. The behavioral choices depended on two intrinsic state variables
148 (female fat mass, pup mass), and one extrinsic state variable that was only applicable when a
149 female was at sea (location, referred to as cell). There is a single backward iteration, where the
150 two habitats are linked by the behavioral choices of going to land or to sea. The following
151 sections provide further detail on each of the key model components, including the specific
152 values and bounds of state variables and the state dynamics, which describe the underlying
153 bioenergetics of how female fat mass and pup mass vary with behavior. A simplified schematic
154 of the model is shown in Fig. 1.

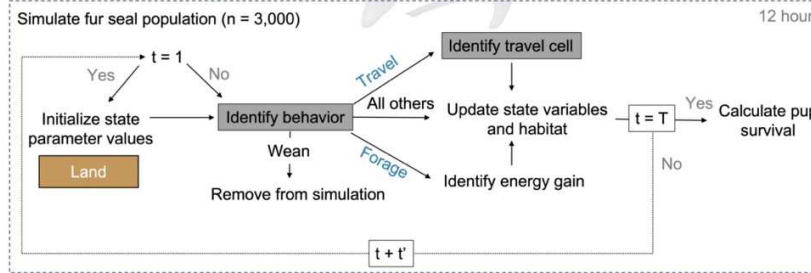
1. Baseline model scenarios



2. Backward iteration



3. Forward simulation



155

156 Figure 1. Conceptual diagram of the stochastic dynamic programming model and different
 157 baseline model scenarios, parameterized for an adult female northern fur seal during lactation.
 158 Model scenarios (1) differed in the location of the high energy cell and the amount of energy
 159 gained from foraging in it, with the high energy cell located in only one of 10 potential locations
 160 for each scenario. In the backward iteration (2), the optimal behavior is the one that maximizes
 161 future reproductive success, with different optimal behaviors depending on whether a female is
 162 on land or at sea. Optimal behaviors were then used in an individual-based forward simulation
 163 (3); at the first time step a female is on land and give birth but thereafter her behaviors are
 164 dictated by the results of the backward iteration given her current habitat (land vs. sea), values of
 165 the state variables, and model time.

166

167 *2.2 Model scenarios*

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

183

184 We developed four alternate models (referred to as ‘trait changes’) to explore how behavioral,
185 physiological, and morphological variation that currently exist within the otariid lineage affected
186 behavioral decisions and reproductive success. These changes included an extension to the time
187 horizon to increase lactation duration, an increase in body size, and reductions in either a
188 female’s or a pup’s metabolic rate (Table 1). We did not include a reduction in body size since
189 female northern fur seals are already among the smallest otariid females. We modeled changes as

190 the endpoint of evolutionary change so that a separate backward iteration determined optimal
191 behaviors under that adapted state. We ran each trait change model using all 30 scenarios of prey
192 location and energy gain. These four models were meant to provide insight into whether there
193 might be selective potential on any of these traits that might help northern fur seals adapt to
194 adverse foraging conditions, such as reduced prey or prey being located further from land. Since
195 each scenario was limited to a single change, results are conditioned on all other factors of their
196 biology remaining the same.

197

198 *2.3 Time horizon*

199 We ran the baseline model from parturition to weaning at a 12-hour interval for a total of 283
200 time steps. The specific date of parturition was assumed to be July 13 (Gentry, 1998). We
201 assumed that within a day, one 12-hour time step corresponded to ‘night’ (even time steps) and
202 one to ‘day’ (odd time steps). This time horizon was approximately two weeks longer than the
203 average lactation duration of northern fur seals (Goebel, 2002; McHuron et al., 2020). Under the
204 trait change scenario for lactation duration, we increased the time horizon to 610 time steps. This
205 value corresponds to a lactation duration typical in temperate otariids (Schulz and Bowen, 2004).

206

207 *2.4 State variables*

208 Female fat mass $X_F(t)$ at time t with particular value denoted by x_F , was the metric used to
209 describe a female’s energy reserves. It was bounded by a lower ($x_{F_{Crit}}$) and upper ($x_{F_{Max}}$) limit,
210 where mortality was assumed to occur when fat mass fell below $x_{F_{Crit}}$. We assumed values of
211 5% of body mass and 20% of body mass for $x_{F_{Crit}}$ and $x_{F_{Max}}$, respectively. Upper limits were

212 informed by fat mass estimates from northern fur seals soon after parturition (Springer et al.,
213 2008). Behavioral choices were assessed at intervals of 0.5 kg.

214

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

221

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

228

229 *2.5 Determining the physiological parameters*

230 The parameters that influenced calculations of how female fat mass or pup mass changed from
231 one time step to the next for each behavior were body size, metabolic rates, pup milk intake
232 (only when nursing), prey energy intake (only when foraging), metabolizable energy (the
233 proportion of ingested energy available after fecal and urinary energy losses), and the

234 composition of new tissue growth (or tissue catabolism). Northern fur seal physiology has been
235 well studied compared with other marine mammal species, and in almost all cases we were able
236 to use empirically derived data from fur seals at two Eastern Pacific stock islands, St. Paul and
237 St. George, to parameterize the model. We chose parameter values based on an 8-year-old
238 female and female pups; focusing on a single female age and pup sex reduced computational
239 time. The choice of pup sex was arbitrary, but we include mention of it because some parameter
240 values differ between male and female pups. A summary of all parameter values under the
241 baseline and trait change models can be found in Table 1.

242

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

247

248 Metabolic rates: Estimates of field metabolic rates (*FMR*) were derived from doubly labeled
249 water studies conducted in 1995 and 1996 on lactating females (McHuron et al., 2019) and pups
250 at different developmental stages (Donohue et al., 2002). For lactating females, we used different
251 metabolic rates for land and sea, and a multiplier that represented the seasonal increase in
252 metabolic rates between summer and fall (Table 1). For pups, we used different metabolic rates
253 for the pre-molt, molt, and post-molt period. Pups are born with their natal coat that they being to
254 molt approximately 1.5 – 2.0 months after birth, which appears to influence their
255 thermoregulatory costs (Donohue et al., 2002). For the perinatal duration model, we used pup

256 metabolic rates derived from Antarctic fur seals (*Arctocephalus gazella*), a fur seal species that is
257 similar in body size and lactation duration to northern fur seals (McDonald et al., 2012).

258

259 Pup milk intake: The amount of milk consumed by a pup for each time step spent suckling was
260 primarily derived from data presented in Donohue et al. (2002), where milk intake was measured
261 in pups that were approximately 15 – 100 days of age using doubly labeled water. We
262 recalculated daily pup milk intake so that it reflected actual daily milk intake as opposed to the
263 typical representation of daily milk intake that is integrated across the entire maternal cycle (trip
264 and land duration). We modeled daily milk intake as a function of body mass (Fig. A1),
265 assuming a non-linear relationship since studies on other fur seal species have found a non-linear
266 relationship (Arnould et al., 1996; Arnould and Hindell, 2002). For the perinatal duration model,
267 we assumed that 4 – 8 kg pups (the likely range of pup mass during this time) consumed 9.95 MJ
268 day⁻¹ (Costa and Gentry, 1986).

269

270 Energy gain: For lactating females, energy gain from foraging (E_{Prey}) depended on cell, with
271 one of the ten cells having high energy gain and the rest low energy gain. Specific values were
272 chosen so that cells with low energy gain ($E_{Prey} = 40$ MJ for all scenarios) were sufficient for a
273 female's own metabolic needs but could not support the entire costs of lactation. In the high
274 energy cell, E_{Prey} was set at a maximum value assuming that a female could not physically
275 consume more than 30% percent of her body mass per day (10.8 kg in the baseline, 13.5 kg in
276 the trait change model for body size). Thus, E_{Prey} in the high energy cell varied depending on
277 the value chosen for prey energy density (Table 1). We used a value of 5.4 MJ kg⁻¹ for the

278 average energy gain scenario, since this is the average prey energy density of the diet of Pribilof
279 Island fur seals (McHuron et al., 2020). The high and low energy gain scenario values were
280 assumed to be 25% higher or lower than this average value (Table 1).

281

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

286

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

296

297

298 Table 1. Parameter values used in the baseline stochastic dynamic programming model and the four trait change models (LD =
 299 lactation duration, BS = body size, FM = female metabolism, PM = pup metabolism). Values for the trait change models are only
 300 shown if they differed from the baseline model. Point estimates are used in the backward iteration. For variables with standard
 301 deviations, values for each simulated individual in the forward simulation were drawn from a normal distribution, with limits indicated
 302 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	0.82 (5.5 - 8.8)	
Land	FMR_{Land}	$FMR_{Sea}/1.8$		
Metabolic multiplier (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	-	
pre molt → molt		1.152
pre molt → postmolt		0.867
Milk intake (MJ day ⁻¹)	E_{Milk}	
Perinatal		9.95
All other times		See Fig. A1

303 ^aOnly used in the forward simulation since optimal decisions were determined for each pup mass

304 2.6 State dynamics

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

306
$$X_{F_{Forage}}(t + 1) = \min \left[X_F(t) + \frac{0.82 \cdot E_{Prey}(c) - FMR_{Sea}(t)}{39.3}, X_{F_{Max}} \right] \quad (1)$$

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

309

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

311
$$X_{F_{GoToLand, Travel, GoToSea}}(t + t') = X_F(t) - \frac{FMR_{Sea}(t)}{39.3} \quad (2)$$

312 where t' is the number of time steps it takes a female to travel from cell c (or land) to her
 313 intended destination; $t' = 1$ except when going to land where t' was estimated based on the
 314 distance of cell c to land and the average transit rate of northern fur seals when traveling (Table
 315 1). In nature, females may forage along the inbound and output portion of their trip (McClintock
 316 and Michelot, 2018), but for simplicity we assumed directed travel with no foraging from their
 317 current cell back to land. To account for this, we assumed that the future expected fat mass of a
 318 female was equivalent to that of traveling a single time step.

319

320 When nursing, a female's fat mass dynamics were

321
$$X_{F_{Nurse}}(t + 1) = X_F(t) - \left(\frac{FMR_{Land}(t) - \frac{E_{Milk}}{2}}{39.3} \right) \quad (3)$$

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

325

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

$$327 \quad X_{P_{Forage,Travel,GoToSea}}(t + 1) = X_P(t) - 1.5 \left(\frac{0.95 \cdot FMR(t)}{39.3} + \frac{0.05 \cdot FMR(t)}{18.0} \right) \quad (4)$$

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

$$335 \quad X_{P_{GoToLand}}(t + t') = X_P(t) - 1.5 \left(\frac{0.95 \cdot FMR(t) \cdot t'}{39.3} + \frac{0.05 \cdot FMR(t) \cdot t'}{18.0} \right) \quad (5)$$

336

337 When the mother was nursing, the pups mass dynamics were calculated as

$$338 \quad X_{P_{Nurse}}(t + 1) = X_P(t) + \frac{0.54 \cdot \left(0.95 \cdot \frac{E_{Milk}}{2} - FMR(t) \right)}{39.3} + \frac{0.46 \cdot \left(0.95 \cdot \frac{E_{Milk}}{2} - FMR(t) \right)}{18.0} \quad (6)$$

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

341

342 2.7 Fitness function and end condition

343 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
344 expected total probability that a female and her pup will survive to return to the breeding grounds
345 given that female fat mass $X_F(t) = x_F$, pup mass $X_P(t) = x_P$, and current cell $C(t) = c$, where
346 the expectation is taken over the stochastic events of survival and food distribution. Since we
347 focus this model on a single age instead of modeling decisions across the entire lifespan of a
348 female, fitness includes her own survival since we assume that some reproduction will occur in
349 the future. There is a fitness function for each habitat type since a female can either be on land or
350 at sea, and there are different behavioral choices associated with each habitat.

