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Behavioral models as a common framework to predict impacts of environmental change on seabirds and fur seals

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ABSTRACT

In this paper, we lay out the theoretical framework for using modeling approaches from behavioral ecology (in particular, state-dependent and game theoretical models) to predict the behavioral responses of central place foragers to changes in their food environment. We develop individual-based models of the state-dependent behavior of individual central place foragers over the course of a breeding season and show how our approach provides a framework for the prediction of trip lengths, foraging location, food delivery, and reproductive success. We formulate a common framework of models for northern fur seals (*Callorhinus ursinus*), black-legged kittiwakes (*Rissa tridactyla*), and thick-billed murre (*Uria lomvia*), and provide worked examples parameterized to represent fur seals and murre. We then develop a game theoretic model at the colony-level for predicting the distribution of multiple individuals across space in the face of potential interference or facilitation, providing a worked example for kittiwakes. We demonstrate how these models can be used to predict near-term aspects of foraging behavior such as diet choice and trip destinations and durations at the individual and colony level. We show how (i) behavioral predictions can be translated into predictions of foraging success, (ii) foraging success can be scaled up to demographically relevant parameters such as survival and reproduction, and (iii) this approach can help predict impacts of environmental change on top-level predators.

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1. Introduction

1.1. Making ecosystem-based fishery management (EBFM) operational

Many scientists, policy-makers, and environmental activists have recommended ecosystem-based fisheries management (Belgrano and Fowler, 2011; Link, 2010), which aims to achieve better management of fisheries by considering larger ecosystem issues (Larkin, 1996; Link, 2002; Sissenwine and Murawski, 2004). There is also increasing emphasis on developing management strategies that are robust to climate change (Lindgren et al., 2010). Combining these two trends will require an improved ability to predict the community and ecosystem level

impacts of environmental change (Montoya and Raffaelli, 2010; Walther, 2010).

The BEST-BSIERP Bering Sea Project (Sigler and Harvey, 2009; Sigler et al., 2010) embodies this approach. Other papers in this issue (Bacheler et al., 2012; DeRobertis and Cokelet, 2012; Hollowed et al., 2012; Lomas et al., 2012; Smart et al., 2012; Stabeno et al., 2012; Wang et al., 2012; Zhang et al., 2012) describe various ways that physical and biological forcing may combine to cause changes in fish communities as a result of predicted environmental change for the Bering Sea. Changes in the fish community can be expected to affect fisheries and human communities and also top predators such as murre, kittiwakes, and fur seals that feed on fish and euphausiids in the Bering Sea (Hunt et al., 2008; Renner et al., 2012).

One approach to predicting the effects of a changing prey base on top predators would be to develop a bioenergetic model and explore the predicted physiological impacts of a change in consumption proportional to the expected changes in fish stocks (many examples of this approach can be found in the *Proceedings of the Fourth William R. and Lenore Mote International Symposium in Fisheries Ecology, Bulletin of Marine Science* 74(3), 2004).

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However such an approach may leave out important consequences of behavior and adaptive adjustments on the part of foragers (Flynn, 2005; Mangel and Switzer, 1998). A retrospective approach (e.g. Mueter and Litzow, 2008) examining statistical relationships between predator success and forage fish abundance may do a better job of describing a relationship that includes the consequences of adaptive behavior because the measured responses will reflect behavioral adjustments made by predators. Historical relationships between environment and demography might be used to project populations into the future (e.g. Barbraud et al., 2011). However, statistical approaches, while possibly well supported over the range of historical data, may not be trustworthy beyond data range of inputs (Bertheaux et al., 2006; Mangel et al., 2001; Molnár et al., 2010). Predictions (especially of relative rather than absolute changes) may provide a better basis for management than simply pleading ignorance, but must be interpreted with caution and in context.

A likely mechanism by which environmental change may affect top predators is via changes in their prey base (Hunt et al., 2002, 2008, 2011). Changes in the abundance of prey will of course have impacts, but changing spatial distributions and potential spatial mismatch (Araujo and Luoto, 2007) may have important effects as well, particularly for central place foragers such as seabirds or fur seals feeding chicks or pups. These animals are constrained by their need to make frequent return trips to their colonies to feed their offspring and thus are limited in their ability to track shifting prey. Potential responses include both diet switches (Sinclair et al., 2008) and changes in trip directions, distances, and duration (Jahncke et al., 2008; Schneider and Hunt, 1984).

We develop a suite of models within a common framework for predicting the foraging ecology of individual northern fur seals (*Callorhinus ursinus*) and thick-billed murrelets (*Uria lomvia*) and the distribution of multiple black-legged kittiwakes (*Rissa tridactyla*) foraging from a single central colony. Our goal is to develop a theoretical framework for predicting the foraging ecology of these species that can then be applied to current and future prey base specifications arising from present day empirical data (Hollowed et al., 2012; Ressler et al., 2012). In some cases, we are also able to predict impacts on reproductive success (c.f. Owen-Smith et al., 2010). Given sufficiently detailed specification of the prey base, model predictions can be validated against empirical observations of seabird (Renner et al., 2012) and fur seal (Call et al., 2008) foraging under present day conditions, and used to predict the impacts of changing prey base (Hollowed et al., 2009). We discuss model validation in greater detail in Section 4. Validation need not imply an ability of the model to reproduce every empirical observation, in fact a model complex enough to do so is likely also complex enough to defy analysis and add little to our understanding (Mangel and Clark, 1988, p. 280). Rather, the most useful models are those that can match broad-scale patterns identified as important by empiricists, and correctly predict at least the direction of responses to specific environmental changes (Clark and Mangel, 2000; Grimm and Railsback, 2005). As a starting point, we will consider very general predictions associated with shifting patterns of the abundance of forage fish as might be brought about by environmental change.

Such pattern oriented modeling (Grimm and Railsback, 2005) may also be informative in that alternate model formulations can be compared and allowed to compete in their ability to generate important patterns. For instance, models could be compared assuming various different assumptions about the importance of reproductive success (offspring survival) versus adult survival in driving foraging behavior, various processes of learning where food is, and varying degrees of knowledge about the distribution of food, ranging up to omniscience. Omniscience might seem unrealistic, but may serve as a useful proxy for unmodeled

processes such as social facilitation, memory from previous years (Sigler et al., 2012), information centers, and long distance visual or olfactory cuing (Nevitt et al., 2008). We might also model limited knowledge early in the breeding season versus better knowledge late in the season to incorporate effects of repeated learning and memory.

1.2. Possible approaches for predicting the behavior of top predators

1.2.1. Classic rate maximization for an individual

In the classical theory of diet choice (Emlen, 1966; MacArthur and Pianka, 1966; Mangel, 2006 for review), one begins by indexing prey species so that they are ranked in the order of single item profitability. We let E_i indicate the net energy (measured, for example, in kilocalories) obtained by consuming a single prey item and h_i the time (measured in an appropriate unit, e.g. seconds or minutes) required to consume it. We rank prey so that

$$\frac{E_1}{h_1} > \frac{E_2}{h_2} > \frac{E_3}{h_3} > \dots > \frac{E_l}{h_l} \quad (1)$$

where l is the maximum number of prey species. These may depend upon predator species, indexed by p , since different predators may require different amounts of time to handle the same prey item and may obtain different energy returns.

