Capital and income breeding: the role of food supply

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Abstract. An aspect of life history that has seen increasing attention in recent years is that of strategies for financing the costs of offspring production. These strategies are often described by a continuum ranging from capital breeding, in which costs are met purely from endogenous reserves, to income breeding, in which costs are met purely from concurrent intake. A variety of factors that might drive strategies toward a given point on the capital–income continuum has been reviewed, and assessed using analytical models. However, aspects of food supply, including seasonality and unpredictability, have often been cited as important drivers of capital and income breeding, but are difficult to assess using analytical models. Consequently, we used dynamic programming to assess the role of the food supply in shaping offspring provisioning strategies. Our model is parameterized for a pinniped (one taxon remarkable for the range of offspring-provisioning strategies that it illustrates). We show that increased food availability, increased seasonality, and, to a lesser extent, increased unpredictability can all favor the emergence of capital breeding. In terms of the conversion of energy into offspring growth, the shorter periods of care associated with capital breeding are considerably more energetically efficient than income breeding, because shorter periods of care are associated with a higher ratio of energy put into offspring growth to energy spent on parent and offspring maintenance metabolism. Moreover, no clear costs are currently associated with capital accumulation in pinnipeds. This contrasts with general assumptions about endotherms, which suggest that income breeding will usually be preferred. Our model emphasizes the role of seasonally high abundances of food in enabling mothers to pursue an energetically efficient capital-breeding strategy. We discuss the importance of offspring development for dictating strategies for financing offspring production.

Key words: capital breeding; energetics of reproduction; fasting; foraging cycle; income breeding; lactation; pinnipeds; seasonal environments.

INTRODUCTION

Energy storage is an aspect of life history of fundamental importance to understanding a range of ecological phenomena. Storage strategies of plants (Chapin et al. 1990) have implications for areas as topical as carbon sequestration and crop yield. Among animals, patterns of energy storage have provided insight into the strategies used by organisms to cope with seasonal environments (McNamara and Houston 2008) and other stressors, including climate change (Anthony et al. 2009, Lehikoinen et al. 2011). A specific aspect of energy storage that has seen increasing interest over recent decades is that of the distinction between capital and income breeders (Jönsson 1997, Bonnet et al. 1998, Meijer and Drent 1999, Klaassen et al. 2001, Houston et al. 2007, Stephens et al. 2009). Capital breeders store energy in advance of breeding, thereby

reducing the extent to which reproductive success is dependent on environmental conditions at the time of breeding; this contrasts with the strategy of income breeders, which finance the costs of reproduction using concurrent intake of energy (Jönsson 1997).

There has been considerable interest in the adaptive value of capital- and income-breeding strategies. A wide range of factors, both intrinsic and extrinsic, has been hypothesized to explain why one or the other strategy might be favored (see review in Stephens et al. 2009). Intrinsic factors relate to morphology and physiology, and include aspects such as body size and the costs of carrying stored reserves. Larger body size is associated with lower costs of carrying stored reserves and, as such, is one of the most widely invoked factors suggested to favor capital breeding. Extrinsic factors usually relate to the abundance and reliability of food, especially at the time of breeding. Capital breeding is often thought to be favored by low or unreliable food availability (Johnson 2006, Pollux and Reznick 2011) or spatial separation between favorable areas for breeding and foraging (Drent and Daan 1980, Jönsson 1997). A third set of

factors involves behavioral trade-offs. In particular, capital breeding dissociates breeding and foraging, allowing organisms to feed and breed at times and in places that are most suitable for these different activities (Bonnet et al. 1998). In some taxa, dissociating feeding from caring for offspring means that the provision of care can be more concentrated; this can reduce the period of offspring dependency, increasing the ratio of energy allocated to offspring growth to that allocated to maternal and offspring maintenance metabolism (Fedak and Anderson 1982). In this context, capital breeding is sometimes viewed as the more energetically efficient maternal strategy (Costa 1993, but see Jönsson 1997). Inevitably, determining when to invest effort in feeding vs. maternal care requires organisms to make trade-offs.

Attempts to assess support for the putative drivers of evolutionary divergences between capital and income breeders have employed two approaches. First, mathematical models have been used to explore the importance of specific factors or sets of factors in isolation (see Stephens et al. 2009:2063). These analytical models have tended to emphasize the importance of maternal mass (e.g., Costa 1993, Boyd 1998, Trillmich and Weissing 2006). By contrast, comparative approaches have emphasized the importance of aspects of food supply, such as seasonality and predictability (Thomas 1988, Schulz and Bowen 2005, Jönsson et al. 2009). Schulz and Bowen (2005), in particular, found that when phylogeny was controlled for, correlates of different breeding strategies were not well explained by maternal body mass. Owing to this discrepancy, and because analytical models are poorly suited to examining the importance of factors such as seasonality and unpredictability of food supplies, several authors have suggested that theoretical models should be constructed within a full life history framework (Jönsson 1997, Houston et al. 2007, Stephens et al. 2009). State-based life history models have now begun to address the adaptive value of capital and income-breeding strategies, showing how behavior can be affected by aspects of the environment, such as the timing of food availability in relation to peak predator abundance (Varpe et al. 2009).

In this paper, we use a dynamic model to examine the role of factors associated with food supply and energetics in driving female behavior toward capital or income-breeding strategies. To take advantage of the availability of data on factors thought to influence capital and income strategies (e.g., Schulz and Bowen 2004), and to facilitate comparisons with several significant investigations into the drivers of capital and income breeding (Costa 1993, Boyd 1998, Schulz and Bowen 2005, Trillmich and Weissing 2006), our model is parameterized for an organism with a life history based on a pinniped (the order comprising seals and their allies). The structure of the model makes it possible to isolate the effects of changes in different aspects of food supply, including overall availability, seasonality, and predictability. The consequences of changes in these parameters are assessed in terms of their effects on the index of capital breeding, a measure of the proportion of maternal energetic outlay between birth and the nutritional independence of offspring that is not offset by income. Using this approach, we show that aspects of food supply alone are capable of driving evolution to any point along the capital–income continuum. This has clear implications for understanding the evolution of these strategies in general, and suggests that resource availability and dynamics could drive divergences between capital and income breeding.

Modeling Methods

Model rationale

We constructed our model with particular reference to the Pinnipedia. All pinnipeds are similarly constrained to forage at sea, but give birth out of the water; as a result, they exhibit a high degree of similarity in ecology and morphology. In spite of this, the order is striking, in that the majority of extant species are sharply divided between those that pursue capital strategies and those that pursue income strategies. Pinnipeds thus offer a particular opportunity to assess the factors underlying the evolution of capital and income strategies. Moreover, although pinniped maternal strategies were formerly believed to be well explained by phylogeny (e.g., Bonner 1984) or maternal mass (Boness and Bowen 1996, Lydersen and Kovacs 1999), neither is consistently supported by evidence. In particular, a range of species of phocid seals (the family typically associated with capital breeding) has been shown to pursue strategies intermediate between pure capital and pure income breeding (e.g., Boness et al. 1994, Thompson et al. 1994, Lydersen and Kovacs 1999, Wheatley et al. 2008); these species span a range of body masses. The primacy of body mass is further undermined by the existence of large-bodied income breeders (e.g., Steller's sea lion, *Eumetopias jubatus*; Rehberg et al. 2009). The factors that could have led to the original divergence between capital- and income-breeding strategies in the pinnipeds thus remain an open question.