351

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

$$355 F_{Wean}(x_F, x_P, T) = \phi_F(x_F) + \phi_P(x_P) \equiv \Phi(x_F, x_P) \quad (7)$$

356 In the absence of empirical data on the functional form of this relationship, we assumed that
357 female survival increased linearly from 0 between the critical fat mass and 50% of the maximum
358 fat mass, which corresponds to 10% of total body mass since 20% was the upper limit. At fat
359 mass levels $> 50\%$ of the maximum fat mass, we fixed survival at 0.95, the age-specific survival
360 of an 8-year old female (Lander, 1981; Fig. A2). This inflection point was based on data
361 indicating that in October and November, fat composition of lactating females was
362 approximately 10% (Banks et al., 2006; Springer et al., 2008). We ran a sensitivity analysis on
363 the specific location of this value using a second fitness function where the value for the

364 inflection point was lowered to 41.6% of the maximum fat mass (8.3% of total body mass; see
 365 further description below). The designation of pup survival to age two is just a reflection of data
 366 availability and does not affect the model output. Once they disperse, most pups do not return to
 367 land until the age of two; thus, this is the first age at which survival is typically estimated
 368 (Lander, 1979).

369

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

$$376 \quad V_{Wean}(x_F, x_P, t) = \phi_F(x_F) + \phi_P(x_P - \Delta x_P(t)) \quad (8)$$

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

379

380 *2.8 Stochastic dynamic programming equations*

381 The dynamic programming equations are then

$$382 \quad F_{Sea}(x_F, x_P, c, t) = \begin{matrix} \text{night} \\ \text{day} \end{matrix} \left[\begin{matrix} \max[V_{Forage}(x_F, x_P, c, t), V_{Travel}(x_F, x_P, c, t), V_{GoToLand}(x_F, x_P, c, t), V_{Wean}(x_F, x_P, t)] \\ \max[V_{Travel}(x_F, x_P, c, t), V_{GoToLand}(x_F, x_P, c, t), V_{Wean}(x_F, x_P, t)] \end{matrix} \right] \quad (9)$$

383 and

$$384 \quad F_{Land}(x_F, x_P, t) = \max[V_{Nurse}(x_F, x_P, t), V_{GoToSea}(x_F, x_P, c, t), V_{Wean}(x_F, x_P, t)] \quad (10)$$

385 where the terms on the right-hand side are the fitness values associated with each behavioral
386 choice, described in further detail below. Because much of the dive activity of northern fur seals
387 occurs at night (Kuhn et al., 2014a), we only allowed a female to forage during the night (even
388 time steps of the model). Doing so allowed us to use maximum daily consumption estimates to
389 limit energy gain while avoiding the inclusion of an additional state variable associated with
390 stomach fullness. The optimal behavior is the one that maximizes fitness. The values of F_{Land}
391 and F_{Sea} are linked by the behaviors of going to sea or going to land. An alternate way to
392 structure the model that would give the same result is to consider land as one of the unique
393 values of the location state variable c , which would result in a single F per time step that would
394 be the maximum across all land and sea behaviors. In theory this structure would be simpler than
395 the one we chose, but in practice it is more challenging to implement given that the state
396 variables, state dynamics, and behavioral choices are somewhat different between land and sea.
397

398 The fitness value of traveling from cell c to land is

$$399 \quad V_{GoToLand}(x_F, x_P, c, t) = e^{-\rho t'} F_{Land}(x'_F, x'_P, t + t') \quad (11)$$

400 where ρ is the per time step probability of mortality ($e^{-\rho}$ is thus the per time step probability of
401 survival), t' is the number of time steps between cell c and land, and x'_F and x'_P are the new
402 states associated with going back to land (Eqs. 2 and 5).

403

404 The fitness value of foraging within cell c is

$$405 \quad V_{Forage}(x_F, x_P, c, t) = e^{-\rho} F_{Sea}(x'_F, x'_P, c, t + 1) \quad (12)$$

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

407

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

$$409 \quad V_{Travel}(x_F, x_P, c, t) = \max_{c \text{ in } \eta(c)} [e^{-\rho} F_{Sea}(x'_F, x'_P, c', t + 1)] \quad (13)$$

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

416

417 The fitness value of nursing is

$$418 \quad V_{Nurse}(x_F, x_P, t) = F_{Land}(x'_F, x'_P, t + 1) \quad (14)$$

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

420

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

$$423 \quad V_{GoToSea}(x_F, x_P, t) = \max_{c \text{ in } \eta(c)} [e^{-\rho} F_{Sea}(x'_F, x'_P, c', t + 1)] \quad (15)$$

424 where $\eta(c)$ is the cell with land and all cells adjacent to it and x'_F and x'_P are the new states
425 associated with traveling (Eqs. 2 and 4). Because we assumed a linear foraging environment,
426 there was only one cell a female could enter from land; however, this equation shows how to
427 modify the model when multiple cells can be accessed from land.

428

429 If at any time x'_F fell below the critical mass, a female died and her fitness was based solely on
430 her pup's mass at that time (assuming $x'_P \geq x_{P_{Crit}}$). Similarly, if at any time x'_P fell below the

431 critical level (assuming $x'_F \geq x_{F_{Crit}}$) then the expected fitness was based solely on the female's
432 mass at that time. We ranked ties in fitness among behavioral states as $V_{Wean} > V_{GoToRook} >$
433 $V_{Forage} > V_{Travel}$ when at sea or $V_{Wean} > V_{GoToSea} > V_{Nurse}$ when on land, using the
434 assumptions that when there is no fitness benefit, land should be preferred over sea and that the
435 most energetically beneficial behavior should be preferred within each habitat. When
436 determining the optimal cell to travel to, ties in fitness were given to the first occurrence of that
437 value.

438

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

446

447 *2.9 Forward simulation*

448 We used the optimal behavioral decisions identified in each backward iteration to quantify the
449 distribution of behaviors and resulting reproductive parameters in a fur seal population. We
450 initiated simulations at birth with all females on land; the initial condition of each female was set
451 at the maximum fat mass. We drew pup mass at birth (Boltnev and York, 2001), and female and
452 pup metabolic rates from normal distributions based on empirical data to incorporate known
453 individual and/or temporal variation in these parameters into the simulations (Table 1). This

454 assumes that decision rules are the same regardless of a female's metabolic rate, an assumption
455 that should be met given that the energy available in the low energy cells would still be too little
456 to meet a female's total energy needs (metabolism + lactation) even with the lowest possible
457 metabolic rate. Between the time a female gave birth and went to sea on her first foraging trip,
458 we used the behavioral decisions derived using the perinatal parameters; after that point we
459 switched to the output from backward iterations using non-perinatal parameters. Females that
460 weaned their pup were removed from future time steps in the simulation.

461
462 We ran a forward simulation for each combination of prey energy gain (3 scenarios), location of
463 the high energy cell (10 scenarios), and trait changes (4 changes), using decisions from the
464 appropriate backward iteration for the scenario combination. A forward simulation was also run
465 for all 10 location scenarios using the average prey energy gain scenario for the fitness function
466 sensitivity analysis. We ran 50 replicates for each unique combination of scenarios. In each
467 replicate, we simulated 3,000 fur seals, which is roughly the number of 8-year-old females in the
468 population from the East complex on St. Paul Island in 2018 (McHuron et al., 2020). We
469 calculated summary statistics (mean \pm SD) for each replicate, including trip and shore durations,
470 pup growth rates, lactation duration, and pup wean mass, all of which were emergent properties
471 of the model. We averaged these values across all replicates in each of the scenario
472 combinations.

473
474 Our approach assumes that female behavior is perfectly matched to the environment, since we
475 used the same prey scenario in the backward iteration and forward simulation. That is, there are
476 no mismatches between what females expect to encounter and what they do encounter. In the

477 real world, this is unlikely to be the case, particularly early in lactation when female fur seals
478 first arrive in the Bering Sea and must learn about the distribution and abundance of prey in that
479 year. Prey distribution and abundance is also dynamic, and there may also be mismatches
480 between expectation and reality throughout lactation. While behavior/environment mismatches
481 and subsequent learning can be incorporated into SDP models (Hilborn and Mangel, 1997;
482 Mangel and Clark, 1988), it increases the complexity of the model and was outside the scope of
483 this paper. Since we ran each prey scenario as a separate forward simulation, results are meant to
484 represent distinct populations with different expectations for prey distribution and abundance,
485 and do not necessarily represent optimal trip and land durations of females within a population
486 that may be switching among different prey patches.

487

488 *2.10 Evaluating the model*

489 We used empirical data collected from fur seals on all three of the Eastern Pacific stock islands
490 (St. Paul, St. George, and Bogoslof) to confront the model output (*sensu* Hilborn and Mangel,
491 1997) with data on the natural behavior of fur seals. At St. Paul Island, fur seals have
492 experienced lower pup growth rates and a population decline since the late 1990s, whereas at
493 Bogoslof Island fur seals have experienced greater pup growth rates and rapid population growth
494 since the colony was established in the 1980s (Kuhn et al., 2014a; Muto et al., 2022; Towell et
495 al., 2006). Foraging trip durations are considerably longer on St. Paul and St. George Islands
496 compared to Bogoslof Island because fur seals at Bogoslof Island travel shorter distances to
497 reach prey patches (Kuhn et al., 2014a).

498

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

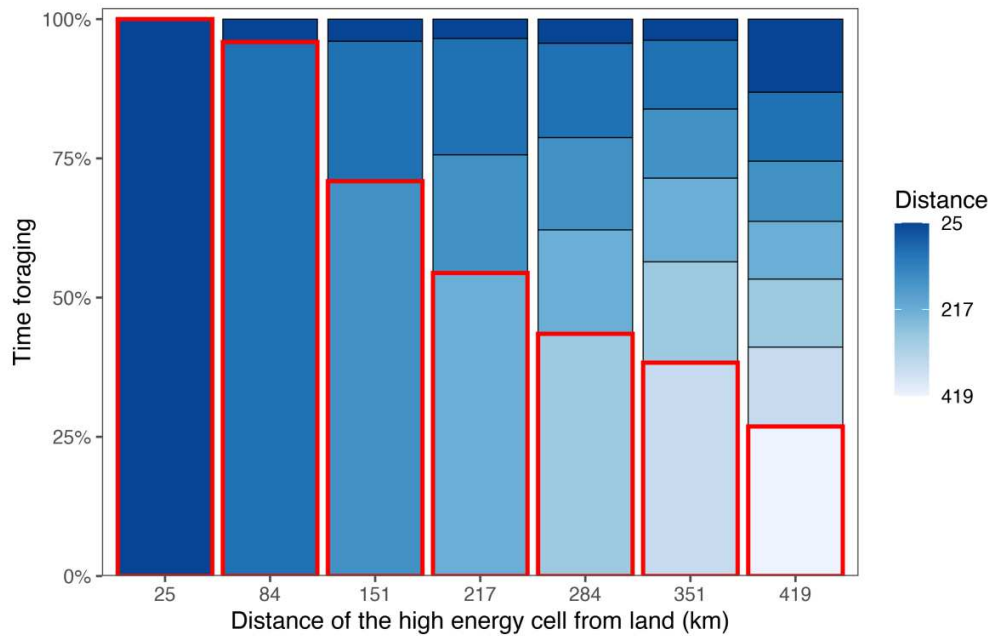
508

509 **3. Results**

510 *3.1 Cell use*

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

519



520

521 Figure 2. An example of the allocation of foraging time among cells when the distance of the
 522 high energy cell from land ranged from 25 – 400+ km. Results are shown for the average prey
 523 energy gain scenario and were averaged across all 3,000 females in a single replicate. Three of
 524 the ten prey location scenarios are not shown since there was no foraging at these distances
 525 because pups were weaned before the first foraging trip. Colors represent different cells, with
 526 darker colors representing cells closer to land. For each distance, the amount of foraging time
 527 spent in the high energy cell is outlined in red.