We then assume that prey species i is encountered at rate λ_i , measured as individuals per time, the value of which will depend upon predator species p and location k , but we suppress that notation for now. If the foraging period is sufficiently long that many encounters occur within it, then the rate of energy return for an individual predator when the first i' prey items are included in the diet (Mangel, 2006) is

$$R_{i'} = \frac{\sum_{i=1}^{i'} \lambda_i E_i}{1 + \sum_{i=1}^{i'} \lambda_i h_i E_i} \quad (2)$$

The energy maximizing diet is then found by maximizing $R_{i'}$ over i' . The classical theory of diet choice leads to the prediction of knife-edge preferences: an item is either included in the diet or it is not. This theory, however, does not treat interference, facilitation, or depletion. In addition, although theory based on rate maximization allows us to make clear predictions about behavior (its great advantage), it provides no idea of the fitness consequences of deviations from the optimal behavior, since there is no explicit connection between rate of energy intake and a measure of Darwinian fitness. Thus, rate maximizing models cannot inform demographic processes. Nor can such models account for trade-offs between starvation and predation mortality.

In addition, for central place foragers energetic return rates are affected by travel time to and from foraging patches and the relative duration of the foraging and traveling periods. If we assume a fixed duration to all foraging trips (perhaps constrained by required feeding intervals for young), the rate of return for foraging in a single patch can be easily modified to account for travel time. However, if foraging occurs in more than one patch, a more complicated model is required, as we describe below.

1.2.2. State-dependent models

Rate maximizing as described above was the paradigm for behavioral predictions in the 1970s and early 1980s. However, since its introduction into ecology and evolutionary biology about 25 years ago (Mangel and Clark, 1986; McNamara and Houston, 1986), state-dependent life history theory as implemented by stochastic dynamic programming (Clark and Mangel, 2000; Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999), has become recognized as a powerful way to analyze evolved systems; it is a tool allowing us to generate

quantitative predictions about stable outcomes of evolution. Natural and sexual selection act to optimize from available variants, which are products of previous optimization events. Thus, state-dependent life history theory is the link between physiology, ecology, and the outcomes of evolution. It provides the means to predict growth, maturation, and behavior as a function of physiological state and environmental conditions. The essence of the method is to work backwards in order to generate state-dependent decisions and then to predict forwards using these decisions and Monte Carlo simulation. In general, the approach requires the following components:

- A characterization of the physiological state (e.g. energy reserves of the organism).
- A characterization of the environment in which the organism is found.
- Characterization of and the dynamics of the state as a function of the state, environment, and actions or allocation processes.
- Connection of the state of the organism at a terminal time with a measure of Darwinian fitness.

In the case in which fitness can be accrued at any moment in time, a characterization of how increments of fitness and state are related is required as well. Given these features, stochastic dynamic programming allows one to compute the fitness-maximizing actions or allocations as a function of the current physiological state and time. At the same time, it provides outputs such as offspring and adult survival that can be used to predict demography.

1.2.3. Game theoretical models

The methods of state-dependent life history theory allow us to incorporate two important features (physiological state and predation) that increase the fidelity of the behavioral models to nature. However, they do not account for the impacts of behaviors of other individuals on a focal individual. Game theoretic models allow this to be done (Maynard Smith and Price, 1973; Maynard Smith, 1982; von Neumann and Morgenstern, 1944). The general treatment of most behavioral games relies on the concept of an Evolutionarily Stable Strategy (ESS).

Maynard Smith (1982) characterized the ESS as follows. Imagine a focal individual is playing against a large number of other individuals and let $W(I,J)$ denote the fitness of a single I -strategist against the rest of the individuals who are J -strategists (an example of such strategies is described below). A sufficient condition for J to be an ESS is that $W(I,J) < W(J,J)$ if $I \neq J$. If there is some strategy K (not equal to J) for which $W(K,J) = W(J,J)$ then an additional condition is required, which asserts that $W(K,J) < W(J,J)$ when the population contains a small proportion of K -strategists (that is, a single K -strategist can do as well as the J 's, but a few cannot so that the K -strategy cannot spread in a population). The ESS is also a Nash equilibrium (Watson, 2002).

In essence, the ESS is the unbeatable strategy that maximizes fitness. Determining ESSs can be a difficult and complicated task and state-dependent behavioral games particularly difficult (e.g. Alonzo et al., 2003). In Section 2.2, we show how this can be done for a colony-level model of kittiwakes, using rate of energy return as the metric for fitness.

1.3. The patch concept

A crucial element of our model formulation is the concept of a foraging patch. We conceive as a patch as a flexibly defined area of space within which prey abundance can be meaningfully described with one set of parameters that distinguishes it from

an adjacent patch described by different values for the same set of parameters. Patch size will depend upon the species being modeled and the resolution of prey data available. When prey data allow, for birds that fly between feeding sites but land on the water surface and dive repeatedly (e.g. murre), patch size might be chosen based on typical minimum flight lengths. For animals that potentially forage more or less continuously as they travel (e.g. fur seals and kittiwakes), patches might be defined in terms of typical travel distances in a given time step, with modeled food consumption potentially adjusted to average over different patches passed through in a single time step. Patches might also be defined based on the distance over which individual predators can meaningfully interact (e.g. interfere and/or facilitate). Patches might be distributed two-dimensionally (with depth adding a third dimension), or if animals from a single colony are assumed to travel in similar directions repeatedly (e.g. Call et al., 2008), a one-dimensional approach may suffice, or space may be treated implicitly by describing a matrix of distances between every pair of patches without an explicit map.

2. Methods

2.1. Individual models

2.1.1. Fur Seals

Fur seals are central place foragers who feed their young via milk during periodic haul outs between extensive feeding trips that may last days and consist of multiple dives (Goebel et al., 1991). We assume that the expected lifetime fitness F of a mother fur seal at the end of the breeding season depends on her future reproductive output, which is predicted by her state (g) at the end of one breeding season, and the expected survival of her newly weaned pup, which we assume depends on its nutritional state (p , cf. Baker and Fowler, 1992; Calambokidis and Gentry, 1985). In general we also track a state variable denoting distance from colony, x . Thus we define

$$F(p,g,x,t) = \text{Maximum Expected \{Current + Future Reproductive Success given that at time } t \text{ the mother is distance } x \text{ from the colony, the current reserves of the pup are } p \text{ and of the mother are } g \}$$
 (3)

The method works backwards in time, because at the final time T we assume to be known the condition-dependent expected survival of weaned pups, denoted by $f_1(p)$, and how the remaining reproductive value of an adult seal, $f_2(g)$, depends on its condition at the end of the current breeding season. Thus, if $x=0$ corresponds to the mother being at the colony

$$F(p,g,0,T) = f_1(p) + f_2(g)$$
 (4)

For previous times, we proceed as follows. Imagine that a mother arrives at the colony ready to provide food when her state is g and the state of the pup is p .