Here, we develop a model intended to be relevantly similar to a generalized pinniped, rather than providing output resembling the life history of any specific pinniped. By modeling a generalized pinniped with minimal constraints on its behavior, we hope to provide insights into the factors underlying the evolution of maternal strategies in this order and more generally. The importance of body mass in determining maternal strategies has been the focus of previous models. Thus, we do not treat mass explicitly, although it is included implicitly through the consequences of several variables that are expected to scale with mass. These include relative intake and the costs of carrying energy reserves. Given that we currently have a very poor understanding of how those variables scale with mass, we prefer to consider a generalized pinniped of fixed lean mass and focus on the consequences of aspects of variability that

TABLE 1. Notation used in the dynamic programming equations.

Parameter	Description
x	Female's energy reserves ($0 \leq x \leq 1$)
a	Age of fetus/pup (in days)
y	Energy reserves of pup ($0 \leq y \leq 1$)
f	Age of a fetus if female implants while tending (in days)
t	Time of year (day)
$V(x,a,y,f,t)$	State-specific residual reproductive value
$R(a,y,t)$	State-specific probability that an independent pup survives to maturity
S_A	Survival of adults to the next time step
$S_P(y)$	State-specific survival of nonindependent young to the next time step
m_R	Resting metabolic costs of an adult during one time step
$m_F(x)$	State-specific metabolic costs of a foraging adult during one time step
$m_P(y)$	State-specific resting metabolic costs of a pup during one time step
L_{max}	Maximum energy transfer by lactation
L	Actual amount of energy transferred to pup by lactation
$e(t)$	Energy gained from a good day's foraging
p	State-specific probability of foraging success
G	Length of gestation (in days)
U_R	Period of uterine recovery between birth and potential implantation (in days)

cannot easily be incorporated in simpler models of life history. Nevertheless, because the role of maternal mass is believed to result from the implications of mass for the ability to carry energetic reserves, the consequences of varying maternal mass are easily inferred from our model by looking at the consequences of variation in the costs of carrying energy stores (and the inevitable impacts of those costs on the ability of females to carry energy stores).

General outline

Our model, programmed in C for Unix (see Supplement), follows the standard algorithms of state-dependent dynamic programs, as applied to annual routines (e.g., Houston and McNamara 1999: Chapter 9, McNamara et al. 2004). Specifically, we are interested in the annual cycle of decisions that females make regarding foraging and resting, implanting or aborting fetuses, and caring for or abandoning pups. We refer to the period between birth and weaning of a pup as the tending period, regardless of whether the female is actively provisioning, or is foraging, at any given time.

We consider a female pinniped to be defined by five state variables: (1) x defines female energy reserves as a proportion of some maximum level ($0 \leq x \leq 1$); (2) a is the age (in days) of a fetus she is carrying or a pup she is caring for (this delineates a number of different situations: $a = 0$, neither pregnant nor tending; $0 < a < G$, pregnant; $a = G$, at term; $a > G$, with a pup of age $a - G$); (3) y is the pup's level of energy reserves, again as a proportion of some maximum level ($0 \leq y \leq 1$); (4) f is the age (in days) of a fetus if the female is simultaneously

pregnant and tending (we assume that a female can only be pregnant with, or tend, one pup at any time, but can tend one while pregnant with another; thus, $0 \leq f \leq G$); and (5) t is time of year in days ($0 \leq t \leq 364$).

These and other symbols used in the model are summarized in Table 1. Note that female age is not a state variable. We return to this point in the discussion, but here we note that life history decisions in pinnipeds are likely to be state dependent (McNamara and Houston 1996, Boyd 2000) and, once the female is reproductively mature, more strongly affected by condition than by age.

For each combination of the five state variables, we use the standard, backward iteration approach of dynamic programming (Houston et al. 1988) to seek the decisions (out of a range of possibilities) that maximize the female's lifetime reproductive success (LRS).

Decision epochs, choices, and dynamic programming equations

Time, t, is measured in days and optimal decisions are determined for each day of the year, with day 365 assumed to be day 0 of the next year. Behavioral decisions are of three types: foraging (the binary decision of whether to forage or rest); reproduction (whether to implant or not, or, if pregnant, whether to abort or not); and caring (whether to tend or abandon, whether to forage or lactate, and, if lactating, how much energy to transfer to the pup). Clearly, not all decisions are relevant to all states. For example, a female that is already pregnant cannot choose to implant, and a female that is not tending need make no decisions about levels of care. Thus, only subsets of the available decisions are relevant to each case. These are summarized in Table 2. Dynamic programming equations relevant to each decision are available in Appendix A.

Energetics, metabolism, and mortality

Mortality is state dependent in that a female dies of starvation when her energy reserves fall to zero. In addition, females are subject to other sources of background mortality. Background mortality is fixed with a value equivalent to an annual survival rate of 0.95 (for an investigation into the effects of varying background mortality, see McNamara et al. 2004). Pup mortality in utero is confined to instances where the mother dies or chooses to abort. As with females, pups die of starvation when their reserves reach zero. Pup background mortality occurs at a rate equivalent to an annual survival of 0.70.

All energetics are scaled to absolute maximum reserves (X_{max} and Y_{max} for adults and pups, respectively). Thus, an intake of F (in megajoules, MJ) by a foraging adult causes a mean increase in her x state variable of F/X_{max}. Similarly, if an adult loses L (in MJ) through lactation, her reserves decrease, on average, by L/X_{max}. Her pup's reserves, by contrast, show a mean

TABLE 2.   State-specific choices available, where G is length of gestation and U_R is period of uterine recovery (in days); notation is summarized in Table 1.

State	Choices available
(a) Neither pregnant nor tending ($a = 0$)	1 Forage and implant
	2 Forage, don't implant
	3 Rest and implant
	4 Rest, don't implant
(b) Pregnant, not tending ($0 < a < G$)	5 Forage and retain
	6 Forage and abort
	7 Rest and retain
	8 Rest and abort
(c) At term, not tending ($a = G$; $f = 0$)†	9 Forage and abort
	10 Rest and give birth
	11 Rest and abort
(d) Tending, not pregnant, cannot implant ($G < a < G + U_R$)	12 Tend and forage
	13 Tend and rest‡
	14 Abandon (then choices as A)§
(e) Tending, can implant ($a \geq G + U_R$; $f = 0$)	15 Tend, forage, implant
	16 Tend, forage, don't implant
	17 Tend, rest, implant‡
	18 Tend, rest, don't implant‡
	19 Abandon (then choices as A)§
(f) Tending and pregnant ($0 < f < G$)	20 Tend, forage, retain
	21 Tend, forage, abort
	22 Tend, rest, retain‡
	23 Tend, rest, abort‡
	24 Abandon (then choices as B with $a = f$; $f = 0$)§
(g) Tending with fetus at term ($f = G$)	25 Tend, forage, abort
	26 Tend, rest, abort‡
	27 Abandon (then choices as C with $a = G$; $f = 0$)§

† Note that giving birth and foraging on the same day is not an option.
‡ If tending and resting, the female also chooses how much energy to transfer to the pup in milk. See further details in Appendix B.
§ Note that abandonment is assumed to be instantaneous, providing the female with the same choices as if that pup had not been present.

increase of $\alpha L / Y_{\max}$, where α is the efficiency with which adult reserves are converted to pup reserves through lactation. Dynamic programming equations in Appendix A reflect this scaling.