528

529 3.2 Land and trip durations

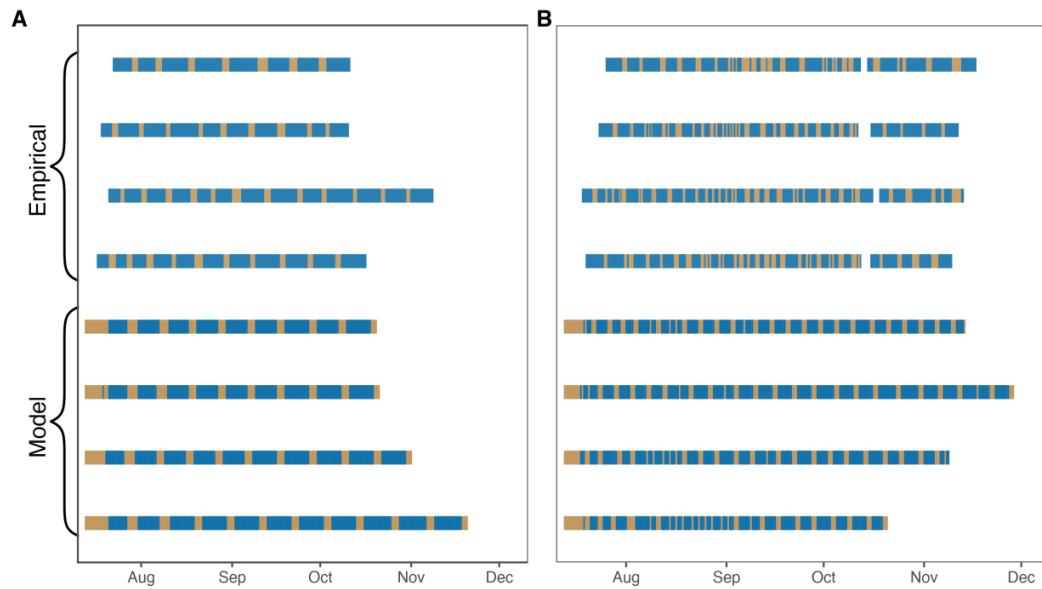
530 During the perinatal period, simulated females spent an extended amount of time on land with
 531 their pup before departing on their first foraging trip (Fig. 3). The average perinatal duration
 532 across all 30 prey scenarios in the baseline model was 6.6 days. After this period, simulated fur
 533 seals adopted a central place foraging strategy, alternating between time spent on land nursing
 534 their pups and foraging at sea (Fig. 3). Across all prey scenarios, trip durations averaged 2.9 –

535 11.2 days with 1.2 – 3.1-day nursing visits onshore. For comparison, trip durations of satellite-
536 tagged fur seals from the empirical dataset ranged from 0.2 – 12.7 days at sea, with 95% of shore
537 durations \leq 3.1 days. Foraging trip durations were generally shortest in July, with trip durations
538 in other months that were on average 32% higher across all prey scenarios. Trip durations of
539 simulated fur seals increased as the distance of the high energy cell from land increased (Fig.
540 4A), with corresponding increases in land durations (Fig. 5B). Decreased prey energy gain in the
541 high energy cell resulted in increased trip durations for a given distance between land and the
542 high energy cell (Fig. 4A).

543

544 Qualitative comparisons between simulated fur seals and empirical data revealed that the model
545 captured the general patterns in trip and land durations of northern fur seals, particularly with
546 respect to how differences in travel distances to foraging grounds affected behavioral patterns
547 (Fig. 3). There was a similar relationship between trip duration and the maximum distance
548 traveled from land between the model output and empirical data, although the model
549 overestimated trip durations for a given distance compared with actual fur seal behavior (Fig.
550 5A). There was close overlap between the model and empirical data for the relationship between
551 land and trip durations (Fig. 5B.)

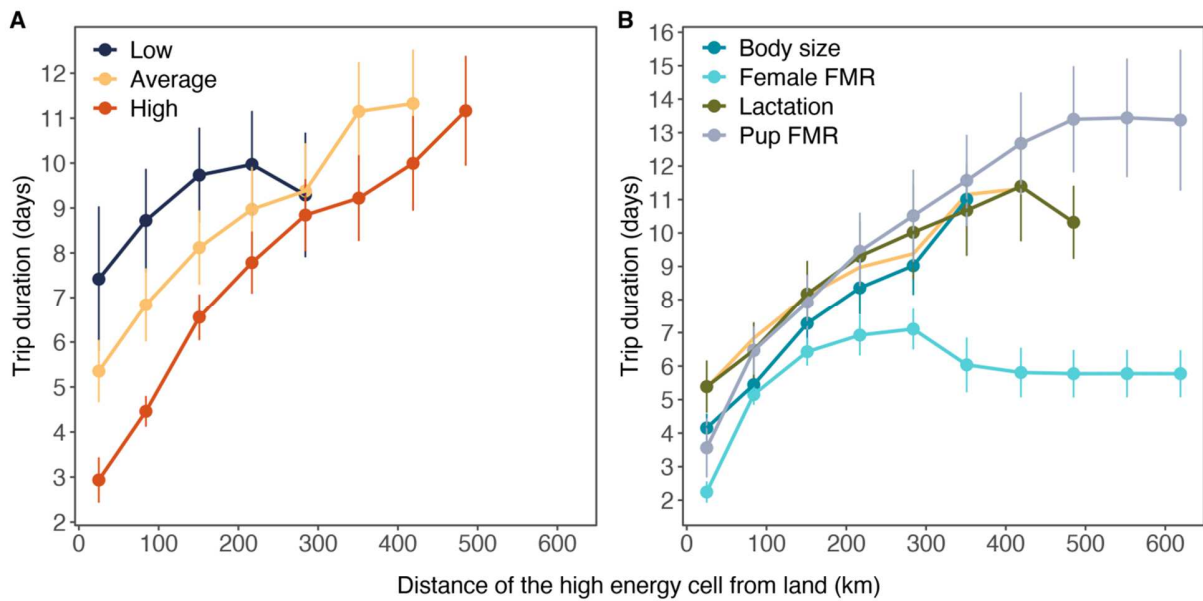
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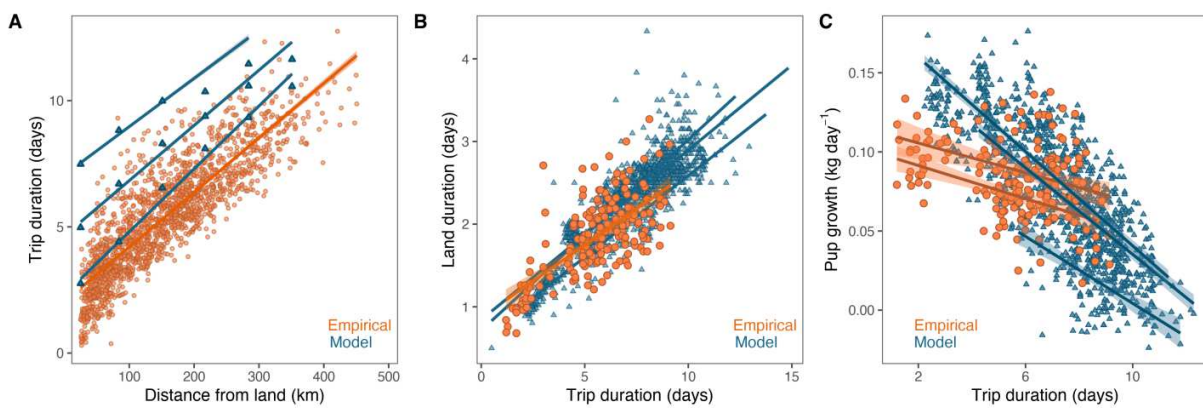
554 Figure 3. Examples of time-location budgets for four simulated fur seals (model) and four
 555 instrumented lactating females from St. Paul Island (empirical, A) and Bogoslof Island (B),
 556 highlighting the similarity in behavior between model output and empirical data (within a plot)
 557 and the effect of environmental differences on behavior (between plots). Colors represent time
 558 spent on land (tan) or at sea (blue). Model comparisons with St. Paul Island were derived from
 559 the average prey energy gain scenario where the location of the high energy cell was 151 km
 560 away from land, whereas comparisons with Bogoslof Island were derived from the high prey
 561 energy gain scenario where the high energy cell was 25 km away from land. These comparisons
 562 were selected to best match the foraging distance of instrumented lactating females and
 563 approximated prey energy density consumed at each island.

564



565

566 Figure 4. The effects of changes in the distance of the high energy cell from land on trip
 567 duration, colored by the different prey energy gain scenarios (A) or trait changes (B). In B, only
 568 results from the average prey energy gain scenario are shown, with the results from the baseline
 569 model in orange for comparison. Each point represents the mean value across 50 replicates. Error
 570 bars represent the average within replicate SD.



571

572 Figure 5. Comparisons between model output and empirical data for the relationships between
 573 trip duration and distance from land (A), land and trip duration (B), and pup growth rate and trip
 574 duration (C). Individual regression lines are presented for each prey energy gain scenario (high,

575 average, low). In A, points are averages for each prey scenario from a single replicate (model) or
576 values for individual foraging trips of instrumented females (empirical). Model results represent
577 the distance of the high energy cell from land, while empirical results are the maximum straight-
578 line distance from land on each foraging trip. In B, each point represents the average trip and
579 land duration for individual females. In C, points are paired mean trip durations and pup growth
580 rates from individual females. In all plots, differences in size and transparency of points are
581 solely for visual purposes. In B and C, a subset of model points are shown for ease of
582 visualization.

583

584 *3.3 Pup growth and lactation duration*

585 Pup growth rates decreased as trip durations increased except when the high energy cell was
586 <100 km from land (Fig. 6A). Mean values ranged from 0.008 – 0.15 kg day⁻¹ (high prey energy
587 gain), 0.005 – 0.10 kg day⁻¹ (average), and -0.03 – 0.01 kg day⁻¹ (low). In comparison, pup
588 growth rates from the empirical dataset ranged from 0.017 – 0.14 kg day⁻¹. Pup mass at weaning
589 followed a similar pattern, with average masses that ranged from 6.5 kg – 21.6 kg (Fig. 6B).
590 There are no corresponding data on wean mass from the empirical dataset. Changes in prey
591 energy gain affected the maximum distance the high energy cell could be from land while still
592 supporting a lactation duration that was considerably longer than the perinatal duration (Fig. 7A),
593 with access to more energy dense prey allowing females to achieve higher pup growth and wean
594 mass for a given distance from land (Fig. 6A and 6B).

