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ORIGINAL ARTICLE

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Lactation patterns of pinnipeds are not explained by optimization of maternal energy delivery rates

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Abstract Within pinnipeds, phocids and otariids show differing maternal care strategies. Phocids rear young out of body stores in a yearly cycle with a single stay ashore when the mother fasts while lactating, whereas otariids provision their young by repeated foraging trips to sea alternating with brief stays ashore where they suckle their young. In a previous optimality model, these differences have been interpreted as adaptations based on differing energy requirements of large (phocid) and smaller (otariid) species, and the time budget of the large elephant and the much smaller Antarctic fur seal were correctly predicted. Our refined model—extended to pinniped species of all sizes—predicts lactation strategies to shift from attendance cycles to 1-year cycles with increasing body mass and provides an explanation for the finding that phocid pups are weaned at lower relative mass than otariid pups. However, other predictions do not correspond to empirical findings. In particular, the model does not explain the behavior of large otariids and small phocids. Thus, maternal metabolic requirements alone appear insufficient to explain observed lactation patterns. In the light of our results, we discuss more generally the scope and limitations of optimality models when applied in a comparative framework to a group of related species.

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Introduction

Mammalian parental strategies evolved to deal with extreme energy demands during brood care. In addition to maintaining their own metabolism, female mammals have to support a litter of dependent young through lactation. Energy management strategies during this period have been described as a continuum ranging from strict “income” to “capital” breeding (Drent and Daan 1980). Income breeders, as one extreme, support all of the additional energy requirements for parental care out of their daily food intake, whereas, capital breeders may fuel their needs entirely, or partially, out of energy reserves stored in the body during a previous time period. Small animals are unable to store enough energy and, thus, must rely mainly on the income strategy during brood care (see Meijer and Drent 1999; Klaassen 2003 for a review of this continuum in birds). In contrast, large animals can store sometimes huge amounts of energy as fat stores (Lindstedt and Boyce 1985) out of which they may fuel all or most of the additional costs during the breeding period.

In pinnipeds, lactation patterns have been described and understood as closely related to phylogeny (Gentry and Kooyman 1986): True seals (belonging to the family Phocidae) were characterized as following the fasting strategy in which mothers come ashore after a prolonged period at sea, give birth, and stay with the pup, fasting until weaning. This maternal strategy corresponds to extreme capital breeding. In contrast, otariids (family Otariidae) and, in a modified form, the walrus (family Odobenidae) seem to follow an income strategy (Trillmich 1996; Boyd 2000). They stay only briefly with the pup after parturition and, thereafter, follow an attendance cycle strategy in which the mother alternates between fasting ashore while suckling the pup and foraging at sea away from the pup, which stays ashore waiting for its mother's return. This cycle is repeated until weaning. Table 1 provides examples for species of both families. Because rearing strategies appear to correspond to the taxonomic division at the family level, it was generally assumed that they represent a phylogenetic constraint.

To explain these differences in maternal strategy along the lines of taxonomic division, Costa (1993) explored how optimal use of maternal resources leads to short lactation periods in phocids to minimize the metabolic overhead, i.e., the cost of maintenance metabolism of mother and pup ashore during lactation. A lower metabolic overhead should result in a more efficient lactational transfer of resources from mother to pup. However, as pointed out by Boyd (1998), this argument would imply that lactation periods should be extremely short, as in the 4-day lactation of the Hooded seal (*Cystophora cristata*; Bowen et al. 1985). In addition, some small phocid seals were found to forage during the lactation period similar to otariid seals (Lydersen and Kovacs 1993; Boness et al. 1994; Bowen et al. 2001), suggesting that lactation patterns represent adaptive suits related to body size. To resolve this problem, Boyd (1998) took the argument one step further by including time and energy costs to the mother, not only those accruing ashore, but also those during foraging.

To understand the differences in maternal strategies of phocids and otariids as adaptations to size-dependent foraging conditions, Boyd (1998) developed an optimality model suggesting that the different strategies relate to inevitable, size-related differences in time–energy budgets. He asked which maternal strategy (i.e., just one provisioning cycle per year, as in phocids, or multiple cycles per year, as in otariids) would maximize the delivery rate of energy to shore. Energy delivery rate was used as a fitness criterion since a more efficient delivery of energy to shore leads to more rapid growth of the pup, resulting in greater mass at weaning and an increased chance of survival (Hall et al. 2001; McMahon et al. 2000). Boyd applied his model to two contrasting pinniped species, the Southern elephant seal (*Mirounga leonina*), a large-sized capital breeder (adult females weigh from about 400–900 kg) and the much smaller (about 40-kg female body mass) Antarctic fur seal *(Arctocephalus gazella*), which is a typical income breeder following the attendance cycle strategy. The model analysis revealed that elephant seals need much higher food density (environmental quality) in the marine ecosystem to achieve a positive energy balance on short foraging trips than the much smaller Antarctic fur seals, even though elephant seals were assumed to have much lower relative metabolic rates at sea than fur seals. Hence, the two different provisioning strategies might indeed be viewed as adaptations related to body size, as body size determines the ability to make efficient use of a given food resource close to or far away from the colony. In conclusion, Boyd argued that the maternal strategies in pinnipeds reflect size-related adaptations to environmental circumstances rather than phylogenetic constraints.