Metabolism could be affected by state and seasonality. Seasonality is included in the model via food availability (as we will show); for simplicity therefore, we model metabolism as independent of time of year (assuming a thermoneutral environment throughout). Blubber is believed to be largely metabolically inert (Rea and Costa 1992, Aarseth et al. 1999), so resting metabolism onshore is fixed at $m_R = 2.2 \times$ BMR, where BMR is an estimate of basal metabolic rate (Boyd 2002, Williams et al. 2007).

In contrast to onshore metabolism, metabolic expenditure while swimming (and foraging) depends on energy reserves. The relationship between fat stores and metabolic costs is likely to be complex, but here we use a highly simplified relationship. Specifically, we assume that the major factor affecting metabolic costs of foraging is likely to be drag, which increases linearly with surface area (Vogel 1994). Although surface area increases as the two-thirds power of mass, bodies also become less dense with increasing volumes of fat storage. For simplicity, therefore, we assume that foraging metabolism is linearly related to energy stores (see *Discussion*), such that

$$m_F(x) = \text{BMR}(b + xc) \qquad (1)$$

for nonpregnant females. Here, the minimum metabolic rate while foraging (m_F) and the rate at which this increases with increasing reserves is determined by the constants b and c, respectively. Metabolic rates, m_R and $m_F(x)$, of pregnant females ($0 < a \leq G$, or $f > 0$) are assumed to be 10% higher than for nonpregnant females with equivalent stores.

Pups are assumed to grow during the tending period, with fat stores representing increasing proportions of body mass as the pup grows. We assumed that proportional body fat of pups would scale linearly with y, the pup state variable, from 10% at birth to a maximum of 49% (Oftedal et al. 1993, Muelbert et al. 2003). Pup basal metabolic rate (BMR_P) was assumed to be proportional to that of their mother, with the proportion based on the relative lean masses of the two individuals (van der Meer 2006: Eq. 1).

Seasonality and predictability in energy gain

Our main focus is on how aspects of food availability affect maternal provisioning strategies. Here, we describe how seasonality and predictability are modeled.

Let $\bar{\mu}$ be a constant (for any modeled scenario) describing the mean daily energy obtained by a foraging adult seal, averaged over the entire year. Seasonality is assumed to result in annual cycles between periods of

high productivity ("summers") and periods of low productivity ("winters"). It is incorporated by calculating the mean intake for day t, $\mu(t)$ as

$$\mu(t) = \bar{\mu}\left[1 + v.\sin\left(\frac{t - 91.25}{182.5}\pi\right)\right] \qquad (2)$$

where v is the amplitude of seasonality ($0 \leq v \leq 1$).

The predictability of the environment is modeled using the parameter p, where $0 \leq p \leq 1$. The actual amount of energy that a foraging seal acquires depends on whether it has a good day's foraging, in which case it will gain $e(t) = \mu(t)/p$, or a bad day's foraging, in which case it will acquire no energy. Metabolizable intake rate cannot rise indefinitely to take advantage of abundant resources. Various cross-species studies suggest possible values for a cap on metabolizable intake (Kirkwood 1983, Hammond and Diamond 1997), but empirical work (e.g., Rosen and Trites 2004) suggests that pinnipeds might sometimes exceed these broad predictions. Here, we use a relatively relaxed limit to intake of $9 \times$ BMR.

The value of independent pups

The value of young released at time t and with reserves y depends on the value of the young they will have in the future. Thus, it is necessary to use a proxy for the value of independent young. Our proxy was the probability that the pup will survive to reach lean adult mass. Specifically, we modeled independent pups foraging in the same environment (characterized by the same levels of seasonality and predictability) as adults, allocating energy acquired to either lean growth or energy reserves (see Appendix B). They were assumed to die if their energy reserves dropped to zero. In this way, the value of pups abandoned with given energy reserves at a certain time of year, $R(y,t)$, is the probability that the pup will survive to reach lean adult size.

Once weaned (i.e., following abandonment by its mother), the pup is assumed to be intermediate between a dependent pup and an adult. Energy gain is apportioned between lean mass and reserves as described in Appendix B. Metabolism is dependent on both size and reserves, and background mortality scales linearly with lean mass. The food source for independent pups is assumed to be the same as that for adult females, but there are two differences between the mean intake of independent pups and that of adults on any given day. First, an independent pup is assumed to be a less efficient forager than an adult. Specifically, the maximum mean energy acquired is given by:

$$\mu_p(t) = q_{rel}\mu(t) \qquad (3)$$

where q_{rel} (the foraging ability of a pup relative to an adult) is defined by the indicator function

$$q_{rel} = \begin{cases} 1/[1 + e^{-Q(t-q_{1/2})}] & t \leq D \\ 1.0 & t > D \end{cases} \qquad (4)$$

with Q being a scaling constant, given by $\ln(999)/(D - q_{1/2})$. This produces a family of sigmoidal curves that ensure a period of learning before the pup asymptotes at 99.9% of adult foraging competence, D days after weaning. Parameter values for D and $q_{1/2}$ are given in Table 3 (but see further). Foraging ability is solely a function of experience, but energy reserves at weaning are useful because they increase the probability that pups will survive the initial post-weaning period until they learn to forage efficiently. This approach ensures a sigmoidal relationship between survival and weaning size, consistent with empirical observation (e.g., Baker 2008). The second difference between pup and adult foraging is that pup intake rate is assumed to scale less steeply with lean body mass than pup metabolic expenditure. This is consistent with one of the fundamental relationships of the metabolic theory of ecology (see van der Meer 2006: Eq. 1). Taken together, these two differences ensure that independent pups do not reach adult body size implausibly rapidly. Preliminary investigations showed that plausible modeled scenarios were associated with a minimum time to full foraging competence of two years; this allowed us to set $D = 728$, producing output consistent with the observation that pinnipeds typically take several years to reach adult size (Winship et al. 2001, Laws et al. 2003). We could then focus investigations on varying $q_{1/2}$ alone.

Other parameters

In this study, we are interested only in the effects of aspects of food supply on maternal provisioning strategies. As a result, several other factors that vary among pinnipeds can be held constant. Where possible, we have used relatively unconstrained parameter values. This reduces the likelihood that strategies are constrained by factors that might apply to only one or a subset of pinniped species. Parameter values used in the basic models are summarized in Table 3.

Among the parameters used, two aspects are particularly poorly understood and might be expected to have an important effect on emergent strategies. These are the parameter affecting mass-dependent costs (c, which determines how steeply foraging metabolism rises with stored energy reserves) and the main parameter affecting the foraging ability of independent offspring ($q_{1/2}$). Baseline values for these parameters are given in Table 3, but we also investigate the importance of these parameters for the findings of our model. Note that, importantly, the strength of mass-dependent costs can be thought of as a substitute for including body mass in the model (because it is through its effects on the strength of mass-dependent costs that body mass is thought to play a role in affecting provisioning strategies). Mass-dependent costs that rise steeply with stored energy are characteristic of small-bodied pinnipeds, whereas costs that rise more gradually with the amount of stores are more associated with large-bodied pinnipeds.

TABLE 3. Parameter and their baseline values.