595

596 Mean lactation durations across all prey scenarios ranged from 6.6 – 131.5 days (out of a
597 maximum allowed of 141.5 days; Fig. 7A). There was a strong bimodality in lactation durations;

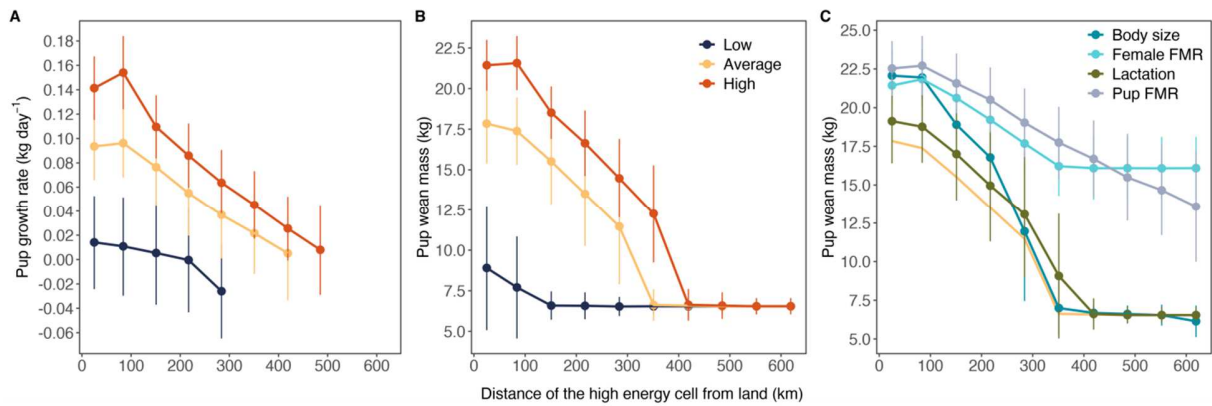
598 most pups were either weaned within 10 days of birth or supported for at least 110 days. This
599 may have been because we used the same prey environment for the backward iteration and
600 forward simulation, so that optimal decisions were based on a perfectly matched environment in
601 the forward simulation, and that each environment was static within a prey scenario. Thus, under
602 suboptimal prey scenarios where the probability of pup survival was virtually zero, simulated
603 females ‘knew’ there was no fitness benefit of continuing lactation beyond the perinatal duration.
604 Scenario means of female fat mass at the time of weaning were 3.5 – 4.1 kg (9.8 – 11.4% of total
605 body mass), with slightly lower values for scenarios where the average age at weaning was at
606 least 110 days vs 10 days or less (overall mean of 10.2% vs 11.4%).

607

608 *3.4 Sensitivity to fitness function*

609 Lowering the fat mass at which female survival plateaued at 0.95 by 20% resulted in small
610 changes to the absolute values of behavioral and reproductive parameters. Across prey location
611 scenarios, it generally increased pup growth rate, wean mass, and land durations, and decreased
612 trip and lactation durations (Fig. A3A). For example, pup growth rates increased by 0.0035 -
613 0.0082 kg day⁻¹ across all prey location scenarios between the baseline and the altered fitness
614 function output, which resulted in pups that were on average 0.02 – 0.63 kg heavier at weaning.
615 Relative changes in trip and land durations, pup wean mass, and lactation durations were all <
616 5%, while relative changes in pup growth rates primarily ranged from 6.5 – 16.2% (Fig. A3A).
617 Altering the fitness function did not change the patterns of how each variable changed in
618 response to increased distance of the high energy cell from land (Fig. A3B).

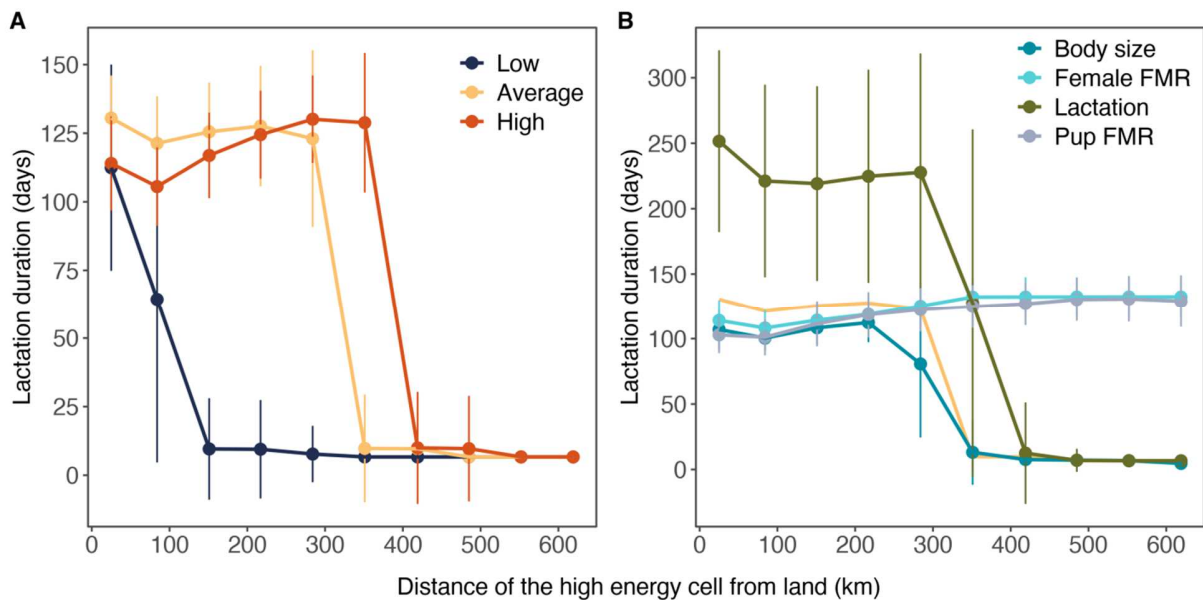
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620

621 Figure 6. The effects of changes in the distance of the high energy cell from land on pup growth
622 rate (A) and pup wean mass (B, C), colored by the different prey energy gain scenarios (A, B) or
623 trait changes (C). Only results from the average prey energy gain scenario are shown in C, with
624 the results from the baseline model in orange for comparison. Each point represents the mean
625 value across 50 replicates. Error bars represent the average within replicate SD.

626



627

628 Figure 7. The effects of changes in the distance of the high energy cell from land on lactation
629 duration, colored by the different prey energy gain scenarios (A) or trait changes (B). In B, only
630 results from the average prey energy gain scenario are shown, with the results from the baseline
631 model in orange for comparison. Each point represents the mean value across 50 replicates. Error
632 bars represent the average within replicate SD.

633

634 *3.5 Trait change models*

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

645

646 The remaining traits had little influence on the ability of a female to successfully reproduce when
647 the high energy cell exceeded 350 km from land. That is, even if traits could evolve, they would
648 not improve reproductive success under our prey scenarios. When the amount of time available
649 for lactation increased, females altered their behavior so that land and trip durations were on
650 average 7.7% shorter and 13.1% longer, respectively compared with the baseline model. This

651 resulted in reduced milk intake rates and pup growth rates, but since pups were being nursed for
652 a longer duration, pup wean masses remained largely unchanged from the baseline model. An
653 increase in body mass was beneficial when the high energy cell was relatively close to land,
654 allowing females to wean pups at a higher mass compared with the baseline model (Fig. 6C).
655 Pup wean masses were higher when foraging closer to land because larger females on average
656 spent less time at sea than females in the baseline model (66 - 71% vs. 69 - 74%). While total
657 metabolic demands increased with body size, larger females could consume greater total
658 amounts of prey per time step than smaller females, which allowed them to have shorter trip
659 durations and thus spend more total time on land with their pups compared with females in the
660 baseline model (Fig. 4B).

661

662 **4. Discussion**

663 In this paper, we explored how optimal behaviors of female northern fur seals, a central-place
664 forager during lactation, changed under different prey scenarios and how beneficial hypothetical
665 trait changes were in facilitating reproduction in the face of prey changes. Behavioral decisions,
666 such as how long to spend at sea foraging and nursing a pup on land, were emergent model
667 properties, allowing for independent comparisons with empirical data. Below we provide further
668 discussion of model and empirical comparisons, focusing in particular on potential causes of
669 discrepancies between the two, and the insights that can be gleaned about wild fur seals despite
670 the hypothetical nature of the prey scenarios and trait change models. While the application of
671 our model here was largely hypothetical, the structure could be relatively easily adapted to
672 incorporate a more realistic foraging environment for northern fur seals or other otariid species
673 that could then be used to predict spatial distribution and reproductive success under hindcasted

674 and forecasted conditions. Since any predictions of spatial distribution would not be constrained
675 by current fur seal behavior, our model provides the framework towards understanding how fur
676 seals may respond to novel environmental conditions in the Bering Sea.

677

678 *4.1 Influences of prey availability on behavior and pup growth*

679 Central-place foraging emerged from the model to balance tradeoffs associated with terrestrial
680 reproduction and aquatic foraging. Following birth, simulated fur seals spent an extended amount
681 of time on land with their pup before leaving on their first foraging trip. The average perinatal
682 duration across all prey scenarios in the baseline model was 6.6 days (individual scenario means
683 ranged from 4.7 – 8.3 days), which is slightly lower than but within the range of the 8.2 day
684 average (range of 4.8 - 13.5 days) exhibited by wild northern fur seals (data from Merrill et al.,
685 2021). Variation in the perinatal duration was largely influenced by a female's expectation of
686 prey availability; durations were shortest when the high energy cell was closest to land, increased
687 quickly to a peak, and then declined to 6.5 days for the remaining distances. This expectation
688 may explain why model values were slightly lower than empirical data, since wild fur seals do
689 not know exactly where prey will be and thus likely provide a buffer to their pup in the case of
690 longer than expected trip durations. Foraging trip durations of simulated fur seals were shortest
691 in July, presumably because pups required less energy and had limited fasting capabilities, with
692 little change in cell use among months. Increases in foraging trip durations throughout lactation
693 are common in northern fur seals (Merrill et al., 2021) and other otariids (Arnould and Hindell,
694 2001; Georges and Guinet, 2000; Higgins and Gass, 1993), and while our model indicates they
695 occur in the absence of shifts in prey availability and distribution, it does not preclude the
696 possibility that shifts in the prey landscape also contribute to these patterns in nature.

697

698 The duration of foraging trips is an influential factor on pup growth rates, weaning mass, and
699 survival for otariids, at least when changes in trip duration are attributable to changes in prey
700 availability and not simply a result of individual behavioral variation (Doidge and Croxall, 1989;
701 Georges and Guinet, 2000; Lunn et al., 1993). Land durations may increase slightly with trip
702 duration but are generally more consistent and not sufficient to compensate for the increased
703 fasting time of the pup. In extreme cases, foraging trips may be so long that the pup starves
704 before the mother returns from her foraging trip (Costa et al., 1989), which for northern fur seals
705 appears to be about 10 - 12 days, at least early in lactation (Calambokidis and Gentry, 1985).
706 Consistent with empirical observations, foraging trip durations of simulated fur seals increased in
707 response to both changes in distribution (the location of the high energy cell) and availability
708 (prey energy gain), which generally had a negative impact on pup growth rates and wean masses.
709 Our observation that trip durations increased when prey energy gain was reduced, even when the
710 distance of the high energy cell from land remained constant, supports suggestions by Boyd
711 (1997) and Costa et al. (1989) that female fur seals may have a set energy target they attempt to
712 reach before returning to their pup.