If she transfers a volume of food (milk for a fur seal) v to the offspring and $m \leq 1.0$ is the efficiency of transfer, then at the start of the next period her state is $g-v$ and the state of the offspring is $p+mv$ and her new position is $x=1$. Thus, for times $t < T$ we have

$$F(p,g,0,t) = \max_v [F(p+mv, g-v, 1, t+1)]$$
 (5)

When seals are away from the colony, at each time step they must allocate effort between travel and foraging. We denote effort expended on foraging as e , constrained such that $e=0$ means all effort is expended in traveling and none on foraging while $e=1$ means all effort is expended on foraging and none on traveling. In addition, foraging seals allocate effort between shallow and deep

dives, with $w=0$ denoting entirely shallow dives, $w=1$ entirely deep dives, and intermediate w the proportion of foraging time spent on deep dives. Each time step the seal also picks a direction to travel ($d=+1$ meaning travel away from the colony, $d=-1$ meaning travel back toward the colony) at speed s . We let $y(x,d,t)$ denote the density of food at a distance x and depth z (0 =shallow, 1 =deep) from the colony at time t . Thus, in a single period when the forager is at distance x and expends effort e the food intake is

$$Y(x,e,w,t) = e \int_x^{x+d(1-e)s} ((1-w)y(x',0,t) + wy(x',1,t)) dx' \quad (6)$$

We assume that the food consumed within a single time period scales as e times the maximum possible consumption. If $p_c(t)$ is the rate at which the pup burns reserves (and may increase with t as the pup grows) and a_c is the rate at which the parent burns reserves, we have

$$F(p,g,x,t) = \max_{d,e} \left\{ F(p-p_c(t),g-a_c + eY(x,e,w,t), \frac{x+d(1-e)}{s}, t+1) \right\} \quad (7)$$

We can constrain the right-hand side of Eq. (7) by critical thresholds p_{crit} such that a pup dies if its reserves drop too low ($p < p_{crit}$ leads to an absorbing state of $p=0$, with no updating of p possible) and g_{crit} such that an adult must be in a minimum sufficient state to provide milk ($v=0$ for $g < g_{crit}$). We neglect survival of the adult on the assumption that predation on adults is minimal in this system during the breeding season; however, this could be readily incorporated by multiplying the expected fitness of foraging by the probability of surviving for one time step.

After identifying the decisions d , w , and e that maximize expected fitness for any combination of state variables x (location), p (pup nutritional state), and g (adult nutritional state), we predict foraging behaviors by specifying starting conditions (nutritional states) at the start of a foraging trip and using forward iteration (Mangel and Clark, 1988) along with the optimal decision rules identified previously to simulate individual foraging trips. If we treat food intake in the forward iteration as a stochastic process with expectation given by $y(x,t)$, repeated simulations will give a distribution of expected trip distances, trip durations, and food intake. In addition, we can examine predicted trip records for patterns in foraging effort—e.g. do we predict seals foraging all along their trip or do we predict rapid travel to a preferred feeding ground, concentrated feeding, and a prompt return. The simulations can be continued over the course of a breeding season (including the milk provisioning decisions when at the colony) to yield a distribution of expected pup state and thus reproductive success.

2.1.2. From fur seals to kittiwakes

The fur seal model can be adapted for individual kittiwakes with minimal modifications since kittiwakes are central place foragers who surface-feed, and provide food to their young via regurgitation (Kitaysky et al., 2000). They likely can observe their accessible prey field, the first 30 cm of the water column, continuously while aloft. Thus they can be modeled using the same framework as fur seals, dropping the depth component and substituting regurgitated food for milk.

2.1.3. Murres

Murres are also central place foragers, but unlike kittiwakes they are divers and feed their young single prey items (Kitaysky et al., 2000). Single-item provisioners require an alternate model formulation. We assume that murres must land before feeding, thus each time step can be spent traveling or foraging but not both. A bird choosing to travel spends time and burns reserves in

proportion to the distance traveled. A bird choosing to forage may encounter a prey item that time step in which case it may consume that prey item (increasing its nutritional state), bring that prey item back to the nest (increasing the chick's nutritional state, after making the return trip), or ignore that prey item and continuing to forage. We model time t with a short time step such that a bird will encounter at most one prey item between time t and time $t+1$.

To begin, we let $S(g)$ denote the overwinter survival rate of parents when their nutritional state at the end of the season is g , R denote the parent's expected remaining lifetime production of offspring conditioned on survival to the next year, and $s(p)$ denote the probability that a chick with terminal state p successfully fledges and recruits to the population.

We denote time- and space-dependent encounter rates with different prey species i with $\lambda_i(x,t)$ with each prey item providing energetic reward e_i . We can model λ_i as known, or birds can learn about it on the basis of foraging success in a patch, with birds tracking how many time they encountered species i (σ_i) out of total time steps spent foraging (α) in the current patch. In the learning scenario, for all values of i we use Bayesian updating to track the probability $r'_{ij}(\alpha, \sigma_i)$ that λ_i takes on a particular value λ_j over a set of j 's indexing the plausible range of λ_i . The set of all r_{ij} provides a prior probability distribution on the value of λ_i (Clark and Mangel, 2000). Assuming encounters with food are a binomial process, r_{ij} is updated to $r'_{ij}(\alpha, \sigma_i)$ after σ_i encounters with species i in α attempts as

$$r'_{ij}(\alpha, \sigma_i) = \frac{\lambda_j^{\sigma_i} (1-\lambda_j)^{\alpha-\sigma_i} r_{ij}}{\sum_k \lambda_k^{\sigma_i} (1-\lambda_k)^{\alpha-\sigma_i} r_{ik}} \quad (8)$$

Then the posterior average for λ_i is

$$\bar{\lambda}_i(\alpha, \sigma_i, x, t) = \sum_j r'_{ij}(\alpha, \sigma_i) \lambda_j \quad (9)$$

We define fitness similarly to Eq. (3), and denote it by $F(p,g,r,x,t)$.

The end condition Eq. (4) now becomes

$$F(p,g,r,0,T) = S(p)R + s(g) \quad (10)$$

for all values of r , the foraging success of the parent in its most recent patch.

When a parent is not at the colony, the behavioral choice is to remain at the current location or move to a new location. Thus we have

$$F(p,g,r,x,t) = \max\{V_{stay}(p,g,r,x,t), V_{move}(p,g,r,x,t)\} \quad (11)$$

where $V_{stay}(p,g,r,x,t)$ is the fitness value of staying at the current location when the states are defined as above and $V_{move}(p,g,r,x,t)$ is the fitness value of moving. If the speed of travel is s , so that the travel time to a new point is $|x-x'|/s$, the fitness values of moving to a new patch is

$$V_{move}(p,g,r,x,t) = \max_{x'} \left\{ F \left(p-p_c \frac{|x-x'|}{s}, g-a_c \frac{|x-x'|}{s}, r_0, t + \frac{|x-x'|}{s} \right) \right\} \quad (12)$$

With r resetting to r_0 (which might itself be informed by surface cues or a longer term expectation of where foraging is profitable) in the new patch where the bird has no recent knowledge.