Description	Parameter	Value	Comment
Adult female lean body mass	M_A	100 kg	Lean body mass excludes fat stores; this therefore represents a pinniped of intermediate size.
Maximum adult energy reserves	X_{max}	4000 MJ	Assumes fat stores could represent half of total body mass (Boyd, 2002:261) at approximately 40 MJ/kg.
Maximum pup energy reserves	Y_{max}	1000 MJ	At weaning, pups are about 1/4 of adult female mass (Schulz and Bowen 2005), so modeled pups have up to 1/4 of adult stores.
Female energy loss in birth	E_{birth}	400 MJ	This includes the energy invested in the pup (which is assumed to be recoverable until the pup is born) and any non-retrievable energy in tissues used to support the pregnancy.
Pup reserves at birth	Y_{birth}	200 MJ	Neither pups nor adults are expected routinely to attain their maximum reserves. Pups typically triple their birth mass by weaning, however, so should be born with about 1/5 of potential reserves.
Gestation period	G	240 d	Gestation is fixed at eight months but beyond this, timing of birth is determined by female decisions regarding implantation.
Minimum age at independence	a_{min}	$G + 3$ d	The low age at which pups can become independent reflects the short weaning period of some species, such as the hooded seal (*Cystophora cristata*), in which weaning can be complete in as little as 4 d (Bowen et al. 1985).
Uterine recovery period	U_R	7 d	This takes a low value to reduce computational load.
Maximum daily energy transfer	L_{max}	135 MJ	Weddell seals achieve the highest daily milk energy transfer relative to body mass (Schulz and Bowen, 2005). We used the same approximate relationship, in order that rates of potential energy transfer would not constrain emergent strategies.
Efficiency of energy transfer	α	80%	This parameter is broadly consistent in pinnipeds.
Adult female basal metabolic rate	BMR_A	10.95 MJ/d	See Boyd (2002) for further details on metabolic rate.
Foraging metabolics parameters (see Eq. 7)	b	2.5	Foraging metabolics parameters were set such that, in the basic model, $m_F(x,a,f)$ for non pregnant females varied from $2.5 \times BMR_A$ to between $5 \times BMR_A$ and $7 \times BMR_A$, depending on the strength of mass dependent costs.
	c	2.5–4.5	
Independent young foraging parameters (see Eq. 14)	D	728	Parameters for independent pup foraging were set to ensure that model outcomes could include situations in which pinnipeds took several years to reach full adult size (Winship et al. 2001, Laws et al. 2003).
	$q_{1/2}$	30–300	

Scenarios and interpretation

Optimal strategies determined from the dynamic program were used in stochastic simulations (Mangel and Clark 1988) of the lives of 10^6 individuals until death. The behavior of individuals was state specific and overall patterns of expected behavior emerged from the optimal strategies. Simulations were started at $t = 0$, with all individuals in condition $x = 0.1$ and neither pregnant nor tending. All results presented (except where specified) are outcomes of the simulations.

Of the parameters controlling food supply, we are primarily interested in absolute levels of food availability ($\bar{\mu}$), amplitude of seasonality (v), and predictability of food availability (p). Absolute food availability was varied on an arbitrary linear scale, but $\bar{\mu} = 1$ approximates the lower limit for the viability of nonreproductive lean females. Scenarios with relatively low food availability are termed low-quality environments. Seasonality and predictability were varied between 0 and 1 (see Appendix C: Fig. C1).

Annual routine models can be used to make predictions about a very wide range of aspects of physiology and behavior (Feró et al. 2008). A variety of emergent behaviors are of interest, including timing of breeding and the degree to which females were entrained to an annual cycle, durations of tending, and absolute levels of investment in offspring (Appendix C: Fig. C3). However, in this paper we focus on the major response variable of interest, the index of capital breeding (K). This is a measure of the extent to which females rely on the fasting strategy for offspring provisioning and is calculated as:

$$K = 1 - E_{in}/E_{out} \tag{5}$$

where E_{in} is total energetic income between birth and weaning and E_{out} is total energy expenditure between birth and weaning.

Total expenditure includes foraging, metabolism, and lactation, but excludes energy lost in birth (which is lost regardless of whether the female then pursues a fasting strategy or a foraging cycle strategy). Estimates of K
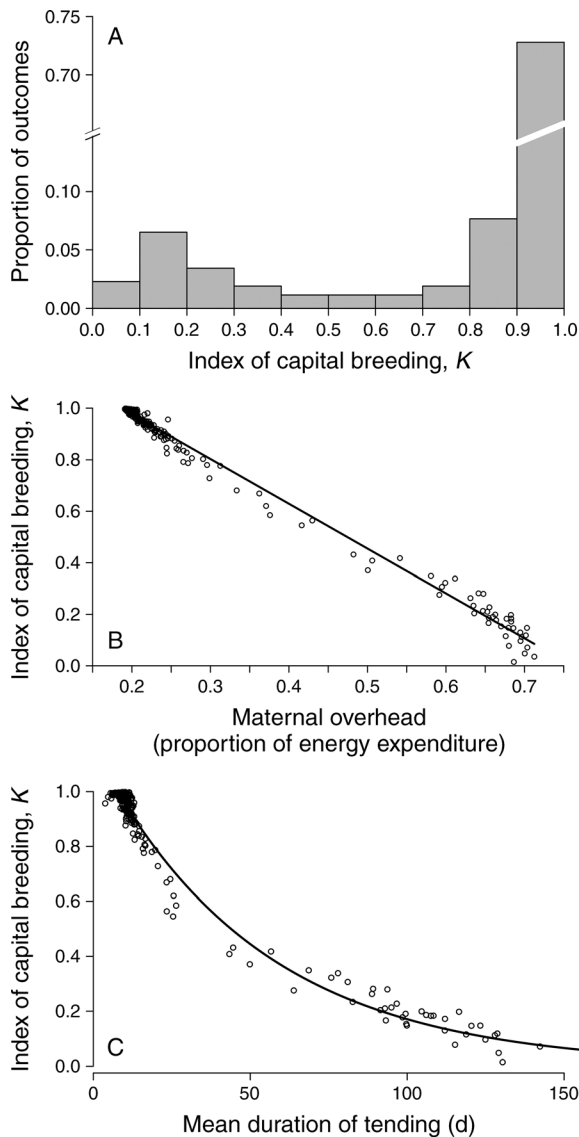
Fig. 1. General outcomes of the simulations: (A) distribution of K emerging from valid parameter combinations (notice the y-axis discontinuity); (B) the relationship between K and maternal overhead (proportion of maternal energy expenditure during weaning that is spent on maternal metabolism); (C) the relationship between K and duration of tending (i.e., the total length of the weaning period). Fitted lines in the lower panels are illustrative only and are: panel (B) $K = 1.33 - 1.74u$ ($R^2 = 0.99$), where u is maternal overhead; and panel (C) $K = 1.16 \exp(-0.02w)$ ($R^2 = 0.95$), where w is duration of tending in days.

from simulations are derived from successful births (that resulted in a viable pup); see Appendix C: Fig. C2. Results of simulations were deemed relevantly similar to pinniped systems if females were broadly entrained to an annual cycle, and strategies had sufficient fitness to suggest that the environment was viable; specifically, double-breeding (i.e., producing more than one pup in a single year) occurred less than once per 100 female years, and pregnant females in moderate condition (with 30%

of maximum reserves) had, at some time of year, an expected LRS ≥ 2.0.