To investigate the generality of Boyd's arguments, we extend his model to pinnipeds of all sizes. By using allometric scaling relationships, all aspects of the maternal strategy will be viewed as functions of a single variable,

Table 1 Time budget data for one cycle of foraging at sea (time at sea, t_s) and attendance ashore (time ashore, t_a) for some well-studied otariids and phocids $t_t/2$ (half travel time) estimates travel time from shore to foraging areas (see text)

Species[a]	Mass (kg)	Time ashore t_a (days)	Travel time $t_t/2$ (days)	Time at sea t_s (days)	References[c]
Otariids					
Galápagos fur seal	29	1.0	0.1	1.5	1
Antarctic fur seal	39	2.1	0.6	4.3	1
Northern fur seal	41	2.2	0.4	6.9	1
Juan Fernandez fur seal	48	5.3	0.5	12.3	2, 3
Subantarctic fur seal	50	3.8	1.4	12.0	3, 4
Steller sea lion	200	0.8	0.1	1.0	5, 6
Phocids					
Harbor seal	85	(24.0)[b]	–	341.0	3
Harp seal	139	12.0	–	353.0	3
Grey seal	190	15.5	–	349.5	3
Hooded seal	213	4.0	–	361	3
Weddell seal	447	47.0	–	318.0	3
Southern elephant seal	525	24.0	–	341.0	3

$t_t/2$ (half travel time) estimates travel time from shore to foraging areas (see text). Note that the Harbour seal does not correspond well to the classical phocid pattern as it tends to forage during lactation

[a] Galápagos fur seal (FS): *Arctocephalus galapagoensis*; Antarctic FS: *A. gazella*; Northern FS: *Callorhinus ursinus*; Juan Fernandez FS: *A. phillippii*; Subantarctic FS: *A. tropicalis*; Steller sea lion: *Eumetopias jubatus*; harbor seal: *Phoca vitulina*; Harp seal: *Pagophilus groenlandicus*; Grey seal: *Halichoerus grypus*; Hooded seal: *Cystophora cristata*; Weddell seal: *Leptonychotes weddelli*; Southern elephant seal: *Mirounga leonina*

[b] Harbor seals are known to forage during lactation (Boness et al. 1994)

[c] (1) Gentry and Kooyman 1986; (2) Francis et al. 1998; (3) Schulz and Bowen 2004; (4) Georges et al. 2000; (5) Merrick and Loughlin 1997; (6) Calkins et al. 1998

maternal body size. We also remove several unrealistic aspects of Boyd's model, including the lack of any coupling between processes of storage at sea and delivery ashore and the absence of an explicit starvation threshold for the pup ashore. Even so, we still treat the pup in an overly simplistic way. It is considered a passive receiver of energy, and its developmental dynamics are not taken into account. In the Discussion, we go back to the limitations this implies. With the refined model, we will be able to compare energy delivery to shore for animals of different sizes, at different distances from food resources, and for differing food abundance at sea. Based on this information, we will determine which strategy optimizes energy delivery rates under various constraints and environmental circumstances. By employing the simple allometric relationship and, thereby, extending the model to a group of related species, we avoid the danger of, perhaps, overfitting an optimality model to the life history of an individual species and, thereby, getting close to adaptive story telling. An explicit comparative approach should allow judging the model results more critically in a broader context and should make it easier to detect its shortcomings. By this refined analysis, we hope to get a better idea whether, and to what extent, the diverse lactation patterns found in pinnipeds can indeed be explained on the basis of size-dependent metabolic requirements.

The model

We first briefly reiterate the salient features of Boyd's (1998) model, thereby pointing out some problems with Boyd's approach. To overcome these problems, we reformulate the main assumptions in terms of the dynamics of maternal body reserves. By solving the dynamical equations, we then derive explicit formulations for the maternal time allocation throughout the season and an optimality criterion allowing us to calculate the time allocation pattern maximizing the rate of energy delivery to shore. In line with Boyd, we argue that the major model parameters are related to maternal body size in a systematic way. By deriving allometric scaling relationships for these parameters from the literature, we arrive at a set of predictions that should be applicable to pinnipeds of widely varying sizes.

Boyd's model

Boyd (1998) assumed that a foraging and lactation cycle of length t can be subdivided into the time t_a spent ashore suckling the pup and the time t_s spent at sea. The time at sea can further be subdivided into the time t_t spent travelling to the foraging grounds and the time t_f spent foraging. Hence,

$$t = t_a + t_s = t_a + t_t + t_f. \tag{1}$$

The energy expenditure of the mother is given by

$$e(t_a, t_s) = m_a t_a + m_s t_s, \tag{2}$$

where m_a and m_s denote the maternal metabolic rates ashore and at sea, respectively. Boyd assumed that the metabolic rate ashore is three times the basal metabolic rate (BMR), while the metabolic rate at sea strongly depends on the size of the animal. In fact, he assumed that m_s=1×BMR for a large pinniped (400 kg), while m_s=4×BMR for a smaller animal (40 kg). Hence, larger animals have a substantially lower specific energy expenditure at sea than smaller ones.