For foraging within a patch, we track acceptance of prey type i as a function of state and location, $b(i,p,g,r,x,t)$, with $b=0$ corresponding to rejecting a prey item, $b=1$ corresponding to consuming it, and $b=2$ corresponding to returning to the nest to provision it to the chick. Then for a bird currently foraging at location x , to compute the fitness value of staying, we let $I_{q=z}$ denote the indicator function that is 1 if $q=z$ and 0 otherwise, and

$s'(i)$ = the vector with s_i updated to $s_i + 1$ for just the species i encountered. Then the fitness value of staying is

$$V_{stay}(p, g, s, a, x, t) = \left(1 - \sum_i \bar{\lambda}_i(a, s_i, x, t)\right) F(p - p_c, g - a_c + y(x, r, t), s, a + 1, t + 1) + \sum_i \lambda_i(r_i, x, t) \max\{F(p - p_c, g - a_c, s'(i), a + 1, t + 1)I_{b=0} + F(p - p_c, g - a_c + e_i, s'(i), a + 1, t + 1)I_{b=1} + F(p - p_c + e_i, g - a_c + e_i, s'(i), a + 1, t + 1)I_{b=2}\} \quad (13)$$

We assume negligible handling times for immediate consumption of prey items, while handling time for provisioning is dominated by flying time to return to the nest. We assume that having fed its chick, the bird moves to $x = 1$ adjacent to the colony to start the next time step.

2.2. Colony model

The individual-based models of the previous section predict that all individuals will forage in the same location, because there is neither interference between foragers nor depletion of the prey base by foragers. In this section, we describe a model that emerges from classical rate maximizing approaches but allows us to take into account the behavior of many individuals, so that intraspecific and interspecific competition or facilitation can be included. Although the model is based on behavioral decisions taken in terms of rate maximization, the rates themselves involve time at sea and location as states. We now explain this idea with an illustrative example based on kittiwakes foraging.

2.2.1. Behavioral decisions

As with classical rate maximizing, we assume that there are no partial preferences so that a prey species is either always included in the diet or is always excluded. Doing so allows us to introduce a behavioral matrix $\mathbf{b}(p)$ describing the diet choice behavior of a predator. The columns of this matrix refer to prey species, the rows of the matrix refer to different diet strategies, and the entries of the matrix are either 0 (prey item excluded from the diet) or 1 (prey item included in the diet). For example, if there are three prey species, the behavioral matrix is

$$\mathbf{b} = \begin{pmatrix} 0 & 0 & 1 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \\ 1 & 1 & 1 \end{pmatrix} \quad (14)$$

The first three rows of the matrix correspond to the situation in which the predator specializes on prey type 3, 2, or 1 respectively. The next three rows the situation in which the predator includes prey types 2 and 3, 1 and 3, or 1 and 2 in its diet, and the last row corresponds to the predator completely generalizing. We use b_{ji} to denote an individual element of the behavioral matrix \mathbf{b} where j corresponds to the row (describing inclusion or not) of the behavioral matrix and i indexes prey type.

We assume that predators interfere with (or facilitate) each other through decreased (or increased) encounter rates rather than changes in handling time. For example, visual cuing onto birds plunging to feed repeatedly could result in facilitation by bringing birds to the most profitable feeding areas, or interference as too many birds cue in on the same spot. Thus we let $\lambda_{ik0}(t)$ denote the encounter rate with prey of type i in patch type k at time t if there were no other predators present. We let f_i measure

the effects of other predator individuals in the patch on the encounter rate with prey species i . When there are $N(k, t)$ kittiwakes in patch k at time t , the encounter rate of any individual in that patch is then

$$\lambda_{ik}(t) = \lambda_{ik0}(t) / [1 + f_i N(k, t)] \quad (15)$$

If the j th row of the matrix \mathbf{b} characterizes the behavior of the kittiwake, the generalization of Eq. (2) is

$$R_k(\mathbf{b}_j, t) = \frac{\sum_{i=1}^I \lambda_{ik}(t) E_i b_{ji}}{1 + \sum_{i=1}^I \lambda_{ik}(t) h_i E_i b_{ji}} \quad (16)$$

Our goal is to predict how a total of N_c birds at the colony will be distributed in space and time. Clearly, as soon as interference occurs, we recognize that the patch that is best when the first bird arrives will ultimately become inferior if we simply fill that one up with individuals.

The conceptual answer to this question (Clark and Mangel, 1984, 1986; Mangel, 1990) is that individuals will distribute themselves according to the ESS or Nash equilibrium (Watson, 2002) in which no single individual can do better for itself by moving. Although Nash equilibria are notoriously difficult to compute analytically for even the simplest problems, a situation like this allows numerical computation of the solution, which we describe in an algorithmic fashion.

We let subscript c denote the colony location and use k and l to denote locations of foraging patches. We let t denote calendar time within a season and τ the length of the current trip, which is constrained to be less than a maximum value τ_{max} , and which may depend upon time in the season. We let τ_{ck} denote the travel time between the colony and patch k , τ_{kl} denote the travel time between patches k and l , with the convention that $\tau_{kk} = 0$, and T denote the end of the chick rearing period. First, we specify the prey characteristics, the behavioral matrix \mathbf{b} , the interference vector $\{f_1, \dots, f_3\}$, the travel times and energetic cost of travel, and the encounter rates in the absence of predators $\{\lambda_{ik0}(t), i = 1, 2, 3; k = 1, \dots, K; t = 0, \dots, T\}$. We let $N_{tot}(k, t)$ denote the number of individuals on patch k at time t and let n and $l(n)$ index the individual kittiwakes (all assumed to be identical) and the location of individual n .

2.2.2. Nash equilibrium patching filling algorithm

We distribute individuals over space using a patch filling algorithm that is based on the concept of a Nash equilibrium. The algorithm is best described as a pseudo-code:

Step 1. Cycle from $t = 0$ to $t = T$. Cycle over k and set $N_{tot}(k, t) = 0$. Set the index counting individuals $n = 1$.

Step 2. For the n th individual, with current location $l(n)$ and current trip length $\tau(n)$ first determine whether it has to return home. That is, if $\tau(n) + \tau_{c, loc(n)} = \tau_{max}$, this individual must return home, at which point its location is reset to the colony and its trip time is reset to 0. We assume that feeding the offspring is very rapid relative to the other times.

Step 3. If the n th individual does not need to return home, then determine which of the possible patches it can visit. In general, this will be constrained as above by the maximum trip length. If the bird is currently at location $l(n)$, travels to patch k and forages for 1 time interval then the new trip length is $\tau(n) + \tau_{loc(n), k} + 1$ and we consider that a patch is potentially visited if this new trip length is less than $\tau_{max} - \tau_{ck}$. That is, a patch is only considered a possible foraging site if the individual can visit that patch and forage for at least 1 time increment before returning home. As the end of the chick rearing period is approached, a similar constraint applies to

patches that will take the individual beyond the chick rearing period.

Step 4. Cycle over all the patches that have potential for visitation. For each patch compute the maximum rate of gain and the behavior that produces this maximum rate of gain taking into account the cost of travel between patches. That is, if α is the energetic cost per unit travel we determine the combination of patch (k) and diet (b) choice that maximize $R_k(b_{j\bullet}, t) - \alpha \bullet \tau_{loc(n), k}$ to identify optimal patch choice k^* .

Step 5. Increase $N_{tot}(k^*, t)$ by 1, and increase n by 1. If $n < N_c$ then return to Step 2; otherwise the algorithm is complete.

2.3. Parameterization

Full parameterization of these models for empirically derived estimates of prey fields is a complicated task beyond the scope of this paper (also see Section 4). Thus, we illustrate the application of the models to simplified, hypothetical scenarios with parameters given in Appendix A. Our goal is to show qualitatively the types of predictions these models can generate, while quantitative predictions await the collection and processing of fine-scale prey abundance estimates or prey fields estimated by other models.