Results

General results

We explored the consequences for maternal strategies of variation in five parameters, using Monte Carlo simulations to draw parameter values from plausible ranges. This process was terminated once we had obtained 260 parameter combinations that met our criteria for viability. Here, we begin by illustrating the general outcomes of our simulations and their relationship with parameters often measured in empirical studies of pinniped breeding behavior. Our random exploration of parameter space yielded more outcomes toward the capital end of the spectrum than toward the income end (Fig. 1A). Intriguingly, the distribution tended to diverge toward its extremes, suggesting that intermediate strategies are less successful in many regions of parameter space. The strong relationship between K, the index of capital breeding, and other parameters more familiar to empirical seal biologists is evident (Fig. 1B, C).

Effects of parameter variation

An initial indication of the importance of each of the focal parameters can be gained from plotting K, the index of capital breeding, against each parameter independently (Fig. 2). Although some structure is evident in each case, clearly neither the major parameters concerned with food availability (Fig. 2A–C) nor the strength of mass-dependent costs (Fig. 2D) has the predominant influence on pup-rearing strategies. Rather, the majority of the variation in the emergent placement on the capital–income continuum is explained by a very poorly understood parameter: the speed at which offspring foraging competence improves (Fig. 2E).

Pinnipeds vary substantially in their placement on the capital–income continuum. Although existing variation might be attributable to different strategies of offspring learning, we are interested in environmental factors that might have promoted early differentiation in offspring-provisioning strategies. Consequently, we concentrated further analyses on intermediate scenarios from Fig. 2E, where the value of $q_{1/2}$ was associated with a wide range of emergent parental strategies. Specifically, we fixed $q_{1/2} = 180$ days and allowed the four remaining parameters to vary as before. We obtained a further 250 parameter combinations that met our criteria for validity. Plotting K against each of the remaining parameters (Fig. 3) revealed considerably more structure than formerly, strongly suggestive (at least for food availability and seasonality) of the direction of effects. To enable these effects to be visualized more clearly, we plotted K against food availability, dividing each of the other focal parameters into "high" and "low" about their median values across all successful simulations (Fig. 4). Some
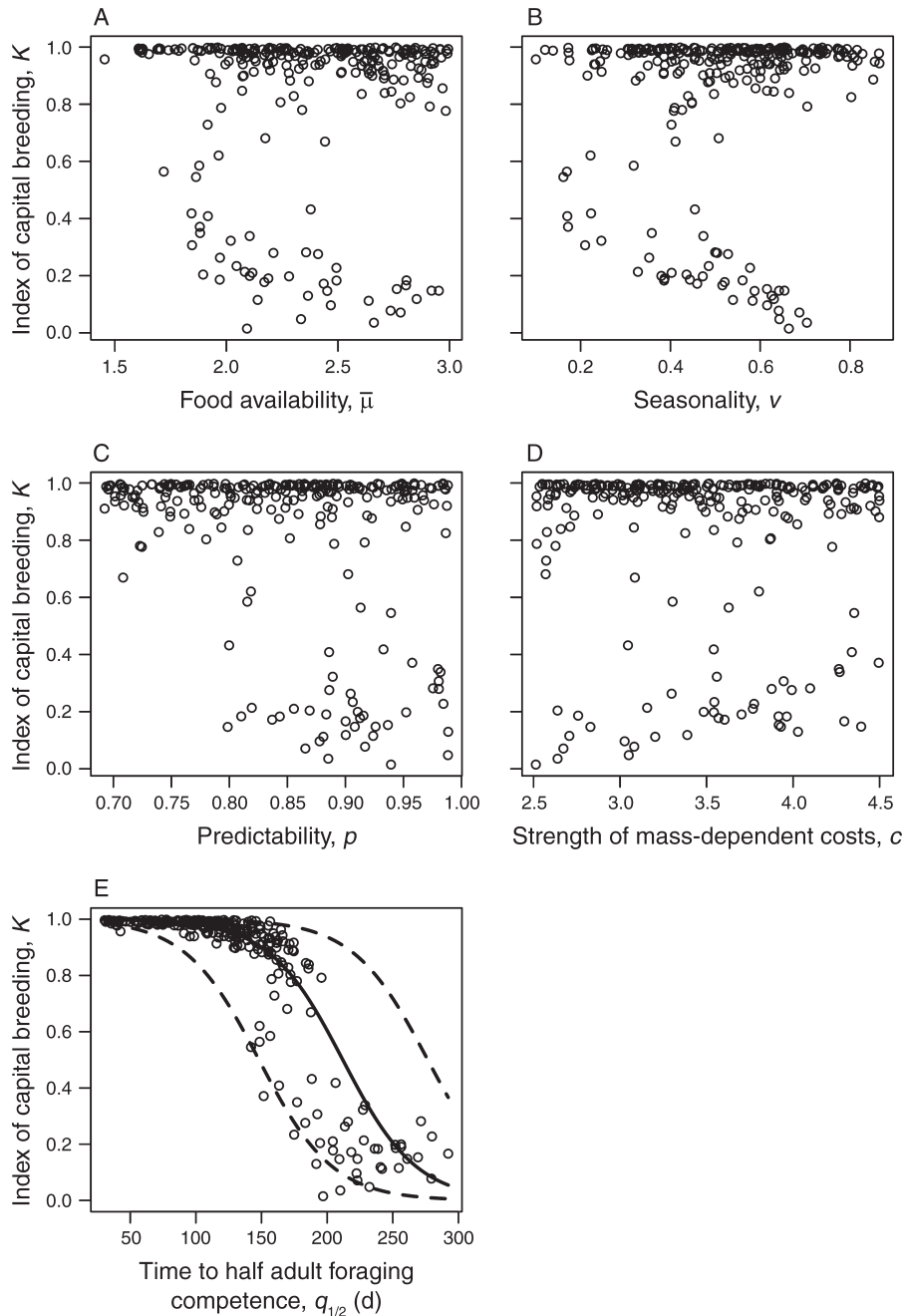
FIG. 2.   Influence of parameters on the index of capital breeding, K, which is shown in relation to: (A) annual mean food availability, $\bar{\mu}$; (B) seasonality, v; (C) predictability, p; (D) strength of mass-dependent costs, c (see Eq. 1); and (E) time taken to reach half of adult foraging competence, $q_{1/2}$. Fitted lines in panel (E) are the mean (solid line) and 95% prediction intervals (broken lines) obtained by fitting a linear function in logit space ($R^2 = 0.74$). For parameter definitions, see *Modeling methods*: subsections *Seasonality and predictability in energy gain; The value of independent pups*; and *Other parameters*.