When foraging, the mother gains energy at a rate α, where the value of α reflects environmental quality. Hence, the total energy gain during a foraging trip is

$$g(t_f) = \alpha t_f. \tag{3}$$

Finally, the delivery of energy to the pup ashore was assumed to be given by

$$d(t_a) = k \cdot \left(1 - e^{-\beta t_a}\right), \tag{4}$$

where k corresponds to the energy storage capacity of the mother, while β represents the rate of delivery of energy to the pup.

Boyd assumed that pinnipeds tend to maximize the delivery of energy to shore per time unit,

$$F(t_a, t_s) = \frac{d(t_a)}{t_a + t_s}, \tag{5}$$

subject to the energy balance equation

$$d(t_a) = g(t_f) - e(t_a, t_s) \tag{6}$$

i.e., subject to the constraint that total energy delivery to the pup corresponds to the net energy gain of the mother. For a fixed travel time t_t, Eq. 6 is an equation of the two variables t_a and t_s (as t_f=t_s−t_t), allowing to write t_a as a function of t_s. Hence, $F(t_a,t_s)$ is essentially a function of the single variable t_a, and the value of t_a maximizing F is readily calculated.

Although we agree, in general, with the above model formulation, we see several points where the model does not seem to be realistic:

(1) The linear gain function while foraging at sea (Eq. 3) potentially leads to the accumulation of unreasonably high energy reserves if a mother stays at sea for a long period of time.

(2) The foraging efficiency of a female is solely determined by the parameter α indicating environmental quality. Accordingly, the size of a female has no effect on her foraging efficiency. However, it seems likely

that larger females would be better at exploiting a given food resource because larger animals are more efficient divers (Kooyman 1989).

(3) In Boyd's model, mothers can spend an unreasonably long period of time at sea. While Boyd introduced starvation thresholds for mothers ashore and pups while the mother is at sea, these thresholds had no influence on the maternal decision to return to the pup while she was foraging. In reality, the mother's decision on when to return from the foraging grounds should be affected by the fact that, in the meantime, the pup might starve to death.

(4) To avoid delivery of excessive energy stores to the pup ashore, the parameter k was introduced in Eq. 4 as an upper limit to maternal body reserves. Assuming k to be fixed corresponds to assuming that the maternal body reserves are independent of maternal energy gain and energy expenditure. In other words, this assumption completely uncouples the dynamics of gain processes at sea from unloading of reserves ashore. We consider this lack of connection between the loading and unloading of energy reserves the most unrealistic aspect of Boyd's model.

A model based on maternal energy reserves

Our model is similar in spirit to Boyd's model, but it systematically focuses on the dynamics of the body reserves R of the mother. We assume the dynamics of R is described by the differential equation

$$\frac{dR}{dt} = \begin{cases} -\beta R - m_a & \text{when delivering ashore} \\ -m_s & \text{when traveling at sea} \\ \alpha - \gamma R - m_s & \text{when foraging at sea} \end{cases} \tag{7}$$

As in Boyd's model, the mother has a fixed metabolic rate m_a ashore and a fixed metabolic rate m_s at sea. When delivering ashore, the pup extracts a fixed proportion β of the maternal body reserves per time unit. When foraging, the energy reserves increase due to food uptake that is dependent on α, where α reflects environmental quality and the foraging efficiency of the female (see below). However, in contrast to Boyd, the transformation of food into body reserves is assumed to proceed at a diminishing rate characterized by the parameter γ. As a consequence, energy storage is limited and can never exceed the value

$$R_{\max} = \frac{\alpha - m_s}{\gamma}. \tag{8}$$

According to our model, a typical foraging cycle has the following properties (Fig. 1). At time t=0 the mother comes ashore with R_0 body reserves. While ashore, the body reserves are reduced due to energy intake by the pup and the mother's metabolism. In this period, the body reserves change according to the equation

$$R(t) = R_0 \cdot e^{-\beta t} - \frac{m_a}{\beta} \cdot \left(1 - e^{-\beta t}\right). \tag{9}$$