3. Results

3.1. Trip dynamics—fur seals

As an example of state-dependent behavior rules, in Fig. 1 we show the predicted direction of movement (Fig. 1A) and allocation of effort to foraging versus traveling (Fig. 1B) of a fur seal parent based on her and her pup's energy state (in this example the parent is at an intermediate distance from the rookery, there is some food available there but more food if she moves out further). Numerous hypotheses can be generated based on this graph. For example: if the pup is going to starve regardless of the parent's actions (far left of graph, i.e. low values on x -axis), we predict abandonment (rapid outward movement facilitated by low foraging effort). If the pup is full and the parent is hungry

(bottom right) we predict outward movement to where food abundance is highest and little to no foraging effort until the parent gets there. As pup state decreases, we predict a well fed parent will return to feed it (upper middle) while a hungry parent must first forage in place to raise its nutritional state high enough to provide milk upon return (lower middle).

3.2. Diet choice, reproductive success, and adaptive behavior—murres

Furthermore, having derived state-dependent rules for all possible states, we can simulate stochastic realizations of individual foraging trips that result from following these rules. As an example, we compared the predicted foraging trip duration, maximum distance, and rate of energy returned to the chick along with what prey type was brought (large fish, small fish, euphausiid, or the chick starved) for murres in a baseline environment and in one with poorer food availability based on either static (followed the old rules in the new environment) or adaptive (new rules developed for the new environment) behavior (Fig. 2). For this model we assumed $\lambda_i(x, t)$ was known to the forager.

In this example, murres consistently chose the same spot to forage (maximum distance showed little variation) but in the food rich environment they stayed in that spot until they found a large or medium fish (Fig. 2A, solid black or dark gray on pie chart), leading to variable trip duration. Following these rules in a food-poor environment (Fig. 2B), trip duration increased, and starvation (white) was more likely. Following adaptive rules for this new environment (Fig. 2C), small fish were more often accepted (light gray), leading to shorter trips and less risk of starvation, at the cost of reduced mean intake rate. By quantifying the probability of chick survival, we can quantify expected changes in demography.

3.3. The colony model

For the parameters given in Appendix A, in the absence of interference between foragers causing a decline of encounter

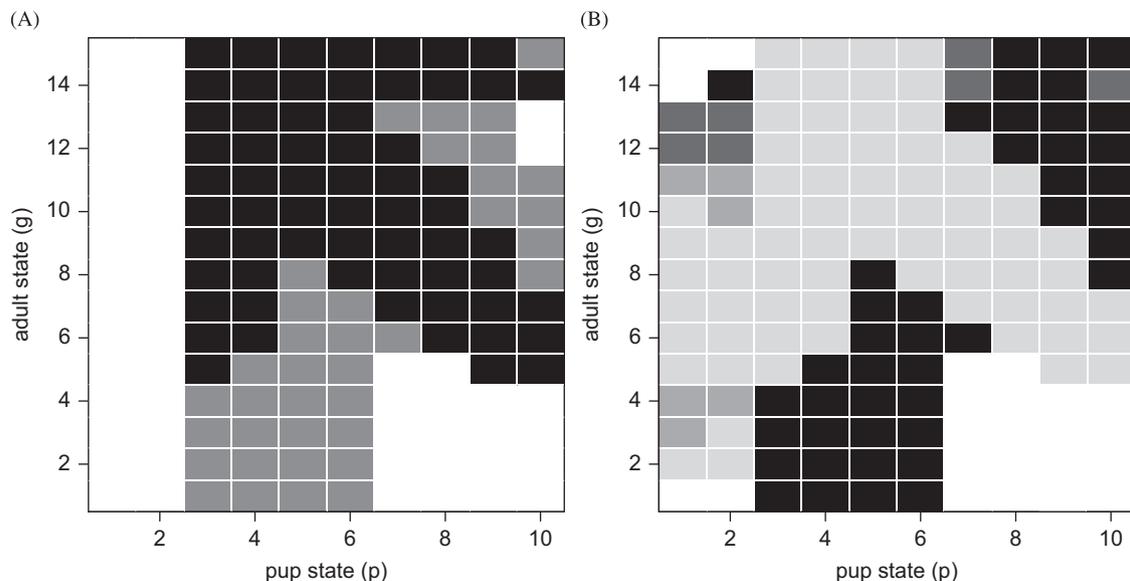


Fig. 1. Movement direction (A) and foraging effort (B) decisions predicted for a fur seal at an intermediate distance from the colony as a function of pup and adult nutritional states. In (A), white represents movement away from the colony, black represents movement back to the colony, and gray represents staying in place. In (B), darker shading indicates increased foraging effort (proportion of effort devoted to foraging rather than travel). (A) Movement direction, $x=5$, (B) foraging effort, $x=5$.