general patterns include: (1) higher food availability consistently favors capital breeding; (2) higher seasonality also tends to be associated with a greater degree of capital breeding; (3) higher predictability reduces reliance on capital, especially when seasonality is low; and (4) high storage costs tend to reduce reliance on capital to a small degree. Identifying these patterns is made more complicated by the interacting effects of parameters on the validity of scenarios. For example, low seasonality seldom produced valid outcomes when combined with high food availability and high predictability, because females did not become entrained to an annual cycle. Likewise, the combination of high seasonality and low food availability was seldom viable,
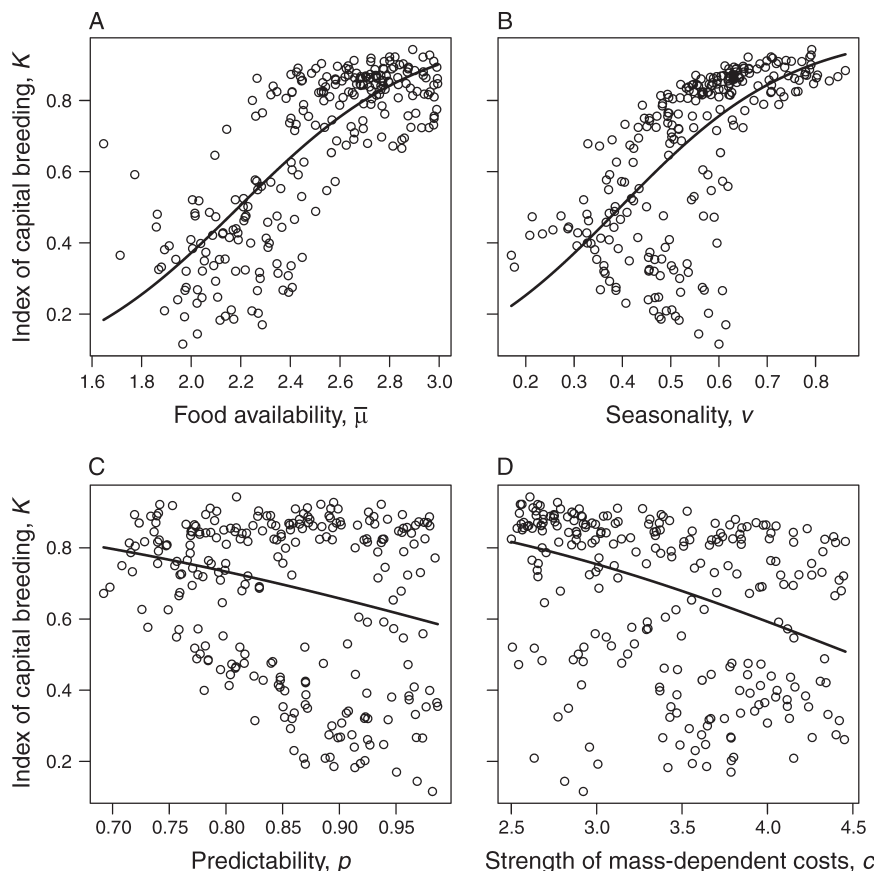
FIG. 3. Influence of parameters on the index of capital breeding, K, when the time taken for independent pups to reach half of adult foraging competence is held constant at $q_{1/2} = 180$. K is shown in relation to: (A) annual mean food availability, $\bar{\mu}$; (B) seasonality, v; (C) predictability, p; (D) strength of mass-dependent costs, c (see Eq. 1). Fitted lines are shown only for ease of visualization and were obtained by modeling $\text{logit}(K)$ as a linear function of the relevant predictor and back-transforming. As an indication of the relative influence of the four predictors, the variance explained by individual predictors in the $\text{logit}(K)$ response is: (A) $R^2 = 0.60$; (B) $R^2 = 0.45$; (C) $R^2 = 0.06$; (D) $R^2 = 0.14$.

owing to the limited potential for females to survive periods of food shortage. These associations between parameters and the regions of parameter space that could be explored confound attempts to fit explanatory statistical models, promoting the risks of identifying artifactual relationships.

Discussion

Our model is focused on aspects of food supply, especially seasonality and predictability, which are hard to incorporate into analytical models of an individual's reliance on stored capital for breeding. We begin by discussing the effects of food supply on capital breeding in our model, together with the broader relevance of these findings to studies of capital and income breeding. We then move on to discuss two intriguing features of the model: the relative difficulty of generating income-breeding scenarios (in spite of the prevailing view that these are the preferred strategies of endotherms; Jönsson 1997) and the strong influence of offspring development.

Finally, we discuss limitations of the model and future directions for research.

Effects of food supply

Our simplified representation of pinniped life history suggests that, in the absence of other constraints on strategy, aspects of food supply alone can determine that females will follow capital, income, or intermediate strategies. Our simulations also suggest that aspects of food supply can interact in complex ways, affecting both the viability of the environment and the emergent strategies of females in viable situations (Fig. 4). As far as it is possible to generalize about the effects that we studied, capital breeding tended to be favored by higher food availability (cf Johnson 2006) and seasonality, whereas higher predictability and storage costs tended to reduce reliance on capital, in keeping with previous findings (Fig. 3). At least within the range of parameter space that we explored, the effects of increasing the costs of carrying fat reserves appeared to be less pronounced than those of overall food availability and seasonality.
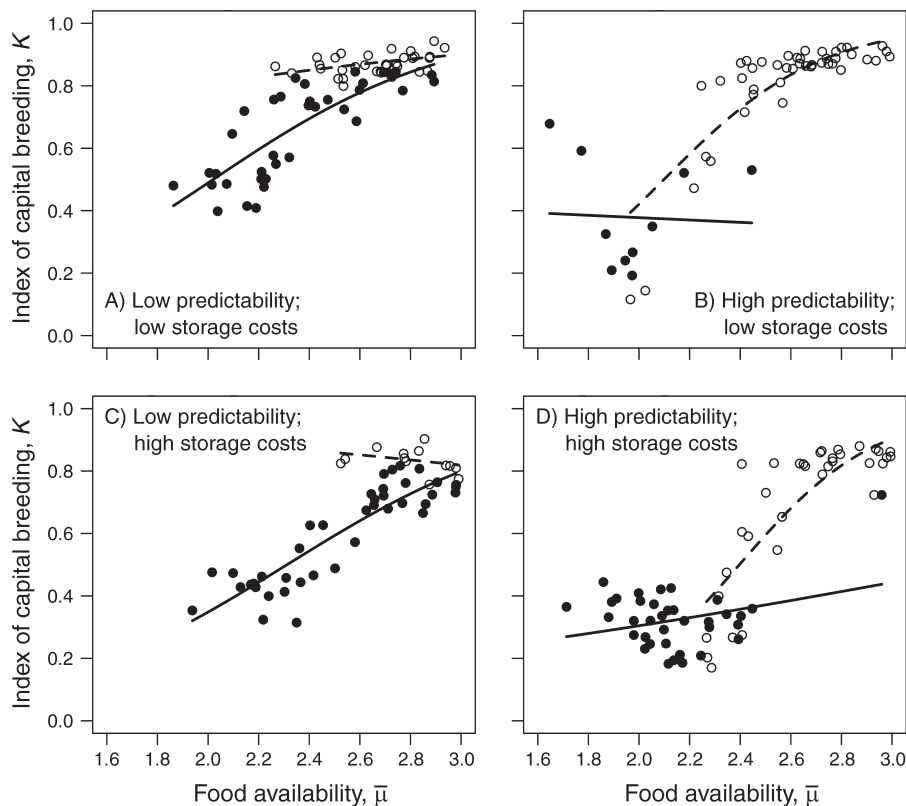
FIG. 4. Effects of parameters on the index of capital breeding, K, when $q_{1/2} = 180$. Each panel shows K as a function of annual mean food availability, $\bar{\mu}$, for low ($v < 0.55$; solid circles and solid lines) and high ($v > 0.55$; open circles and broken lines) seasonality. Predictability is low ($p < 0.86$) in panels (A) and (C) and high ($p > 0.86$) in panels (B) and (D). Mass-dependent costs are low ($c < 3.39$) in panels (A) and (B) and high ($p > 3.39$) in panels (C) and (D). Fitted lines are shown only for ease of visualization and were obtained by modeling logit(K) as a linear function of $\bar{\mu}$ and back-transforming. Fitted lines for low seasonality (solid lines) in panels (B) and (D), and for high seasonality (broken line) in panel (C) were nonsignificant ($P > 0.05$).