At time t_a, when the mother leaves again for the following foraging cycle, her body reserves have been depleted to the level R_a=$R(t_a)$. The mother has used an amount $m_a t_a$ for her own metabolism; the rest of the reduction in reserves, R_0−R_a has been delivered to the pup:

$$d(t_a) = R_0 - R_a - m_a t_a. \tag{10}$$

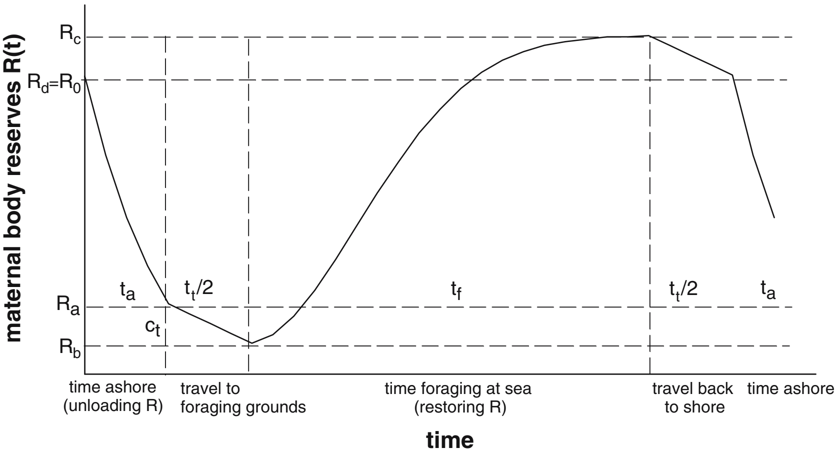

Fig. 1 Maternal reserves (R) as a function of time ashore and time at sea. At time t=0 the mother comes ashore with R_0 body reserves. When she leaves again after t_a time units, her reserves have been depleted to level R_a. During the trip to the foraging area, her reserves are further depleted by an amount c_t. Having arrived at the foraging ground with reserves $R_b = R_a - c_t$, the female accumulates reserves to a level R_c, which cannot exceed the asymptotic maximum $R_{\max}$. After travelling back, the mother arrives ashore again with reserves $R_d = R_c - c_t$. We assume R_d=R_0, i.e., the state of the mother at the end of a foraging and lactation cycle is the same as at the start of the cycle

During the trip to the foraging grounds, the maternal body reserves are reduced linearly (with slope $-m_s$), yielding body reserves

$$R_b = R_a - \frac{1}{2} m_s t_t = R_a - c_t \tag{11}$$

upon arrival at the foraging grounds. The term $c_t = \frac{1}{2} m_s t_t$ corresponds to the metabolic cost of the trip to the foraging grounds, which takes $\frac{1}{2} t_t$ time units. On the foraging ground, body reserves increase again according to

$$R(t) = R_b \cdot e^{-\gamma t} + R_{\max} \cdot (1 - e^{-\gamma t}), \tag{12}$$

where, for simplicity of notation, the arrival time at the foraging grounds corresponds to t=0. When the mother leaves the foraging grounds after t_f time units, her reserves have increased to a level R_c=$R(t_f)$. The return trip to shore reduce these reserves again by $c_t = \frac{1}{2} m_s t_t$, such that the mother arrives ashore with reserves $R_d = R_c - c_t$.

Model analysis

In line with Boyd (1998), we assume that the maternal state at the end of the cycle equals her state at the start: R_d=R_0. In other words, net energy storage when foraging has to equal total energy expenditure when ashore and when travelling:

$$R_c - R_b = R_0 - R_a - 2 c_t. \tag{13}$$

Using this consistency requirement and assuming a fixed travel time t_t, we can now calculate the time t_a spent ashore to transfer a given amount of energy to the pup, thereby reducing maternal energy reserves by R_0–R_a,

$$t_a = \frac{1}{\beta} \cdot \left[\ln\left(R_0 + \frac{m_a}{\beta} \right) - \ln\left(R_a + \frac{m_a}{\beta} \right) \right] \tag{14}$$

and the time at sea t_s required to achieve the corresponding energy gain

$$t_s = \frac{1}{\gamma} \cdot \left[\ln\left(R_{\max} + 2 c_t - R_a \right) - \ln\left(R_{\max} - R_0 \right) \right]. \tag{15}$$

For any given combination of R_0 and R_a, we can now calculate the corresponding time ashore t_a and the resulting amount of energy delivered to the pup (which is given by Eq. 10). With the help of Eq. 15, we can also calculate the time at sea and, hence, the total length of the foraging and attendance cycle. Taken together, this yields $F(t_a, t_s)$, the amount of energy delivered to the pup per time unit (see Eq. 5), which is assumed to be maximized by natural selection. For each parameter combination, we can, therefore, determine the optimal combination of R_0 and R_a and the corresponding optimal time budget t_a and t_s (Fig. 2). In the following, this strategy will be called the "unconstrained solution" of the optimality problem. We will compare this solution with two other ones: the "t_s-constrained solution", where only those combinations of t_a and t_s are considered when the time at sea is below the starvation threshold of the pup (see Fig. 2 and below), and the "one-cycle solution", where the situation of only one cycle between sea and land within a given year is considered (i.e., $t_a + t_s = 360$).