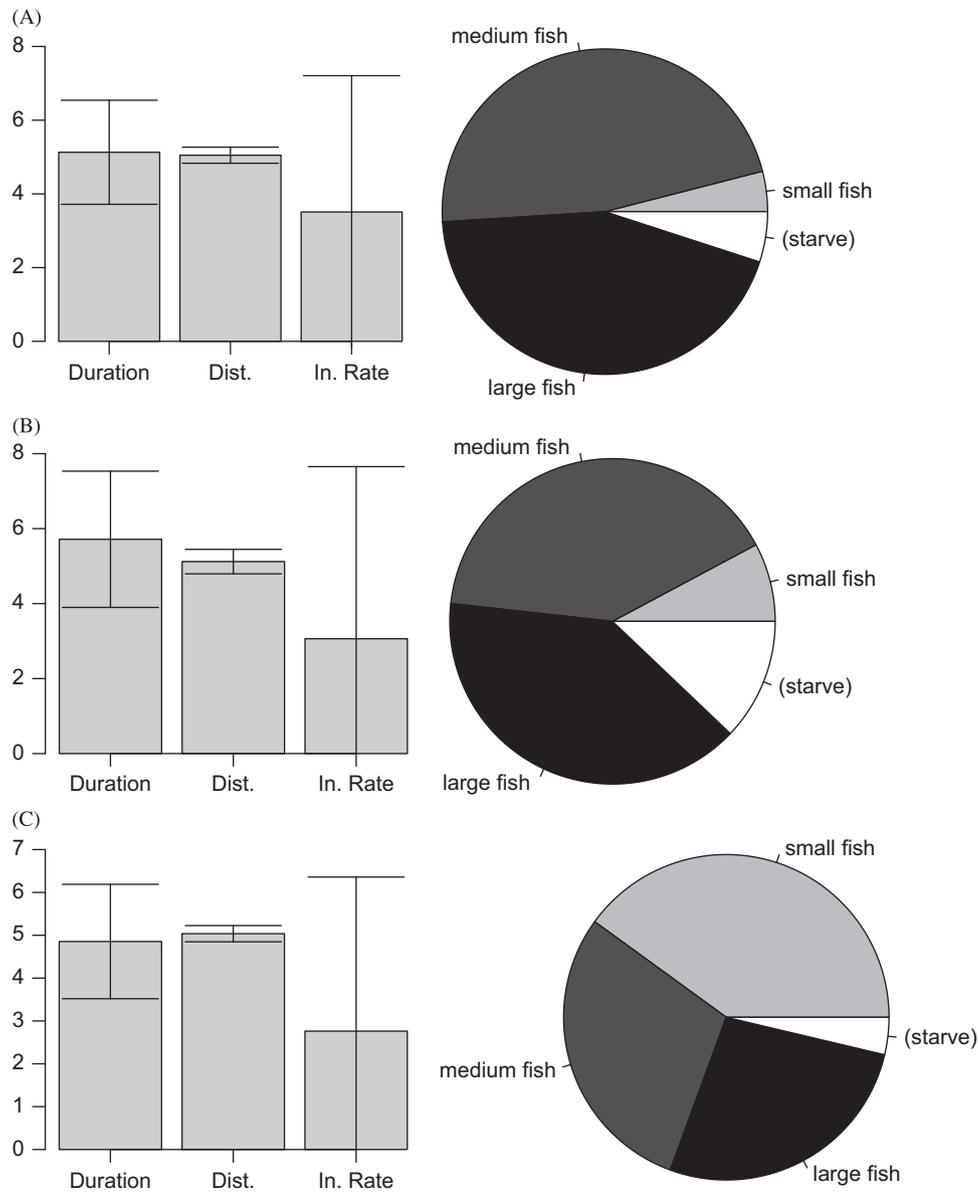


Fig. 2. Predicted trip duration, maximum distance, and energy intake (E/t) rate along with diet choice for the baseline environment (A), a reduced food environment with static behavior (B), and a reduced food environment with adaptive behavior (C).

Table 1

Optimal Strategy (row of the behavioral matrix \mathbf{b} , see Eq. (14) in text) and associated rate of energetic return for each patch in the absence of behavioral interactions.

Patch	Optimal strategy	Return rate
1	1	2.9566
2	1	2.9566
3	4	11.4534
4	4	11.4534
5	4	11.4534
6	5	40.7225
7	5	40.7225
8	3	33.6293
9	3	33.6293
10	3	33.6293

rates, we show the rate of return and optimal behavior in each patch in Table 1. These results also lead to testable hypotheses, conditioned on knowing how encounter rates with food vary

though space. For example, if kittiwakes are following rate maximizing without consideration of interference, then we predict individuals will only be found in patches 6 and 7, in equal numbers.

A second hypothesis (H2) can be generated from Table 1: we predict that the individuals from the colony will distribute themselves on average according to the energy return from the patch. Although this hypothesis may seem overly simplistic, we include it because it emphasizes the importance of the Nash equilibrium. The patch filling Nash equilibrium approach also generates a hypothesis concerning the distribution of birds in space and time. We show typical results in Fig. 3. Note that only patches 3–10 are occupied and for them the rate of energy return is essentially constant (it actually differs by about 0.4% between patches 5 and 6 and 7–10). These results suggest a number of testable hypotheses, such as: (a) birds will be distributed across patches, but need not occupy all patches (Fig. 3A); (b) at those patches that are occupied, individuals will have essentially the same rate of energy intake (Fig. 3B); (c) however, individuals may have different behaviors in different patches (Fig. 3C); or (d) although individuals will leave the

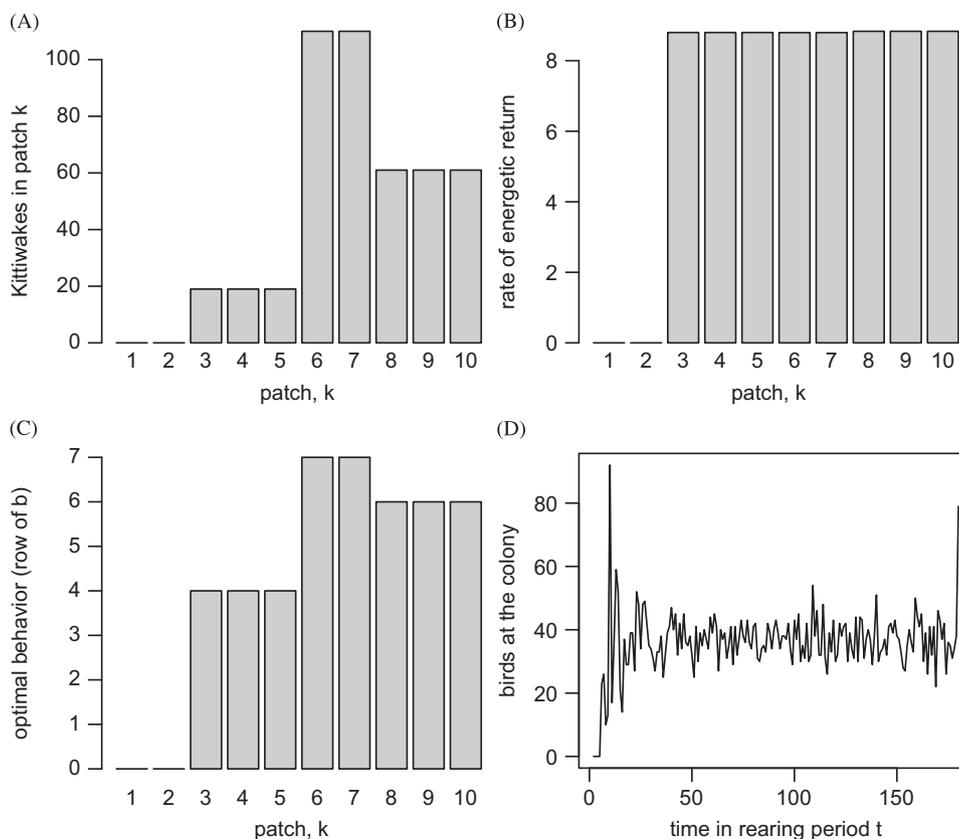


Fig. 3. Results of the Nash patch filling algorithm. (A) The distribution of birds across patches at $t=90$ (halfway through the chick rearing period) (distribution of predators). (B) The energetic return for individuals (patch return). (C) The optimal behavior (row of the behavioral matrix) according to patch (diet choice by patch). (D) The number of birds at the colony during the breeding season (colony attendance).

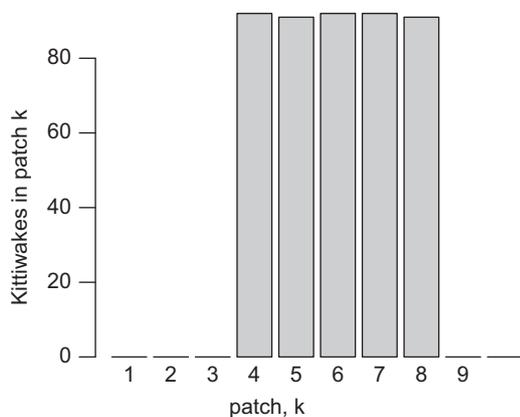


Fig. 4. Predictions of the distributions of kittiwakes under a climate change scenario in which pollock move further off-shore (see text for details). This should be compared with (Fig. 4A).

colony in synchrony, throughout most of the breeding season only a fraction of them will be at the colony (Fig. 3D).

We emphasize these are strong qualitative predictions, perhaps the best for comparison of behavioral predictions and theory (Hilborn and Mangel, 1997, Chapter 6; Clark and Mangel, 2000 especially Chapters 3, 4, and 6; Mangel, 2006, Chapter 5).