That increasing the costs of carrying fat reserves had a negative effect on the extent of capital breeding was expected (Trillmich and Weissing 2006, Houston et al. 2007), and we do not consider that outcome further here. Instead, we focus on the effects of food availability, seasonality, and predictability.

To some extent, the effects of aspects of food supply can all be explained with reference to two phenomena. First, in pure energetic terms, income breeding is much more expensive than capital breeding. This can be seen from the much greater maternal overheads (sensu Fedak and Anderson 1982) associated with income breeding (see Fig. 1B), and also from examining the overall amounts of energy required to finance offspring provisioning in the two strategies (e.g., Appendix C: Fig. C3 shows examples of capital and income breeding; energy spent on lactation and metabolism is about five times greater in the income-breeding example). Second, in our model, the only costs to accumulating capital arise from increased metabolic expenditure. This means that capital accumulation is a self-limiting process, but it also suggests that there is no reason why females should not store capital whenever possible. These two phenom-

ena combine to promote capital breeding wherever possible and help to identify why food availability, seasonality, and predictability have the observed effects. Specifically, increased food availability makes it much easier to accumulate capital, allowing females to opt for the greater efficiency of capital breeding. Likewise, in highly seasonal environments, and especially those associated with relatively abundant food, periods of high food abundance provide good opportunities to accumulate stores and wean offspring rapidly, before recovering stores in advance of periods of low food abundance. When seasonality and food availability are high, the extent of predictability makes little difference; however, when conditions make accumulating capital harder, some degree of unpredictability can actually promote the ability to accumulate capital. Furthermore, in unpredictable environments, income breeding becomes an increasingly risky strategy, because the chances of obtaining income reliably over a long period are low.

Identifying the effects of different parameters in our model was made more difficult by the influence of those same parameters on the regions of parameter space

explored. This might suggest that we should not have constrained the regions of parameter space that we explored; however, models that encompass large regions of biologically inapplicable parameter space are seldom looked on favorably. In spite of this limitation, our model does highlight the point that, when females can raise more reserves than the minimum required for birth, some degree of capital investment is expected. In a stochastic world, regardless of the form of mass-dependent costs, females will seldom raise exactly the minimum reserves required for birth (unless there are some additional penalties for carrying reserves that are not included in our model). Rather, in some years females will fail to raise the required reserves (resulting in year-skipping; Pomeroy et al. 1999, McKenzie et al. 2005), whereas in other years they will raise excess reserves, resulting in some degree of capital breeding (e.g., Boyd et al. 1997).

In the Pinnepedia, specifically, phylogenetically controlled analyses of factors affecting breeding strategies suggest that extant strategies are constrained by a range of coevolved traits, including body size, metabolic rate, mammary gland physiology, and behavior, including choice of breeding substrates (Schulz and Bowen 2005). Consequently, it is hard to identify reasons for the original divergence by studying extant strategies. Nevertheless, Schulz and Bowen (2005) build on the work of Costa (1993) to suggest that the evolution of large body size among phocids enabled them to exploit colder waters and patchier prey. A number of positive feedbacks ensued, all of which promoted an abbreviated lactation; these included improved fasting ability, breeding on pack ice, and producing high-lipid milk (Schulz and Bowen 2005). Our modeling is consistent with this interpretation. However, rather than patchier prey, our results emphasize the importance of seasonally high abundances of prey in enabling the adoption of more energetically efficient capital-breeding strategies. In this way, there is no need to invoke any of the additional pressures (such as the need for ice-breeding to avoid predation) to explain the selective advantages of capital breeding for ancestral pinnipeds exploiting higher latitudes.

The role of seasonally abundant prey in promoting capital breeding might be reflected in current distributions of pinnipeds. For example, phocids tend to occur at higher latitudes than otariids (Riedman 1990:61), and otariids show negative relationships between the duration of offspring provisioning and latitude (Schulz and Bowen 2005). Among birds, species that exemplify high levels of capital breeding (e.g., Adelie Penguin *Pygoscelis adeliae*, Lesser Snow Goose *Chen caerulescens*, and Common Eider *Somateria mollissima*, Meijer and Drent 1999) are also strongly associated with more extreme latitudes, especially during the breeding season. For cetaceans, the picture is less clear. Different populations of the same species might vary substantially in their exploitation of different latitudes (Martin and Reeves

2002) and in their movements between latitudes (Stevick et al. 2002). Vast size differences among extant cetaceans suggest that coadaptations associated with offspring-provisioning strategies might conceal the origins of those strategies. Nevertheless, it is interesting to note that, although the earliest cetaceans are recognized from the tropical waters of the eastern Tethys Sea, the earliest mysticetes (the suborder associated most strongly with capital breeding) have been identified from the waters of the late Eocene Antarctic (Heyning and Lento 2002).

Foraging by independent offspring and the prevalence of capital breeding

Our model was designed with the potential to include the physical separation of feeding and pupping locations. For obvious reasons, such a separation is thought likely to promote capital breeding (Bonnet et al. 1998), especially if foraging intervals are sufficiently long to cause mammary gland regression (Reich and Arnould 2007). However, the vast majority of viable scenarios in our model were toward the capital breeding end of the continuum (see Fig. 1A); consequently, the major challenge was to determine conditions that would lead to viable income breeding. Thus, we did not explore further aspects of model design that might promote capital breeding.

That capital breeding emerged so readily from our model is intriguing. Income breeding is often viewed as a preferred strategy for endotherms (Jönsson 1997), with capital breeding arising only in adverse conditions, such as when food is scarce or unreliable (Trexler and DeAngelis 2003, Johnson 2006). In light of this, pinnipeds appear to be more akin to the view on ectotherms held by Bonnet et al. (1998) than to Jönsson's (1997) view of endotherms. There are two possible reasons for this. First, regardless of whether they follow an income- or a capital-based strategy, marine mammals need to convert their intake into milk prior to supplying it to their offspring. This means that the costs of conversion will be similar for the two strategies. Second, the costs of maintaining stored capital also appear to be fairly low for marine mammals. In our model, these costs are included only through an increase in the metabolic cost of foraging (which is a cost only in the sense that it reduces the rate at which further capital can be accumulated). Whether there are other costs to capital storage (such as increased disease or predation) is unclear; however, that these are not obvious does challenge the perception that storage is inherently costly. Indeed, fat storage might even confer benefits from increased insulation in some environments. Overall, if significant costs of fat storage cannot be identified in pinnipeds, our model suggests that neither time pressures (due to ice breeding; Stirling 1983, Bowen et al. 1985), separation from food resources (Costa 1993), nor even body mass (e.g., Boyd 1998, Lydersen and Kovacs 1999, Trillmich and Weissing

2006) need be invoked to explain the origin of capital breeding in pinnipeds.