Parameterisation of the model

Boyd parameterized his model for two species, a 40-kg and a 400-kg pinniped. By making plausible assumptions on allometric relationships, we extend this range and make our model applicable to the whole spectrum of pinniped species. We take these two species (roughly corresponding to a subpolar fur seal and an elephant seal) as broadly delimiting the range of maternal body sizes, ignoring

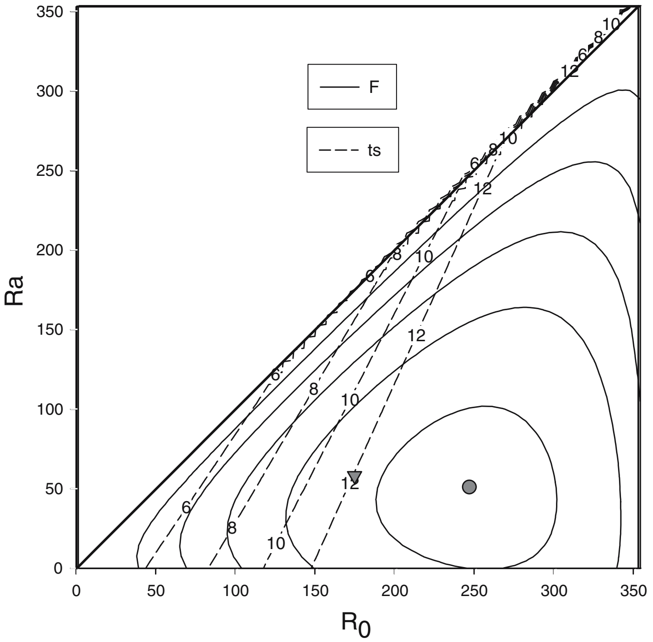

Fig. 2 Fitness isoclines for a species with body mass m=50 kg as a function of maternal reserves when returning from a foraging trip (R_0) and when leaving again for the next trip (R_a). In this example, fitness (F=energy delivery rate) is maximized for the combination R_0=245.5 MJ and R_a=50.5 MJ, corresponding to times t_s=19.5 days at sea and t_a=4.4 days ashore. However, this maximum is not feasible, as the pup starvation threshold (here t_a=12.0 days) prevents the mother from staying at sea until optimal body reserves are acquired. In this time-at-sea constrained case, the optimal solution corresponds to the combination R_0=173.0 MJ and R_a=50.5 MJ that maximizes fitness subject to the constraint t_s=12.0 days (see the *dashed* iso-t_s-*lines*). At this constrained solution, t_a=3.0 days. Other parameters in this example: t_t=6.0 days and EQ=40.0. The *circle* marks the unconstrained optimum, the *triangle* the time-at-sea constrained optimum

potential differences, for example in lipid storage, between phocids and otariids.

Metabolic costs ashore and at sea

Maternal metabolic costs are closely related to BMR. Following Boyd, and as the general applicability of Kleiber's law has been questioned (Dodds et al. 2001), we use the formula of Lavigne et al. (1986) that was specifically derived for pinnipeds:

$$BMR = 0.17 \cdot M^{0.87}\,[MJ/d],$$

where M denotes body mass in kilogram. Following Boyd, we assume that metabolic rate ashore is three times BMR:

$$m_a = 3 \cdot BMR = 0.5 \cdot M^{0.87}.$$

From empirical data, Boyd argued convincingly that the metabolic rate at sea, measured in multiples of BMR, will be lower in larger animals. To implement this, we use the allometric formula

$$m_s = 12 \cdot M^{-0.3} \cdot BMR = 2.0 \cdot M^{0.57}$$

This results in four times BMR for a 40-kg animal and two times BMR for a 400-kg animal, a reasonable estimate in the light of empirical evidence.

Foraging efficiency

Boyd implicitly assumed that energy intake and assimilation are mainly dependent on food availability and, hence, the productivity of the environment. Here, we take into account that, in addition, the intake rate will strongly depend on the size of the foraging animal. Larger pinnipeds are more efficient foragers than smaller pinnipeds, partly because the aerobic dive limit (ADL) increases with size (Kooyman 1989). As a consequence, larger divers can stay underwater longer without incurring an oxygen debt, particularly at maximum depth where prey is most likely encountered. To quantify the change in ADL and, hence, foraging efficiency, with body mass, we used the formula

$$ADL = 0.4 \cdot M^{0.25},$$

yielding a factor of 1.0 for a 40-kg animal and a factor of 1.8 for a 400-kg animal. We assume that energy intake rate α is given by the product of ADL and EQ, a measure of environmental quality or productivity:

$$\alpha = ADL \cdot EQ.$$

This means that in the same environment of quality EQ, a larger animal can achieve a higher intake rate than a smaller one. The parameter γ that describes the transformation of food into body reserves can be inferred from Eq. 8, as it is inversely proportional to $R_{\max}$, the maximal storage capacity of the mother. We assume that the maximal storage capacity (i.e., transferable lipids, excluding blubber layer lipids needed for thermoregulation, membranes, and the like) is about 7 kg of lipids (at 38 MJ/kg) for a 40-kg female and 115 kg for a 400-kg female (Costa 1993). Fitting this to an allometric equation leads to