We can also consider predictions about the effects of potential environmental change. For example, suppose that environmental change has no effect on euphausiid distribution but causes pollock to move further offshore, with age-0 pollock occupying patches 4–8, and age-1 pollock occupying patches 8–10. In this case, at time $t=90$ we predict that about 40 birds will be at the colony,

essentially the same as in the base case, but the remainder will be uniformly distributed as shown in Fig. 4. Furthermore, the rate of energetic return for birds in the occupied patches drops from ~ 8.8 in the base case to about ~ 5.6 in the case of environmental change. This raises the question of what will the effect of such change be on reproductive success, which we cannot answer with a rate-maximizing model, but revisit in Section 4.

4. Discussion

We have described a framework that can be used to predict the behavior and reproductive success of murre, kittiwake, and fur seals foraging under different environmental conditions. This framework allows us to explicitly acknowledge the role of adaptive behavior in determining how the demography of real organisms is likely to change in response to a changing environment. Thus, when tied to a quantitative model of environmentally induced changes in the prey base (e.g. a predicted decline in forage fish due to increased piscivorous fish, Hunt et al., 2008), our work allows prediction of the impacts of such changes on the behavior and reproductive success of kittiwakes, murre, and fur seals. Given a fine-scale description of prey distribution, our model provides a framework for predicting how foraging locations of central place foragers might shift, and allows comparison of the expected foraging success for different rookeries.

Full parameterization of these models will be challenging. The most substantial challenge is an adequate description of the prey field, summarized on the spatial scale that is relevant to the behavioral models (Wolf and Mangel, 2008). However, even with a coarse approximation of the prey field we can make predictions about the impacts of various changes in the environment by

looking at predicted relative success based on plausible changes in the prey field, and sensitivity analyses can identify the most important environmental drivers and most crucial uncertainties, assisting in the prioritization of future research.

In addition, encounter rates in these models, and especially how they change, do not need to be calculated exclusively from prey densities. For example, variations from baseline encounter rates could easily be used to explore the relative effects of changes in foraging efficiency, such as those caused by storm effects or windshear, or the predictability of fronts that provide high prey concentrations (Decker and Hunt, 1996). Thus our approach can be directly tied to physical as well as biological models of environmental change.

Handling time (as required by classic rate maximization models, or the colony model) is also difficult to characterize. Arguably, time spent actually handling prey may be small enough to ignore for food limited predators, who may spend far more time searching for prey than they spend handling prey after rare encounters. However, handling time might be conceived to include time wasted through unsuccessful attacks (Jeschke et al., 2002 and references therein) and might include pursuit times, which could be estimated using a model similar to Barkley (1964). For murrets and fur seals, handling time might be dominated by the time required to surface to consume large prey items and then return to depth to continue foraging.

Physiological parameters are generally available (e.g. Costa and Gentry, 1986; Croll and McLaren, 1993; Jodice et al., 2003), although it is also common to model state variables as a fraction of some maximal sated state (Clark and Mangel, 2000; Mangel and Clark, 1988). Travel speeds can be inferred from tracking studies or direct measurements (e.g. Benvenuti et al., 1998; Oldén and Peterz, 1985). The links between organismal state and terminal fitness could take on assumed shapes that span the observed variation in adult and offspring survival, or be parameterized based on known relationships between pup size and survival in fur seals (Calambokidis and Gentry, 1985) and relationships between food stress and survival in kittiwakes (Kitaysky et al., 2010; Satterthwaite et al., 2010).

In summary, modelers consistently face the challenge of deciding whether it is more important to acquire more data on direct physiological links, or to document the range of possible outcomes and assume they represent some range of some unmeasurable state variable. We advocate a mixed approach, using direct measures of state whenever possible to yield directly testable predictions, but pragmatically acknowledging that in some cases such data will never be available and there is still much to be learned from qualitative predictions and models based on general principles.

For the case of colony foraging, we have shown that a Nash equilibrium in which no individual can improve its own energy intake by moving can be computed using a relatively simple algorithm, even if the analytical solution is virtually impossible to discover even for a very simple case. However, because this is a rate-maximizing model we are unable to make direct comments on either parental survival or reproductive success (chick survival). The astute reader has surely recognized already that what is needed is a combination of a dynamic state variable model, as done for individuals, and the dynamic game as done for rate-maximizing. Such dynamic state variable games are indeed possible to solve and implement (e.g. Alonzo et al., 2003 for the other polar ocean), but beyond the scope of the current paper and is a major effort for our continued work.

Our models generate testable field predictions, which is good because model validation (*sensu* Oreskes et al., 1994) may be challenging. Owen-Smith et al. (2010) provide a framework for analyzing GIS data in light of optimality models of foraging

behavior that might be adapted to tracking and location data on fur seals and seabirds in this system (e.g. Renner et al., 2012). However, prey fields are highly uncertain, temporally variable, and sparsely sampled empirically. Quantitative model validation may be difficult in the face of so much uncertainty in the prey base, such that a pattern oriented modeling approach (Grimm and Railsback, 2005) comparing alternate assumptions (e.g. relative weighting of parent and offspring in the terminal fitness function, learning vs. omniscience (perhaps due to large colonies functioning as information centers) on the part of foragers, as well as the best values for uncertain parameters) might be the most appropriate approach for this system. A well supported model should be able to capture patterns such as differences between colonies in the predominant foraging locations (Call et al., 2008; Coyle et al., 1992; Schneider and Hunt, 1984; Jahncke et al., 2008), attendance (Kitaysky et al., 2000), the relative performance of individuals (Banks et al., 2006; Benowitz-Fredericks et al., 2008), and demography (Byrd et al., 2008a; Towell et al., 2006). Potential cross species comparisons include their relative flexibility in time budgets (Piatt et al., 2007), differing performance of species with different foraging strategies (Kitaysky and Golubova, 2000), and apparently stronger response to sea ice for kittiwakes than for murrets (Byrd et al., 2008b). At the same time, it is important to realize that a model complicated enough to capture every last empirical detail will be no easier to interpret than nature itself, so there is value in models that capture some but not all patterns in nature. Thus one of the major contributions that empiricists can make for modeling work is to identify the patterns that they consider to be the crucial ones for understanding the system. Doing so will allow the continued interaction of modeling and empirical work.

5. Conclusion

Predicting responses to environmental change is widely acknowledged to be a formidable task, fraught with uncertainty (Berteaux et al., 2006; Krebs and Berteaux, 2006). Even adequately characterizing the present-day prey base is a monumental undertaking given the vast geographic scale of the Bering Sea, the cryptic nature of fish and plankton, and huge spatial and temporal variability. Thus highly precise, quantitative predictions of long term impacts on top predators may not be achievable with this or any other model. Nevertheless, explorations of different scenarios with this modeling framework are useful to document sensitivities to various uncertainties and expected environmental changes, and to assess the plausibility of various hypothesized responses. When combined with data on other parts of the life cycle, the model's predictions of reproductive success can inform demographic projections for species of interest as well, with the same sort of uncertainty and caveats associated with any other demographic projections (e.g. Brook et al., 2000). Mechanistic models such as these are the only option for moving beyond simply extrapolating observed correlations beyond the observed historical range of conditions, and doing the latter is fraught with danger (Mangel et al., 2001).

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Appendix A. Model parameterizations

As described in the main text, full parameterization of these models is challenging but much can be learned from sensitivity analyses and scenario exploration rather than trying to reproduce a particular system. Nevertheless, we provide information and justification on the numeric values chosen for the illustrative model runs.