713

714 Model predictions of pup growth rates in response to trip durations were more extreme than
715 relationships derived from empirical data, with maximum mean pup growth rates (0.15 kg day^{-1})
716 that were higher than the mean of 0.11 kg day^{-1} that has been reported in female pups from
717 Bogoslof Island where the population has experienced rapid growth (Banks et al., 2006; Springer
718 et al., 2008). Since the model did well in predicting land durations as a function of trip duration
719 (i.e., we did not overestimate milk energy delivery because of too much time spent on land), this

720 discrepancy may be related to our simplification of milk delivery decisions that resulted in a
721 constant value of milk energy transfer (relative to pup body mass) during nursing regardless of
722 the female's fat reserves, behavior, and pup's metabolic needs or body condition. Milk energy
723 delivery varies depending on female mass and trip and land durations (Arnould et al., 1996;
724 Costa and Gentry, 1986; Georges et al., 2001), and is likely also influenced by pup suckling
725 efficiency and the amount of time spent suckling in a given period. The majority of suckling
726 events are initiated and terminated by the pup (Macy, 1982; Ono et al., 1987) and it may be that
727 pup body condition influences motivational state while the female is present (Arnould et al.,
728 2001a). It also is possible that a female may be less receptive to nursing attempts when her pup is
729 in good body condition and foraging trips are short, preferentially retaining fat reserves to
730 mitigate potential future periods of poor foraging success. Pups also exhibit several behavioral
731 strategies to cope with extended maternal trip durations, such as reductions in activity and
732 attempts to suckle on other females (Lunn, 1992; Macy, 1982; Ono et al., 1987), which may
733 reduce the severity of weight loss and temper declines in pup growth rates. The data we used to
734 parameterize the milk energy delivery and pup metabolic rates in the model were collected over
735 two decades ago (Donohue et al., 2002); additional data collection would help illuminate how
736 these values may be changing in response to environmental conditions, which would refine our
737 ability to parameterize pup growth dynamics and lactation costs. Indeed, one important role of
738 models such as this one is to suggest those empirical data that are most valuable to collect.

739

740 Poor prey quality (i.e., 'junk-food') has been hypothesized by some as a contributing factor to
741 the decline of two Alaskan otariids, northern fur seals and Steller sea lions (*Eumetopias jubatus*),
742 as well as other marine central-place foragers (Gomez et al., 2016; Österblom et al., 2008; Trites,

743 2021; Wanless et al., 2005; Wolf and Mangel, 2008). Our model shows that prey energy density
744 impacts the behavior and reproductive success of fur seals, with fur seals in the low prey energy
745 gain scenario having the longest foraging trips and lowest pup growth rates for a given distance.
746 Pup growth rates in this scenario were near zero, even when females traveled very short
747 distances (25 km) to the foraging patch. These results highlight the dramatic impact that poor
748 quality prey can have on reproductive success, but also show that the interaction between prey
749 energy density and prey distribution is an important driver of changes in pup growth rates. For
750 example, in the average prey energy gain scenario, which was parameterized based on recent fur
751 seal diet and prey energy density estimates from the Pribilof Islands (McHuron et al., 2020), fur
752 seals were able to achieve pup growth rates comparable to those from a population experiencing
753 rapid growth (Banks et al., 2006) if the high energy cell was relatively close to land. Thus, the
754 same prey item could likely result in rapid population growth in some scenarios and population
755 declines in others, even if the energy density of that prey remains the same. High-quality prey
756 did provide a buffer to changes in prey distribution, with simulated females maintaining pup
757 growth rates exceeding 0.1 kg day^{-1} when the high energy cell moved to just over 200 km from
758 land. While modeled as a change in prey energy density, these conclusions are broadly
759 applicable to other situations that would influence the amount of energy gained while foraging,
760 such as changes in prey abundance.

761

762 *4.2 Influences of trait changes on behavior and pup growth*

763 Trait changes that affected pup fasting ability or durations were the only viable way to support
764 reproduction when the distance of the high energy cell from land resulted in trip durations that
765 consistently exceeded 10 days. The two trait changes that accomplished this did so through

766 different mechanisms: i) reduced female metabolic rates allowed females to maintain short
767 foraging trips by exploiting lower quality prey patches close to land, whereas ii) reduced pup
768 metabolic rates allowed females to extend foraging trip durations to reach distant prey patches. It
769 seems unlikely that there would be strong selective pressure for reduced female metabolic rates
770 to evolve solely in response to changes in prey distribution, as the positive effect on pup wean
771 mass was contingent on the availability of other prey resources close to land. In addition, low
772 adult metabolic rates appear to be largely confined to tropical species as an adaptation to
773 environmental factors, such as low productivity and warm air temperatures (Careau et al., 2007;
774 Costa and Trillmich, 1988; Villegas-Amtmann et al., 2017; Wiersma et al., 2007), so it is unclear
775 if these are attainable in temperate or polar environments. Reduced pup metabolic rates have
776 been documented in subantarctic fur seals (*Arctocephalus tropicalis*), a species where maternal
777 trip durations can last upwards of 3 weeks (Arnould et al., 2003; Verrier et al., 2009). These
778 reductions occur because pups are able to decrease thermoregulation costs by reduced swimming
779 activity, intense fat deposition, and a temperate climate (Arnould et al., 2003; Verrier et al.,
780 2009). While our results indicate that, of those examined, reductions in pup metabolic rates may
781 be the best mechanism for northern fur seals to adapt to long maternal trip durations, this can
782 delay the development of diving capabilities (Arnould et al., 2003; Verrier et al., 2011). It is
783 unclear how selective pressure to reduce thermoregulation costs would balance with the need to
784 develop diving capabilities in a species like northern fur seals that have such a short lactation
785 period, particularly when they need to forage independently very soon after weaning. It is likely
786 that changes in milk energy density also play a role in a pup's fasting ability, as milk fat content
787 increases with trip duration within and across otariid species (Georges et al., 2001; Ochoa-Acuna
788 et al., 1999; Trillmich and Lechner, 1986). These changes were not investigated here because

789 northern fur seals already have one of the highest milk fat content of otariids (Costa and Gentry,
790 1986).

791

792 Variability in otariid lactation durations, which range from four months to several years, has
793 been attributed to environmental differences associated with latitude (Ofstedal et al., 1987; Schulz
794 and Bowen, 2005; Trillmich, 1990). To optimize energy efficiency, lactation durations should be
795 as short as possible since costs increase with longer durations because the female is supporting
796 both growth and metabolic costs of her pup (Costa, 1993; Stephens et al., 2014). At roughly four
797 months, northern fur seals have one of the shortest lactation durations of any otariid, a duration
798 that is largely consistent despite the wide latitudinal range among breeding rookeries (34° N -
799 57° N). When we extended the lactation duration to 10 months, simulated females altered their
800 trip and land durations so that less energy was provided to the pup per unit time. Thus, pup
801 growth rates were reduced but pups were weaned at similar masses as in the baseline model,
802 regardless of the prey scenario. It was somewhat surprising that a longer lactation duration did
803 not result in increased pup wean masses under the low energy gain scenario compared with the
804 baseline model; however, it is important to consider that we did not alter any other lactation
805 parameters, such as milk energy delivery per unit time. Instead, simulated females spent more
806 time at sea and less time on land to achieve this reduction, and since these durations are so
807 influential on pup growth, further model exploration as to how changes in multiple factors
808 interact (e.g., milk energy delivery, female or pup body size) might provide better insight into the
809 conditions under which a longer lactation period would be beneficial. What we can conclude is
810 that under current rates of milk delivery, there is unlikely to be strong selective pressure for a

811 longer lactation duration for northern fur seals, which may explain the consistency in lactation
812 duration across their breeding range.

813

814 **5. Conclusions**

815 Our model provides insights that are applicable to northern fur seals and the current population
816 decline despite the simplified and hypothetical aspects of the model. Results indicate that a
817 rookery is unlikely to be viable if a female fur seal must consistently travel 400 km (straight line
818 distance) or farther to reach the primary foraging grounds, unless there are physiological changes
819 that affect the fasting capabilities of the pup. Whether or not a reduction in pup metabolic rate is
820 a viable strategy remains unknown, since it is unclear how flexible this parameter is, particularly
821 as reductions in activity rates could adversely affect other aspects of pup development.

822 Regardless, our results indicate that further empirical studies of pup metabolic rates may be
823 warranted. To obtain pup growth rates approaching those of a population experiencing rapid
824 growth (Banks et al., 2006; Springer et al., 2008), our model indicates the potential foraging
825 grounds need to be <150 km from the rookery assuming an average prey energy density of 5.4
826 MJ kg⁻¹. These conclusions assume that a female is able to consume a maximum of 30% of her
827 body mass per day, which is within the range estimated from captive juveniles (Rosen et al.,
828 2012) but may be slightly high given previous consumption estimates for free-ranging fur seals
829 of ~26% (Perez and Mooney, 1986). The ability of the model to reproduce behavior (and
830 behavioral responses to prey) consistent with northern fur seals and other otariids indicate its
831 utility in additional applications to this and other systems. Such applications include a model
832 extension to encompass the lifetime of a female fur seal and the incorporation of empirically
833 derived prey energy landscapes to predict the impact of a changing climate and commercial

834 fishing pressures on behavior, reproductive success, and population dynamics of northern fur
835 seals from the Eastern Pacific stock.

836

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847

848 **Literature Cited**

849 Arnould, J., Boyd, I.L., 1995. Temporal patterns of milk production in Antarctic fur seals
850 (*Arctocephalus gazella*). J. Zool. 237, 1–12.

851 Arnould, J., Boyd, I.L., Socha, D.G., 1996. Milk consumption and growth efficiency in Antarctic
852 fur seal (*Arctocephalus gazella*) pups. Can. J. Zool. 74, 254–266.

853 <https://doi.org/10.1139/z96-032>

854 Arnould, J.P.Y., Boyd, I.L., Rawlins, D.R., Hindell, M.A., 2001a. Variation in maternal
855 provisioning by lactating Antarctic fur seals (*Arctocephalus gazella*): Response to
856 experimental manipulation in pup demand. Behav. Ecol. Sociobiol. 50, 461–466.

857 <https://doi.org/10.1007/s002650100386>

858 Arnould, J.P.Y., Green, J.A., Rawlins, D.R., 2001b. Fasting metabolism in Antarctic fur seal
859 (*Arctocephalus gazella*) pups. *Comp. Biochem. Physiol. Part A* 129, 829–841.

860 Arnould, J.P.Y., Hindell, M.A., 2002. Milk consumption, body composition and pre-weaning
861 growth rates of Australian fur seal (*Arctocephalus pusillus doriferus*) pups. *J. Zool.* 256,
862 351–359. <https://doi.org/10.1017/S0952836902000389>

863 Arnould, J.P.Y., Hindell, M.A., 2001. Dive behaviour, foraging locations, and maternal-
864 attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Can. J. Zool.*
865 79, 35–48. <https://doi.org/10.1139/cjz-79-1-35>

866 Arnould, J.P.Y., Luque, S.P., Guinet, C., Costa, D.P., Kingston, J., Shaffer, S.A., 2003. The
867 comparative energetics and growth strategies of sympatric Antarctic and subantarctic fur
868 seal pups at Îles Crozet. *J. Exp. Biol.* 206, 4497–4506. <https://doi.org/10.1242/jeb.00703>

869 Ashmole, N.P., 1963. The regulation of numbers of tropical oceanic birds. *Ibis (Lond. 1859).*
870 103b, 458–473. <https://doi.org/10.1111/j.1474-919X.1963.tb06766.x>

871 Baker, J.D., Donohue, M.J., 2000. Ontogeny of swimming and diving in northern fur seal
872 (*Callorhinus ursinus*) pups. *Can. J. Zool.* 109, 100–109.