$$R_{\max} = 3.3 \cdot M^{1.2}\,[MJ]. \tag{16}$$

Energy delivery

Following Boyd, we used actual data for various pinnipeds (Boyd's Fig. 1, excluding the outlying data point for the Hooded seal) to estimate energy delivery to the pup per day ashore [MJ/day] as a function of maternal body weight:

$$d(t_a)/t_a = 8.0 \cdot M^{0.4}$$

According to Eq. 7a, this corresponds to βR, where R is the amount of energy stored by the mother. Taking $\frac{1}{2} R_{\max}$ as a representative value for R, we can estimate β by

$$\beta = \frac{d(t_a)/t_a}{\frac{1}{2} R_{\max}} = 5.0 \cdot M^{-0.8}.$$

From the allometry of fat storage (Eq. 16) and that for BMR ashore, we assume that a young pup of a 40-kg pinniped, weighing about 4 kg, can starve for 10–12 days and that of a 400-kg pinniped for about 20–25 days. If so, the starvation threshold of the pup is given by

$$T = 3.7 \cdot M^{0.3},$$

yielding about 11 days for the newborn pup of a 40-kg pinniped and 22 days for that of a 400-kg pinniped.

Results

We demonstrate the model behavior by applying the model to three body sizes corresponding to a small (40 kg, e.g., Antarctic fur seal), an intermediate (200 kg, medium-sized phocid or large otariid female), and a large-sized species (400 kg, elephant seal-sized). These three examples cover the range of female body sizes in pinnipeds quite well. We will first use the allometric relationships outlined above and later explore how variation of these relationships affects our results.

Environmental quality

Figure 3 shows how the rate of energy delivery to shore (Eq. 5) increases with environmental quality (EQ). Given a fixed, intermediate travel time (t_t=3 days), delivery to shore initially increases rapidly with increasing EQ, but then levels off much more rapidly in the small animal than in the larger ones. At high EQ, delivery to shore is strongly and positively related to body size due to allometric increase in foraging efficiency and storage capacity. At low EQ, larger females deliver ashore less than smaller females and finally cannot achieve any positive energy gain at very low EQ because metabolism at sea (m_s) uses up more energy than can be gained through foraging at such low food availabilities. For a given travel time, small animals are able to successfully exploit environments that do not provide sufficient food for larger animals, even though the latter are assumed to be more efficient foragers. In case of a travel time of 1 day, for example, a 40-kg animal can survive whenever the environmental quality is above EQ=17, while a 200-kg and a 400-kg animal require an EQ of at least 29 and 36, respectively. Notice that these values are the thresholds for achieving energy balance (survival), but will be insufficient for raising a pup.

Figure 4 shows how environmental quality influences the time budget of females, again only considering a fixed travel time of 3 days. Over a wide range of high environmental qualities, time at sea t_s and, in particular, time ashore t_a change little. It is only towards low values of environmental quality that t_s tends to increase, while t_a simultaneously decreases. The stronger decrease in t_a at lower environmental qualities is typical for the lower range of t_s-constrained solutions, i.e., those solutions where time at sea is constrained in order to prevent starvation of the pup (t_s<T). In this range, model females cannot fully replenish reserves in the available time at sea, and, therefore, deliver less energy ashore which is depleted to C_t (the energy required for travelling to the foraging area) much faster, and, thus, leads to earlier departure from shore. At the very lowest environmental quality at which an animal of a given size

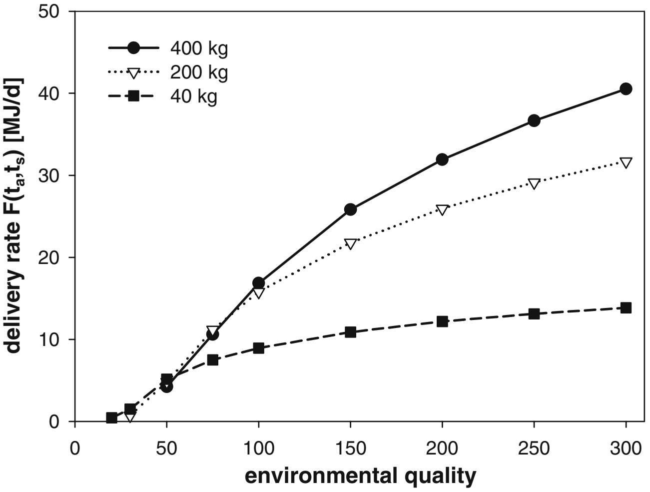

Fig. 3 Rate of energy delivery to shore (d(t_a)/t in MJ/d) as a function of environmental quality for females of three different body size classes (40, 200, and 400 kg). Travel time was fixed to 3 days in all three cases