A.1. Fur seal individual model

(decisions plotted for $x=5$, $t=1$)

A.1.1. Constraints

$p_{max}=10$ (This scales relative pup nutritional state, there are no explicit units.)

$g_{max}=15$ (This scales how much nutritional surplus the parent has available, there are no explicit units.)

$T=40$ (For illustrative purposes we model the first 40 day of the breeding season, this could be extended to 120 day to capture the full season, Gentry, 1998).

$x_{max}=20$ (Each block of x units can be assumed to be 20 km long to encompass maximum trip lengths up to about 400 km reported in Call et al. (2008)).

A.1.2. Terminal fitness functions

$$f_1(p) = \frac{p}{10+p} \quad \text{if } p > p_{crit}, 0 \text{ otherwise}$$

$$f_2(g) = \frac{g}{100}$$

These impose starvation upon a pup with very poor nutritional state, while imposing a saturating relationship between increased nutritional state and fitness.

A.1.3. Metabolic rates

$p_c(t)=0.1*(5+2t/51)^{0.83}$, i.e. scales with increasing pup mass. The 0.83 allometric scaling of metabolic needs comes from Donohue et al. (2002), while the pattern of mass increase follows Trites (1993).

$$p_{crit} = 2$$

$$a_c = 0.5$$

$g_{crit}=3$ (These are unitless nutritional/metabolic scalars. $g_{crit} > 1$ allows the parent to continue foraging even with a nutritional surplus currently too low to provide milk.)

A.1.4. Efficiency of milk transfer

$$m = 1$$

A.1.5. Travel speed

$s=5$ (how many spatial cells traveled in one time step if devote 100% effort to travel, 0 to feeding). Assuming 20 km cell widths, this corresponds to 100 km/day. Total distance/trip durations reported by Call et al. (2008) were typically closer to 50 km/day, but this would include time spent foraging and traveling at

submaximal speed, and some trips approached mean speeds of 100 km/day.

A.1.6. Food distribution

We chose an arbitrary formulation with food abundance peaking ~ 11 cells away from the colony:

$$y(x,d,t) = \begin{cases} 0 & \text{for } x < 3 \\ \frac{3}{0.5+|x-10|/10} & \text{for } d = 0 \\ \frac{3}{0.5+|x-10|/10} & \text{for } d = 1 \end{cases} \quad \text{for } 3 \leq x < 11$$

$$\begin{cases} \frac{8}{0.5+|x-10|/10} & \text{for } d = 0 \\ \frac{25}{0.5+|x-10|/10} & \text{for } d = 1 \end{cases} \quad \text{for } x > 11$$

Feeding is continuous over a day, it depends on location but not prey type.

A.2. Murre individual model

A.2.1. Constraints

$$p_{max} = 10$$

$$g_{max} = 15$$

(As for fur seals, these are unitless measures of relative nutritional state).

$T=36$ (This was an arbitrary choice, long enough to allow for multiple trips and long enough to allow starvation of chicks given p_{max} and how fast they burn reserves.)

$x_{max}=20$ (Given travel speed of 3 cells/time step (see below), this allows for travel beyond that which a round trip is possible before the chick starves, so that there is no external imposition of maximum trip length).

A.2.2. Terminal fitness functions

$$f_1(p) = p \quad \text{if } p > p_{crit}, 0 \quad \text{otherwise}$$

$$f_2(g) = \frac{g}{10+g}$$

(This allows chicks to starve, while parents benefit slightly from a nutritional surplus).

A.2.3. Metabolic rates

$$p_c = 1$$

$$a_c = 1$$

$$g_{crit} = 4$$

(These are in arbitrary units of relative nutritional state).

A.2.4. Travel speed

$s=3$ (we chose speed so that x_{max} is not a direct constraint on birds, since even fully fed chicks starve before the parent can return from a round trip to x_{max}).

A.2.5. Food distribution

$E=(2,4,8)$ for small fish, medium fish, and large fish respectively—these are in arbitrary units of relative energy content (learning about food is suppressed, thus only $\bar{\lambda}$ needed, a and s suppressed):

$$\bar{\lambda}_i = 0 \quad \text{if } x < 2$$

$$\bar{\lambda}_i = \begin{cases} 0.8m & \text{if } i = 1 \\ 0.1m & \text{if } i = 2 \\ 0.1m & \text{if } i = 3 \end{cases} \quad \text{if } 2 \leq x < 5$$

Table A.1

Energy content and handling time of prey items in the colony model ranked by profitability.

Prey type	Species	Energy/prey item	Handling time	Profitability
1	Age 1-pollock	52.8	0.22	240.0
2	Age 0-pollock	10.4	0.052	199.4
3	Euphausiid	0.34	0.015	22.7

$$\bar{\lambda}_i = \begin{cases} 0.4m & \text{if } i = 1 \\ 0.3m & \text{if } i = 2 \\ 0.3m & \text{if } i = 3 \end{cases} \text{ if } x > 5$$

$$\text{where } m = \frac{0.5}{0.5 + |x-6|/6}$$

for the reduced food scenario, encounter rate was decreased 25% in all locations for all species. This formulation makes food most abundant at $x=6$, falling off in either direction. The area near the colony is dominated by small prey, larger prey become relatively more abundant further away.)

A3. Kittiwake colony-level model

We envision the prey to be euphausiids (21 mm, 4.8 kJ/g wet weight, Nishiyama, 1977 in Davis, 2003), age 0 pollock (7 cm fork length, 4.2 kJ/g wet weight, Logerwell and Schaufler, 2005), and age 1 pollock (12 cm fork length since kittiwakes can only eat the smaller of the age-1 fish, same energy density) and use weight-length allometries (from Wiedenmann et al., 2008 for euphausiids and Katakura et al., 2007 for pollock) to compute the energy content of prey items. We picked handling times based on rough approximations, and in a manner that the prey were ranked as described in Table A.1.

We assume 10 patches, that euphausiids are found in all 10 at the same density in all patches $\lambda_{30}(k) = \bar{\lambda}_3 = 10$ and that age-0 pollock are found in patches 3–7 ('inshore') at constant density $\lambda_{20}(k) = \bar{\lambda}_2 = 1.0$. In addition to assuming that age 0-pollock are an order of magnitude less abundant than euphausiids, we assume that pollock are at a stable age distribution corresponding to an annual mortality rate 0.3 and that age-1 pollock are found in patches 6–10 ('offshore') at constant density $\lambda_{30}(k) = \bar{\lambda}_3 = \exp(-0.3)\bar{\lambda}_2$.

We assume that the travel time between the colony and patch k is $\tau_{ck} = 0.035k$, that between patches k and l is $\tau_{kl} = \tau_{lk} = 0.035|k-l|$ and that the energetic cost of travel per unit time is $\alpha = 0.01$.

We assume that colony size is $N_c = 500$ individuals, for the interference vector we assume $\{f_1, f_2, f_3\} = \{0, 0.025, 0.075\}$, and assume that a single time interval is 6 h. The chick rearing period is about 45 days, so that $T = 180$. We set $\tau_{max} = 5$, corresponding to a maximum trip of 20 h (within the range reported by Kotzerka et al. (2010) their Table 2). We assume patch locations are fixed. For simple illustrative purpose rates here, we assume patch return rates (energy/time) are constant through time, but they could be varied.

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