In terms of its ability to produce a range of strategies comparable to the observed variety among pinnipeds, the performance of our model was mixed. The range of maternal overheads (proportion of maternal energy expenditure during weaning that is spent on maternal metabolism, ~0.2–0.7; see Fig. 1B) is well in line with the range of maternal overheads collated by Schulz and Bowen (2005): hooded (*Cystophora cristata*) and harp (*Pagophilus groenlandicus*) seals, 0.2–0.3; Antarctic (*Arctocephalus gazella*) and northern (*Callorhinus ursinus*) fur seals, 0.7–0.8. Another straightforward comparator to observed systems is the length of the weaning period. In this respect, our model performed less well. Although it captured a range of strategies from weaning periods of a few days (comparable to those of hooded seals; Bowen et al. 1985) to about four months (again comparable to Antarctic and northern fur seals; Schulz and Bowen 2005), the model never predicted some of the more extreme durations of lactation that have been observed in at least 12 species of fur seals and sea lions (frequently in the range of 200–550 days; Schulz and Bowen 2005). That these strategies never arose in the model suggests that they cannot easily be explained with reference to aspects of food supply. One possible explanation lies in the fact that several otariid species can suckle both a yearling (or even older) pup and a newborn pup, while simultaneously pregnant (Trillmich 1986); whether this results in survival of the newborn appears to depend on the abundance of food (Trillmich and Wolf 2008). This exposes a fundamental constraint in our model, which only permits a female to suckle one young at a time. Relaxing this limit would greatly increase the computational burden, but might be worthwhile to explore the origins of these very long weaning periods.

The individual factor that most strongly influenced whether capital or income breeding emerged from the model was associated with the development of foraging ability among weaned young (see Fig. 2E). Given the sensitivity of the model to factors affecting the value of independent young, even subtle effects, such as basing the relative fat content of weaned young on a phocid, might have biased the model toward capital-breeding outcomes. Despite considerable work on the development of diving ability (Prewitt et al. 2010, Villegas-Amtmann and Costa 2010, LaRosa et al. 2012), the development of foraging ability itself is poorly understood, making the process of offspring development difficult to model with confidence. Particularly important in this regard is our assumption that the foraging competence of young seals developed only after weaning, thereby being related only to the time since weaning and not to the age of the pups as well. Otariid pups typically reach independence after many months of active learning, swimming, and diving (e.g., Fowler et al. 2006, Jeglinski et al. 2012). Moreover, the intensity of active learning appears to be higher among species reaching independence at a younger age (Arnould et al. 2003). To a lesser extent, pups of bearded (*Erignathus barbatus*) and ringed (*Pusa hispida*) seals also learn to swim and dive during the nursing period (Lydersen and Kovacs 1999). By contrast, the pups of most other phocid species are weaned very rapidly, are relatively inactive during the lactation period, and reach independence often without having entered the water (Lydersen and Kovacs 1999); rapid development of foraging ability is thus critical (Zeno et al. 2008). Differences in age and experience at weaning might well underlie the substantial differences in pup survival after weaning (e.g., 19% of capital-breeding northern elephant seal *Mirounga angustirostris* pups survive to breeding age, compared to 38% of income-breeding northern fur seal pups) (Arnould 1997). Differences in the development of foraging ability appear to be strongly associated with maternal provisioning strategies and strongly suggest a role for pup behavioral development in determining the length of the lactation period (a suggestion that is further reinforced by the limited impact of supplemental feeding on the time to weaning; Arnould et al. 2001). The different requirements for pup behavioral development among pinniped species remain poorly understood and a primary area for further investigation, especially in light of the consequences for maternal provisioning strategies.

Model constraints and future directions

Our results should be viewed in light of several important caveats. Framed in the context of annual routines that maximize lifetime reproductive success, our model is necessarily more detailed than previous models of offspring provisioning in pinnipeds (Costa 1993, Boyd 1998, Trillmich and Weissing 2006). In spite of this, it does not include every aspect of pinniped life history, admit the full range of offspring rearing strategies (e.g., simultaneous lactation of more than one offspring), or consider individual variability in provisioning strategies (e.g., Crossin et al. 2012). Neither does it consider the role of offspring in determining the timing of independence, a consideration that would require a game-theoretic approach to resolve. In Appendix D, we discuss our assumptions about several aspects of pinniped life history and physiology that might have a bearing on model outcomes, including: our emphasis on levels of energy reserves, rather than age, as the major state variable; our assumption that offspring are born in a fixed condition (rather than allowing variable levels of in utero investment); our focus on maternal provision of energy, rather than on other nutrients important to offspring development; and our omission of the processes of mating and molting and the impacts of these demands on female allocation of time. These considerations might all have limited our ability to reproduce the specific life histories of pinnipeds, but do not undermine our more general interpretations

regarding the influence of food supply on the evolution of capital- and income-breeding strategies.

The heuristic value of model construction is often overlooked as a benefit of modeling studies. Collating the required information for our model has highlighted a number of poorly understood processes that would benefit from further research. These include pup development, as discussed previously. In addition, we were greatly limited in our ability to ascribe costs to the accumulation of energy stores. Such costs have been considered for birds (e.g., see Witter and Cuthill 1993) and are often assumed to apply to other taxa also (Higginson et al. 2012). However, we were unable to find evidence for any costs of fat storage among pinnipeds. Indeed, even the metabolic consequences of fat storage (which should probably be regarded as limitations, rather than costs) are difficult to ascertain. Our simplistic approach was to treat metabolic rate while active as rising linearly with the amount of stores. A rigorous treatment of the problem would almost certainly require a detailed model of fluid dynamics. A further insight from our model is that, even with a relatively liberal cap on maximum daily intake, foragers might often be unable to take advantage of seasonally abundant food (e.g., see Appendix C: Fig. C1A, B). This raises the intriguing possibility that seasonality might affect many foragers as much through variation in the predictability of resources, as through variation in their abundance. In addition, the cap on potential intake has the effect that above a certain level of unpredictability, foragers will be unable to take full advantage of good days. This means that increasing daily unpredictability beyond a certain level will be equivalent to decreasing mean food availability. This might explain the relatively weak effect of predictability in the model, in spite of the parameter's known importance in dictating energy storage (McNamara and Houston 1990, Houston and McNamara 1993). Ideally, it would be possible to examine the effects of interannual unpredictability, and this remains a challenge for life history modelers.

CONCLUSIONS

Our model shows that food parameters can have a strong impact on the extent of female reliance on capital during offspring rearing. Factors that increase the ability of females to accumulate significant energy reserves (including higher overall food availability and seasonality of resources) tend to favor reliance on capital, which, in turn, enables more energetically efficient breeding. These general findings should apply to other taxa. Our results highlight that pinnipeds do not conform well to more general assumptions about endotherms, specifically because they do not appear to incur significant costs from capital accumulation. This point could be general to marine mammals (for which the costs of carrying additional mass might be low relative to those incurred by terrestrial taxa). As such, our model highlights the need for a better understanding

of the true costs of capital accumulation in these and other taxa. The early divergence of capital- and income-breeding strategies in several taxa might have arisen as different types of environment were exploited. Given that optimal strategies are now associated with a range of coadaptations, this does not require that taxa remain divided in terms of the resources they exploit. Nevertheless, capital breeding among extant pinnipeds and birds, as well as in ancestral cetaceans, seems to be strongly associated with higher latitudes. A particularly poorly understood process that had a strong impact on model outcomes is that of the development of offspring foraging competence. Our model highlights the need to understand pronounced differences in offspring maturity at independence among taxa in which both capital- and income-breeding strategies are seen.

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SUPPLEMENTAL MATERIAL

Appendix A

Dynamic programming equations (*Ecological Archives* E095-074-A1).

Appendix B

Additional details on energetics and modeling (*Ecological Archives* E095-074-A2).

Appendix C

Additional figures to illustrate methods (*Ecological Archives* E095-074-A3).

Appendix D

Limitations of the model for capturing pinniped life histories (*Ecological Archives* E095-074-A4).

Supplement

C code for dynamic modeling of pup rearing decisions by adult female pinnipeds, plus simulations using optimal strategies (*Ecological Archives* E095-074-S1).