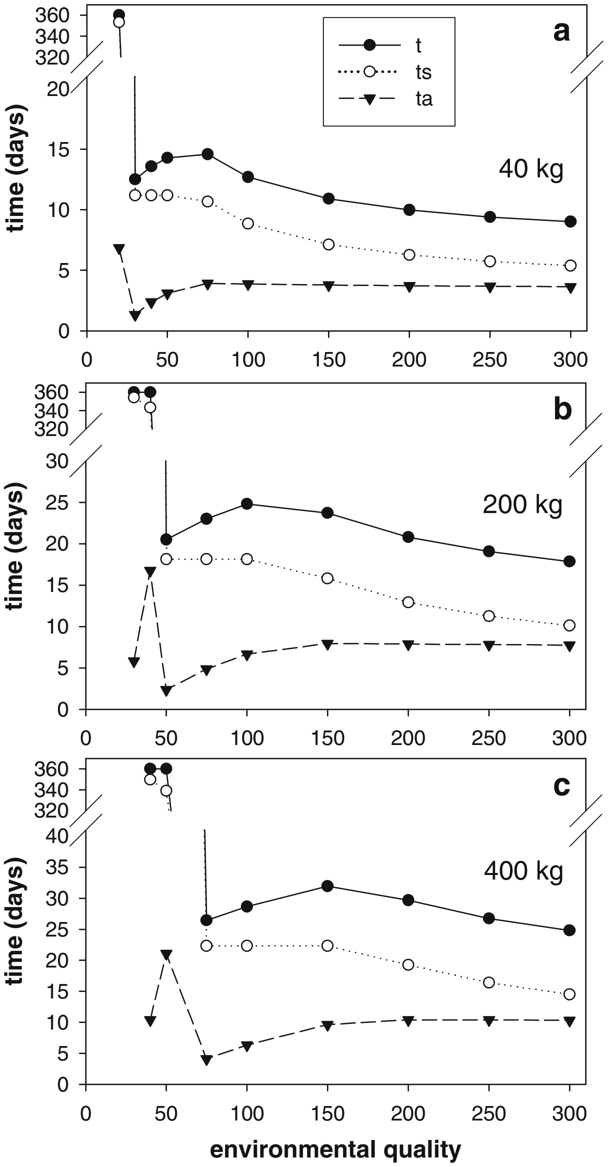

Fig. 4 Time budget of pinniped mothers as a function of environmental quality (EQ, arbitrary units). In all cases, travel time is t_t=3 days. Plotted are time at sea (t_s), time ashore (t_a) and the total time of a cycle ($t = t_a + t_s$) for females of body mass 40 (**a**), 200 (**b**), and 400 kg (**c**)

can still achieve a positive energy balance, a switch to a yearly cycle occurs, which then leads to a sudden increase in t_a. When comparing animals of different sizes, it becomes obvious that the optimal solution for larger animals always favors longer cycles. In absolute time, loading and unloading reserves take longer for larger animals.

Travel time

Travel time to the foraging area has the strongest influence on female time budgets (Fig. 5). At low environmental quality, as used in this figure (EQ=40), small mothers (40 kg; Fig. 5a) can find an unconstrained solution up to about a travel time of 0.5 days. At such low environmental quality, the number of cycles possible within 1 year drops rapidly with increasing travel time. Especially for the smaller animals, for a broad range of travel time ($0.5<t_t<5.5$), the optimal time budget is t_s-constrained, i.e., time at sea corresponds to the starvation threshold T of the pup. In that range, time ashore slowly declines with an increase in travel time. As a consequence, the number of cycles increases until $t_t>5.5$, where a single yearly cycle is the optimal solution. At the one-cycle solution, time ashore increases again, but for a small animal, only allows about 5 days ashore. For larger animals (Fig. 5b,c), the pattern remains essentially the same, but unconstrained solutions do not exist at this low environmental quality. Even for very low travel times, time at sea is constrained by pup starvation, and the one-cycle solution becomes optimal at travel times of 2–3 days. Larger animals have a wider range of one-cycle solutions than small females and are found to spend about twice as much time ashore. Delivery to shore in the range of one-cycle solutions is marginal at best for a small female. As environmental quality increases, the t_s-constrained solution becomes optimal over a wider range of travel times, and it replaces the one-cycle solution until it is, in turn, replaced by the unconstrained solution at EQ values above 80 to 100. The larger the animal the higher the environmental quality it needs to allow the unconstrained and t_s-constrained solution. Again, time ashore varies little. In the majority of environmental circumstances, the model produces optimal solutions in the range of multiple cycles. At long travel times, it depends mainly on environmental quality whether the optimal solution turns out to be a t_s-constrained or a one-cycle solution.