873 Banks, A., Iverson, S., Springer, A., Ream, R., Sterling, J., 2006. Consequences of fur seal
874 foraging strategies (COFFS). North Pacific Research Board Final Report 414.

875 Baylis, A.M.M., Orben, R.A., Arnould, J.P.Y., Christiansen, F., Hays, G.C., Staniland, I.J., 2015.
876 Disentangling the cause of a catastrophic population decline in a large marine mammal.
877 *Ecology* 96, 2834–2847. <https://doi.org/10.1890/14-1948.1>

878 Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J.,
879 Nordstrom, C.A., Paredes, R., Suryan, R.M., Waluk, C.M., Trites, A.W., 2013. Prey patch

880 patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS
881 One 8, e53348. <https://doi.org/10.1371/journal.pone.0053348>

882 Bogich, T., Shea, K., 2008. A state-dependent model for the optimal management of an invasive
883 metapopulation. *Ecol. Appl.* 18, 748–761. <https://doi.org/10.1890/07-0642.1>

884 Boltnev, A.I., York, A.E., 2001. Maternal investment in northern fur seals (*Callorhinus ursinus*):
885 Interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. *J.*
886 *Zool.* 254, 219–228. <https://doi.org/10.1017/S0952836901000735>

887 Boltnev, A.I., York, A.E., Antonelis, G.A., 1998. Northern fur seal young: interrelationships
888 among birth size, growth, and survival. *Can. J. Zool.* 76, 843–854.

889 Bost, C.A., Cotté, C., Terray, P., Barbraud, C., Bon, C., Delord, K., Gimenez, O., Handrich, Y.,
890 Naito, Y., Guinet, C., Weimerskirch, H., 2015. Large-scale climatic anomalies affect marine
891 predator foraging behaviour and demography. *Nat. Commun.* 6.
892 <https://doi.org/10.1038/ncomms9220>

893 Boyd, C., Castillo, R., Hunt, G.L., Punt, A.E., Vanblaricom, G.R., Weimerskirch, H., Bertrand,
894 S., 2015. Predictive modelling of habitat selection by marine predators with respect to the
895 abundance and depth distribution of pelagic prey. *J. Anim. Ecol.* 84, 1575–1588.
896 <https://doi.org/10.1111/1365-2656.12409>

897 Boyd, I.L., 1997. Foraging and provisioning in Antarctic fur seals: interannual variability in
898 time-energy budgets. *Behav. Ecol.* 10, 198–208.

899 Browning, E., Bolton, M., Owen, E., Shoji, A., Guilford, T., Freeman, R., 2018. Predicting
900 animal behaviour using deep learning: GPS data alone accurately predict diving in seabirds.
901 *Methods Ecol. Evol.* 9, 681–692. <https://doi.org/10.1111/2041-210X.12926>

902 Burke, C.M., Montevecchi, W.A., 2009. The foraging decisions of a central place foraging

903 seabird in response to fluctuations in local prey conditions. *J. Zool.* 278, 354–361.
904 <https://doi.org/10.1111/j.1469-7998.2009.00584.x>

905 Calambokidis, J., Gentry, R.L., 1985. Mortality of northern fur seal pups in relation to growth
906 and birth weights. *J. Wildl. Dis.* 21, 327–330.

907 Careau, V., Morand-Ferron, J., Thomas, D., 2007. Basal metabolic rate of Canidae from hot
908 deserts to cold Arctic climates. *J. Mammal.* 88, 394–400. [https://doi.org/10.1644/06-mamm-](https://doi.org/10.1644/06-mamm-a-111r1.1)
909 [a-111r1.1](https://doi.org/10.1644/06-mamm-a-111r1.1)

910 Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P.,
911 McConnell, B., 2021. AgentSeal: Agent-based model describing movement of marine
912 central-place foragers. *Ecol. Modell.* 440. <https://doi.org/10.1016/j.ecolmodel.2020.109397>

913 Clark, C.W., Mangel, M., 2000. Dynamic state variable models in ecology: methods and
914 applications. Oxford University Press, New York and Oxford.

915 Cohen, L.A., Pichegru, L., Grémillet, D., Coetzee, J., Upfold, L., Ryan, P.G., 2014. Changes in
916 prey availability impact the foraging behaviour and fitness of Cape gannets over a decade.
917 *Mar. Ecol. Prog. Ser.* 505, 281–293. <https://doi.org/10.3354/meps10762>

918 Costa, D.P., 2008. A conceptual model of the variation in parental attendance in response to
919 environmental fluctuation: foraging energetics of lactating sea lions and fur seals. *Aquat.*
920 *Conserv. Mar. Freshw. Ecosyst.* 17, S44–S52. <https://doi.org/10.1002/aqc>

921 Costa, D.P., 1993. The relationship between reproductive and foraging energetics and the
922 evolution of the Pinnipedia. *Symp. Zool. Soc. London* 66, 293–314.

923 Costa, D.P., Croxall, J.P., Duck, C.D., 1989. Foraging energetics of Antarctic fur seals in relation
924 to changes in prey availability. *Ecology* 70, 596–606.

925 Costa, D.P., Gentry, R.L., 1986. Reproductive energetics of northern fur seals, in: Gentry, R.L.,

926 Kooyman, G.L. (Eds.), *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton
927 University Press, Princeton, New Jersey, USA, pp. 79–101.

928 Costa, D.P., Trillmich, F., 1988. Mass changes and metabolism during the perinatal fast: a
929 comparison between Antarctic (*Arctocephalus gazella*) and Galapagos fur seals
930 (*Arctocephalus galapagoensis*). *Physiol. Zool.* 61, 160–169.

931 Cuddington, K., Fortin, M.J., Gerber, L.R., Hastings, A., Liebhold, A., O’connor, M., Ray, C.,
932 2013. Process-based models are required to manage ecological systems in a changing world.
933 *Ecosphere* 4, 1–12. <https://doi.org/10.1890/ES12-00178.1>

934 Davoren, G.K., 2013. Distribution of marine predator hotspots explained by persistent areas of
935 prey. *Mar. Biol.* 160, 3043–3058. <https://doi.org/10.1007/s00227-013-2294-5>

936 Doidge, D.W., Croxall, J.P., 1989. Factors affecting weaning weight in Antarctic fur seals
937 *Arctocephalus gazella* at South Georgia. *Polar Biol.* 9, 155–160.
938 <https://doi.org/10.1007/BF00297170>

939 Donohue, M.J., Costa, D.P., Goebel, E., Antonelis, G.A., Baker, J.D., 2002. Milk intake and
940 energy expenditure of free-ranging northern fur seal, *Callorhinus ursinus*, pups. *Physiol.*
941 *Biochem. Zool.* 75, 3–18. <https://doi.org/10.1086/338284>

942 Eisner, L.B., Zuenko, Y.I., Basyuk, E.O., Britt, L.L., Duffy-Anderson, J.T., Kotwicki, S., Ladd,
943 C., Cheng, W., 2020. Environmental impacts on walleye pollock (*Gadus chalcogrammus*)
944 distribution across the Bering Sea shelf. *Deep. Res. Part II Top. Stud. Oceanogr.* 181–182,
945 104881. <https://doi.org/10.1016/j.dsr2.2020.104881>

946 Elith, J., Leathwick, J.R., 2009. Species distribution models: Ecological explanation and
947 prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677–697.
948 <https://doi.org/10.1146/annurev.ecolsys.110308.120159>

949 Elliott, K.H., Woo, K.J., Gaston, A.J., Benvenuti, S., Dall'Antonia, L., Davoren, G.K., 2009.
950 Central-place foraging in an Arctic seabird provides evidence for Storer-Ashmole's Halo.
951 Auk 126, 613–625. <https://doi.org/10.1525/auk.2009.08245>

952 Fauchald, P., Erikstad, K., Skarsfjord, H., 2000. Scale-dependent predator – prey interactions:
953 the hierarchical spatial distribution of seabirds and prey. Ecology 81, 773–783.

954 Fiechter, J., Huckstadt, L.A., Rose, K.A., Costa, D.P., 2016. A fully coupled ecosystem model to
955 predict the foraging ecology of apex predators in the California Current. Mar. Ecol. Prog.
956 Ser. 556, 273–285. <https://doi.org/10.3354/meps11849>

957 Gentry, R.L., 1998. Behavior and ecology of the northern fur seal. Princeton University Press,
958 Princeton, New Jersey, USA.

959 Georges, J.Y., Groscolas, R., Guinet, C., Robin, J.P., 2001. Milking strategy in subantarctic fur
960 seals *Arctocephalus tropicalis* breeding on Amsterdam Island: evidence from changes in
961 milk composition. Physiol. Biochem. Zool. 74, 548–559. <https://doi.org/10.1086/322164>

962 Georges, J.Y., Guinet, C., 2000. Maternal care in the subantarctic fur seals on Amsterdam Island.
963 Ecology 81, 295–308. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2000)081[0295:MCITSF]2.0.CO;2)
964 [9658\(2000\)081\[0295:MCITSF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0295:MCITSF]2.0.CO;2)

965 Gladics, A.J., Suryan, R.M., Parrish, J.K., Horton, C.A., Daly, E.A., Peterson, W.T., 2015.
966 Environmental drivers and reproductive consequences of variation in the diet of a marine
967 predator. J. Mar. Syst. 146, 72–81. <https://doi.org/10.1016/j.jmarsys.2014.06.015>

968 Goebel, M.E., 2002. Northern fur seal lactation, attendance and reproductive success in two
969 years of contrasting oceanography. University of California Santa Cruz.

970 Gomez, M.D., Rosen, D.A.S., Trites, A.W., 2016. Net energy gained by northern fur seals
971 (*Callorhinus ursinus*) is impacted more by diet quality than by diet diversity. Can. J. Zool.

972 94, 123–135. <https://doi.org/10.1139/cjz-2015-0143>

973 Griffen, B.D., 2018. Reproductive skipping as an optimal life history strategy in the southern
974 elephant seal, *Mirounga leonina*. *Ecol. Evol.* 8, 9158–9170.
975 <https://doi.org/10.1002/ece3.4408>

976 Higgins, L. V., Gass, L., 1993. Birth to weaning: Parturition, duration of lactation, and
977 attendance cycles of Australian sea lions (*Neophoca cinerea*). *Can. J. Zool.* 71, 2047–2055.
978 <https://doi.org/10.1139/z93-290>

979 Higginson, A.D., McNamara, J.M., Houston, A.I., 2016. Fatness and fitness: Exposing the logic
980 of evolutionary explanations for obesity. *Proc. R. Soc. B Biol. Sci.* 283.
981 <https://doi.org/10.1098/rspb.2015.2443>

982 Hilborn, R., Mangel, M., 1997. The ecological detective: confronting models with data.
983 Princeton University Press.

984 Holsman, K.K., Haynie, A.C., Hollowed, A.B., Reum, J.C.P., Aydin, K., Hermann, A.J., Cheng,
985 W., Faig, A., Ianelli, J.N., Kearney, K.A., Punt, A.E., 2020. Ecosystem-based fisheries
986 management forestalls climate-driven collapse. *Nat. Commun.* 11.
987 <https://doi.org/10.1038/s41467-020-18300-3>

988 Houston, A., Clark, C., McNamara, J., Mangel, M., 1988. Dynamic models in behavioural and
989 evolutionary ecology. *Nature* 332, 29–34. <https://doi.org/10.1038/332029a0>

990 Houston, A.I., Stephens, P.A., Boyd, I.L., Harding, K.C., McNamara, J.M., 2006. Capital or
991 income breeding? A theoretical model of female reproductive strategies. *Behav. Ecol.* 18,
992 241–250. <https://doi.org/10.1093/beheco/arl080>

993 Jeglinski, J.W.E., Werner, C., Robinson, P.W., Costa, D.P., Trillmich, F., 2012. Age, body mass
994 and environmental variation shape the foraging ontogeny of Galapagos sea lions. *Mar. Ecol.*

995 Prog. Ser. 453, 279–296. <https://doi.org/10.3354/meps09649>

996 Jonsen, I.D., Basson, M., Bestley, S., Bravington, M. V., Patterson, T.A., Pedersen, M.W.,
997 Thomson, R., Thygesen, U.H., Wotherspoon, S.J., 2013. State-space models for bio-
998 loggers: A methodological road map. Deep. Res. Part II Top. Stud. Oceanogr. 88–89, 34–
999 46. <https://doi.org/10.1016/j.dsr2.2012.07.008>

1000 Kuhn, C.E., Baker, J.D., Towell, R.G., Ream, R.R., 2014a. Evidence of localized resource
1001 depletion following a natural colonization event by a large marine predator. J. Anim. Ecol.
1002 83, 1169–1177. <https://doi.org/10.1111/1365-2656.12202>

1003 Kuhn, C.E., Ream, R.R., Sterling, J.T., Thomason, J.R., Towell, R.G., 2014b. Spatial segregation
1004 and the influence of habitat on the foraging behavior of northern fur seals (*Callorhinus*
1005 *ursinus*). Can. J. Zool. 92, 861–873. <https://doi.org/10.1139/cjz-2014-0087>

1006 Lander, R.H., 1981. A life table and biomass estimate for Alaskan fur seals. Fish. Res. 1, 55–70.
1007 [https://doi.org/10.1016/0165-7836\(81\)90007-2](https://doi.org/10.1016/0165-7836(81)90007-2)

1008 Lander, R.H., 1979. Role of land and ocean mortality in yield of male Alaskan fur seal,
1009 *Callorhinus ursinus*. Fish. Bull. 77, 311–314.

1010 Le Bot, T., Lescroël, A., Fort, J., Péron, C., Gimenez, O., Provost, P., Grémillet, D., 2019.
1011 Fishery discards do not compensate natural prey shortage in Northern gannets from the
1012 English Channel. Biol. Conserv. 236, 375–384.
1013 <https://doi.org/10.1016/j.biocon.2019.05.040>

1014 Lunn, N.J., 1992. Fostering behaviour and milk stealing in Antarctic fur seals. Can. J. Zool. 70,
1015 837–839. <https://doi.org/10.1139/z92-119>

1016 Lunn, N.J., Boyd, I.L., Barton, T., Croxall, J.P., 1993. Factors affecting the growth rate and mass
1017 at weaning of Antarctic fur seals at Bird Island, South Georgia. J. Mammal. 74, 908–919.

1018 Macy, S.K., 1982. Mother-pup interactions in the northern fur seal. University of Washington.

1019 Mangel, M., 2015. Stochastic Dynamic Programming illuminates the link between environment,
1020 physiology, and evolution. *Bull. Math. Biol.* 77, 857–877. <https://doi.org/10.1007/s11538->
1021 014-9973-3

1022 Mangel, M., Clark, 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton University Press,
1023 Princeton, NJ.

1024 Maniscalco, J.M., 2014. The effects of birth weight and maternal care on survival of juvenile
1025 Steller sea lions (*Eumetopias jubatus*). *PLoS One* 9, e96328.
1026 <https://doi.org/10.1371/journal.pone.0096328>

1027 Martin, J., O’Connell, A.F., Kendall, W.L., Runge, M.C., Simons, T.R., Waldstein, A.H.,
1028 Schulte, S.A., Converse, S.J., Smith, G.W., Pinion, T., Rikard, M., Zipkin, E.F., 2010.
1029 Optimal control of native predators. *Biol. Conserv.* 143, 1751–1758.
1030 <https://doi.org/10.1016/j.biocon.2010.04.023>

1031 McCarthy, M.A., Possingham, H.P., Gill, A.M., 2001. Using stochastic dynamic programming to
1032 determine optimal fire management for *Banksia ornata*. *J. Appl. Ecol.* 38, 585–592.
1033 <https://doi.org/10.1046/j.1365-2664.2001.00617.x>

1034 McClintock, B.T., Michelot, T., 2018. momentuHMM: R package for generalized hidden
1035 Markov models of animal movement. *Methods Ecol. Evol.* 9, 1518–1530.
1036 <https://doi.org/10.1111/2041-210X.12995>

1037 McDonald, B.I., Goebel, M.E., Crocker, D.E., Costa, D.P., 2012. Biological and environmental
1038 drivers of energy allocation in a dependent mammal, the Antarctic fur seal pup. *Physiol.*
1039 *Biochem. Zool.* 85, 134–47. <https://doi.org/10.1086/664948>

1040 McHuron, E.A., Luxa, K., Pelland, N.A., Holsman, K., Ream, R., Zeppelin, T., Sterling, J.T.,

1041 2020. Practical application of a bioenergetic model to inform management of a declining fur
1042 seal population and their commercially important prey. *Front. Mar. Sci.* 7, 597973.
1043 <https://doi.org/10.3389/fmars.2020.597973>

1044 McHuron, E.A., Schwarz, L.K., Costa, D.P., Mangel, M., 2018. A state-dependent model for
1045 assessing the population consequences of disturbance on income-breeding mammals. *Ecol.*
1046 *Modell.* 385, 133–144. <https://doi.org/10.1016/j.ecolmodel.2018.07.016>

1047 McHuron, E.A., Sterling, J.T., Costa, D.P., Goebel, M.E., 2019. Factors affecting energy
1048 expenditure in a declining fur seal population. *Conserv. Physiol.* 7, coz103.
1049 <https://doi.org/10.1093/conphys/coz103>

1050 Merrill, G., Testa, J., Burns, J., 2021. Maternal foraging trip duration as a population-level index
1051 of foraging and reproductive success for the northern fur seal. *Mar. Ecol. Prog. Ser.* 666,
1052 217–229. <https://doi.org/10.3354/meps13694>

1053 Meyer-Gutbrod, E.L., Greene, C.H., Sullivan, P.J., Pershing, A.J., 2015. Climate-associated
1054 changes in prey availability drive reproductive dynamics of the North Atlantic right whale
1055 population. *Mar. Ecol. Prog. Ser.* 535, 243–258. <https://doi.org/10.3354/meps11372>

1056 Michelot, T., Langrock, R., Bestley, S., Jonsen, I.D., Photopoulou, T., Patterson, T.A., 2017.
1057 Estimation and simulation of foraging trips in land-based marine predators. *Ecology* 98,
1058 1932–1944. <https://doi.org/10.1002/ecy.1880>

1059 Milner-Gulland, E.J., 1997. A stochastic dynamic programming model for the management of
1060 the saiga antelope. *Ecol. Appl.* 7, 130–142. [https://doi.org/10.1890/1051-](https://doi.org/10.1890/1051-0761(1997)007[0130:ASDPMF]2.0.CO;2)
1061 [0761\(1997\)007\[0130:ASDPMF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1997)007[0130:ASDPMF]2.0.CO;2)

1062 Muhling, B.A., Brodie, S., Smith, J.A., Tommasi, D., Gaitan, C.F., Hazen, E.L., Jacox, M.G.,
1063 Auth, T.D., Brodeur, R.D., 2020. Predictability of Species Distributions Deteriorates Under

1064 Novel Environmental Conditions in the California Current System. *Front. Mar. Sci.* 7, 1–22.
1065 <https://doi.org/10.3389/fmars.2020.00589>

1066 Murray, C.C., Hannah, L.C., Doniol-Valcroze, T., Wright, B.M., Stredulinsky, E.H., Nelson,
1067 J.C., Locke, A., Lacy, R.C., 2021. A cumulative effects model for population trajectories of
1068 resident killer whales in the Northeast Pacific. *Biol. Conserv.* 257, 109124.
1069 <https://doi.org/10.1016/j.biocon.2021.109124>

1070 Muto, M.M., Helker, V.T., Delean, B.J., Young, N.C., Freed, J.C., Angliss, R.P., Friday, N.A.,
1071 Boveng, P.L., Breiwick, J.M., Brost, B.M., Cameron, M.F., Clapham, P.J., Crance, J.L.,
1072 Dahle, S.P., Dahlheim, M.E., Fadely, B.S., Ferguson, M.C., Fritz, L.W., Goetz, K.T.,
1073 Hobbs, R.C., Ivanshchenko, Y. V., Kennedy, A.S., London, J.M., Mizroch, S.A., Ream,
1074 R.R., Richmond, E.L., Shelden, K.E.W., Sweeney, K.L., Towell, R.G., Wade, P.R., Waite,
1075 J.M., Zerbini, A.N., 2022. Alaska marine mammal stock assessments, 2021. U.S. Dep.
1076 Commer., NOAA Tech. Memo. NMFS-AFSC-441, 295 p.

1077 Noren, D.P., Mangel, M., 2004. Energy reserve allocation in fasting northern elephant seal pups:
1078 inter-relationships between body condition and fasting duration. *Funct. Ecol.* 18, 233–242.
1079 <https://doi.org/10.1111/j.0269-8463.2004.00840.x>

1080 Noren, D.P., Rea, L.D., Loughlin, T.R., 2009. A model to predict fasting capacities and
1081 utilization of body energy stores in weaned Steller sea lions (*Eumetopias jubatus*) during
1082 periods of reduced prey availability. *Can. J. Zool.* 87, 852–864. [https://doi.org/10.1139/Z09-](https://doi.org/10.1139/Z09-074)
1083 074

1084 Ochoa-Acuna, H., Francis, J.M., Oftedal, O.T., 1999. Influence of long intersuckling interval on
1085 composition of milk in the Juan Fernandez fur seal, *Arctocephalus philippii*. *J. Mammal.* 80,
1086 758–767. <https://doi.org/10.2307/1383245>

1087 Oftedal, O.T., Boness, D.J., Tedman, R.A., 1987. The behavior, physiology, and anatomy of
1088 lactation in the pinnipedia, in: Geneoways, H.H. (Ed.), Current Mammology. Springer US,
1089 pp. 175–245.

1090 Ono, K.A., Boness, D.J., Oftedal, O.T., 1987. The effect of a natural environmental disturbance
1091 on maternal investment and pup behavior in the California sea lion. *Behav. Ecol. Sociobiol.*
1092 21, 109–118.

1093 Ortiz, C.L., Le Boeuf, B.J., Costa, D.P., 1984. Milk intake of elephant seal pups: an index of
1094 parental investment. *Am. Nat.* 124, 416–422.

1095 Österblom, H., Olsson, O., Blenckner, T., Furness, R.W., 2008. Junk-food in marine ecosystems.
1096 *Oikos* 117, 967–977. <https://doi.org/10.1111/j.2008.0030-1299.16501.x>

1097 Palacios, D.M., Baumgartner, M.F., Laidre, K.L., Gregr, E.J., 2014. Beyond correlation:
1098 Integrating environmentally and behaviourally mediated processes in models of marine
1099 mammal distributions. *Endanger. Species Res.* 22, 191–203.
1100 <https://doi.org/10.3354/esr00558>

1101 Perez, M.A., Mooney, E.E., 1986. Increased food and energy consumption of lactating northern
1102 fur seals, *Callorhinus ursinus*. *Fish. Bull.* 84, 371–381.

1103 Pichegru, L., Ryan, P.G., Crawford, R.J.M., van der Lingen, C.D., Grémillet, D., 2010.
1104 Behavioural inertia places a top marine predator at risk from environmental change in the
1105 Benguela upwelling system. *Mar. Biol.* 157, 537–544. [https://doi.org/10.1007/s00227-009-](https://doi.org/10.1007/s00227-009-1339-2)
1106 1339-2

1107 Pirotta, E., Mangel, M., Costa, D.P., Mate, B.R., Goldbogen, J.A., Palacios, D.M., Hückstädt,
1108 L.A., McHuron, E., Schwarz, L.K., New, L.F., 2018. A dynamic state model of migratory
1109 behavior and physiology to assess the consequences of environmental variation and

1110 anthropogenic disturbance on marine vertebrates. *Am. Nat.* 191, E40–E56.

1111 Reimer, J.R., Mangel, M., Derocher, A.E., Lewis, M.A., 2019. Modeling optimal responses and
1112 fitness consequences in a changing Arctic. *Glob. Chang. Biol.* 25, 3450–3461.
1113 <https://doi.org/10.1111/gcb.14681>

1114 Ronconi, R.A., Burger, A.E., 2008. Limited foraging flexibility: Increased foraging effort by a
1115 marine predator does not buffer against scarce prey. *Mar. Ecol. Prog. Ser.* 366, 245–258.
1116 <https://doi.org/10.3354/meps07529>

1117 Rosen, D.A., Young, B.L., Trites, A.W., 2012. Rates of maximum food intake in young northern
1118 fur seals (*Callorhinus ursinus*) and the seasonal effects of food intake on body growth. *Can.*
1119 *J. Zool.* 90, 61–69. <https://doi.org/10.1139/Z11-112>

1120 Rosen, D.A.S., 2021. The effect of food restriction on growth rates in Steller sea lions,
1121 *Eumetopias jubatus*. *Mar. Mammal Sci.* 1–7. <https://doi.org/10.1111/mms.12813>

1122 Russell, D.J.F., McClintock, B.T., Matthiopoulos, J., Thompson, P.M., Thompson, D.,
1123 Hammond, P.S., Jones, E.L., Mackenzie, M.L., Moss, S., McConnell, B.J., 2015. Intrinsic
1124 and extrinsic drivers of activity budgets in sympatric grey and harbour seals. *Oikos* 124,
1125 1462–1472. <https://doi.org/10.1111/oik.01810>

1126 Salvadeo, C.J., Gómez-Gallardo, A., Nájera-Caballero, M., Urbán-Ramirez, J., Lluch-Belda, D.,
1127 2015. The effect of climate variability on gray whales (*Eschrichtius robustus*) within their
1128 wintering areas. *PLoS One* 10, e0134655. <https://doi.org/10.1371/journal.pone.0134655>

1129 Satterthwaite, W.H., Mangel, M., 2012. Behavioral models as a common framework to predict
1130 impacts of environmental change on seabirds and fur seals. *Deep Sea Res. Part II Top. Stud.*
1131 *Oceanogr.* 65–70, 304–315. <https://doi.org/10.1016/j.dsr2.2012.02.016>

1132 Scheffer, V.B., Wilke, F., 1953. Relative growth in the northern fur seal. *Growth* 17, 129–145.

- 1133 Schulz, T.M., Bowen, W.D., 2005. The evolution of lactation strategies in pinnipeds: A
1134 phylogenetic analysis. *Ecol. Monogr.* 75, 159–177. <https://doi.org/10.1890/04-0319>
- 1135 Schulz, T.M., Bowen, W.D., 2004. Pinniped lactation strategies: evaluation of data on maternal
1136 and offspring life history traits. *Mar. Mammal Sci.* 20, 86–114.
1137 <https://doi.org/10.1111/j.1748-7692.2004.tb01142.x>
- 1138 Sherley, R.B., Barham, B.J., Barham, P.J., Campbell, K.J., Crawford, R.J.M., Grigg, J., Horswill,
1139 C., McInnes, A., Morris, T.L., Pichegru, L., Steinfurth, A., Weller, F., Winker, H., Votier,
1140 S.C., 2018. Bayesian inference reveals positive but subtle effects of experimental fishery
1141 closures on marine predator demographics. *Proc. R. Soc. B Biol. Sci.* 285.
1142 <https://doi.org/10.1098/rspb.2017.2443>
- 1143 Soto, K.H., Trites, A.W., Arias-Schreiber, M., 2004. The effects of prey availability on pup
1144 mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *J.*
1145 *Zool.* 264, 419–428. <https://doi.org/10.1017/S0952836904005965>
- 1146 Springer, A.M., Ream, R., Iverson, S., 2008. Seasonal foraging strategies and consequences for
1147 northern fur seals at colonies with opposite population trends - Year 2. North Pacific
1148 Research Board Final Report Project 514.
- 1149 Stephens, P., Uk, D.A., Houston, A.I., Harding, K.C., Boyd, I.L., McNamara, J.M., 2014. Capital
1150 and income breeding: The role of food supply. *Ecology* 95, 882–896.
- 1151 Tinker, M.T., Mangel, M., Estes, J.A., 2009. Learning to be different: Acquired skills, social
1152 learning, frequency dependence, and environmental variation can cause behaviourally
1153 mediated foraging specializations. *Evol. Ecol. Res.* 11, 841–869.
1154 <https://doi.org/10.1.1.158.1420>
- 1155 Towell, R.G., Ream, R.R., York, A.E., 2006. Decline in northern fur seal (*Callorhinus ursinus*)

1156 pup production on the Pribilof Islands. *Mar. Mammal Sci.* 22, 486–491.
1157 <https://doi.org/10.1111/j.1748-7692.2006.00026.x>

1158 Trillmich, F., 1990. The behavioral ecology of maternal effort in fur seals and sea lions.
1159 *Behavior* 114, 3–20.

1160 Trillmich, F., 1986. Maternal investment and sex-allocation in the Galapagos fur seal,
1161 *Arctocephalus galapagoensis*. *Behav. Ecol. Sociobiol.* 19, 157–164.
1162 <https://doi.org/10.1007/BF00300855>

1163 Trillmich, F., Lechner, E., 1986. Milk of the Galapagos fur seal and sea lion, with a comparison
1164 of the milk of Eared seals (Otariidae). *J. Zool.* 209, 271–277.

1165 Trites, A.W., 2021. Behavioral insights into the decline and natural history of Steller sea lions,
1166 in: Campagna, C., Harcourt, R. (Eds.), *Ethology and Behavioral Ecology of Otariids and the*
1167 *Odobeniid*. Springer, pp. 489–519. https://doi.org/10.1007/978-3-030-59184-7_23

1168 Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., Watters, G.M., 2011.
1169 Variability in krill biomass links harvesting and climate warming to penguin population
1170 changes in Antarctica. *Proc. Natl. Acad. Sci.* 108, 7625–7628.
1171 <https://doi.org/10.1073/pnas.1016560108>

1172 Verrier, D., Groscolas, R., Guinet, C., Arnould, J.P.Y., 2009. Physiological response to extreme
1173 fasting in subantarctic fur seal (*Arctocephalus tropicalis*) pups: metabolic rates, energy
1174 reserve utilization, and water fluxes. *Am. J. Physiol. Integr. Comp. Physiol.* 297, R1582–
1175 R1592. <https://doi.org/10.1152/ajpregu.90857.2008>

1176 Verrier, D., Guinet, C., Authier, M., Tremblay, Y., Shaffer, S.A., Costa, D.P., Groscolas, R.,
1177 Arnould, J.P.Y., 2011. The ontogeny of diving abilities in subantarctic fur seal pups:
1178 developmental trade-off in response to extreme fasting? *Funct. Ecol.* 25, 818–828.

- 1179 Villegas-Amtmann, S., McDonald, B.I., Páez-Rosas, D., Aurióles-Gamboa, D., Costa, D.P.,
1180 2017. Adapted to change: low energy requirements in a low and unpredictable productivity
1181 environment, the case of the Galapagos sea lion. *Deep. Res. Part II* 140, 94–104.
1182 <https://doi.org/10.1016/j.dsr2.2016.05.015>
- 1183 Wanless, S., Harris, M.P., Redman, P., Speakman, J.R., 2005. Low energy values of fish as a
1184 probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog. Ser.*
1185 294, 1–8. <https://doi.org/10.3354/meps294001>
- 1186 Weber, S.B., Richardson, A.J., Brown, J., Bolton, M., Clark, B.L., Godley, B.J., Leat, E., Oppel,
1187 S., Shearer, L., Soetaert, K.E.R., Weber, N., Broderick, A.C., 2021. Direct evidence of a
1188 prey depletion “ halo ” surrounding a pelagic predator colony. *Proc. Natl. Acad. Sci.* 118,
1189 e2101325118. <https://doi.org/10.1073/pnas.2101325118>
- 1190 Wiedenmann, J., Cresswell, K.A., Goldbogen, J., Potvin, J., Mangel, M., 2011. Exploring the
1191 effects of reductions in krill biomass in the Southern Ocean on blue whales using a state-
1192 dependent foraging model. *Ecol. Modell.* 222, 3366–3379.
1193 <https://doi.org/10.1016/j.ecolmodel.2011.07.013>
- 1194 Wiersma, P., Muñoz-García, A., Walker, A., Williams, J.B., 2007. Tropical birds have a slow
1195 pace of life. *Proc. Natl. Acad. Sci. U. S. A.* 104, 9340–9345.
1196 <https://doi.org/10.1073/pnas.0702212104>
- 1197 Wilson, R.P., Scolaro, J.A., Grémillet, D., Kierspel, M.A.M., Laurenti, S., Upton, J., Gallelli, H.,
1198 Quintana, F., Frere, E., Müller, G., Straten, M.T., Zimmer, I., 2005. How do magellanic
1199 penguins cope with variability in their access to prey? *Ecol. Monogr.* 75, 379–401.
1200 <https://doi.org/10.1890/04-1238>
- 1201 Wolf, N., Mangel, M., 2008. Multiple hypothesis testing and the declining-population paradigm

1202 in Steller sea lions. *Ecol. Appl.* 18, 1932–1955.

1203 Yoshioka, H., Tanaka, T., Aranishi, F., Izumi, T., Fujihara, M., 2019. Stochastic optimal
1204 switching model for migrating population dynamics. *J. Biol. Dyn.* 13, 706–732.
1205 <https://doi.org/10.1080/17513758.2019.1685134>

1206 Zeppelin, T.K., Ream, R.R., 2006. Foraging habitats based on the diet of female northern fur
1207 seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska. *J. Zool.* 270, 565–576.
1208 <https://doi.org/10.1111/j.1469-7998.2006.00122.x>

1209