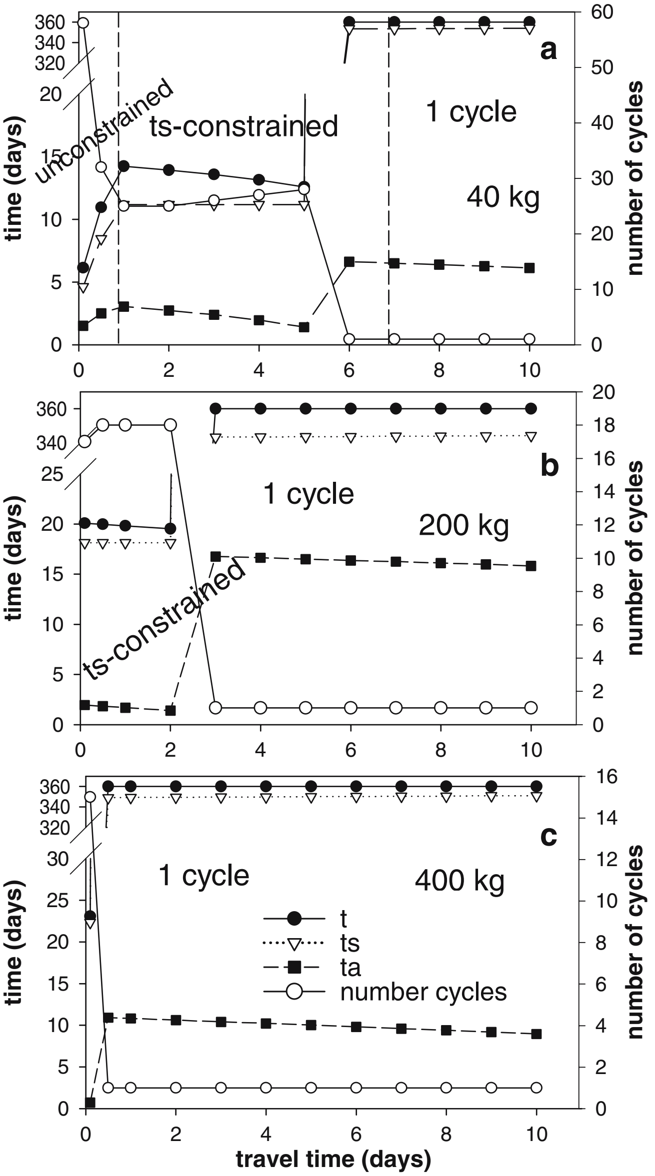

Fig. 5 The effect of travel time (t_t) on optimal maternal time budget and the resulting number of cycles per year for females of body mass 40 (**a**), 200 (**b**), and 400 kg (**c**). EQ is always 40. Vertical hatched lines separate the ranges where unconstrained, t_s-constrained and one-cycle solutions are optimal

Delivery to shore as a function of travel time

Travel time, i.e., the time it takes a mother to swim to and from the foraging site at sea to shore is the most decisive factor for energy delivery to the pup ashore. As shown by Fig. 6, females of all body sizes deliver increasingly less

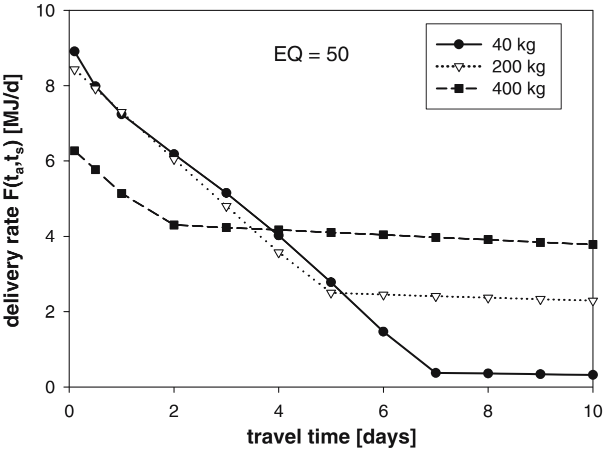

Fig. 6 Rate of energy delivery to shore as a function of travel time (t_t) for animals of three sizes. EQ=50

energy to shore as t_t increases. The rate of energy delivery to shore, $d(t_a)/t$, approaches very low levels when the yearly cycle becomes the optimal solution. For the 40-kg animal, this is only a theoretical solution as delivery ashore appears too small to raise a pup successfully. Note that energy delivery is greater for the 200-kg than for the 400-kg female up to a travel time of about 3.5 days, but is lower when it comes to a yearly cycle. The 200-kg animal has sufficiently lower metabolic rate at sea and ashore in the t_s-constrained range of solutions that it is able to transfer more energy to its pup over all of this range than the larger 400-kg animal.

From a pure energy efficiency point of view, a yearly cycle is most efficient for the mother as delivery of energy to the pup from body stores minimizes the energetic overhead, which, otherwise, needs to be paid for travelling to and from the foraging area and for metabolic expenditure of mother and pup during the periods when the mother is at sea replenishing her body stores for the next period ashore. Nevertheless, the yearly cycle is always the solution with lowest total energy delivery to shore. As demonstrated by Fig. 7 in our model, energy delivery to the pup, almost always, increases with the number of cycles, irrespective of animal size. This effect is most dramatic for the smallest animal. The next best solution, and one that is feasible under a wide range of environmental qualities, is a t_s-constrained strategy. For females of all sizes, this becomes the best strategy over a wide range of environmental qualities. Unconstrained optimal solutions only occur at high environmental quality and short travel times.

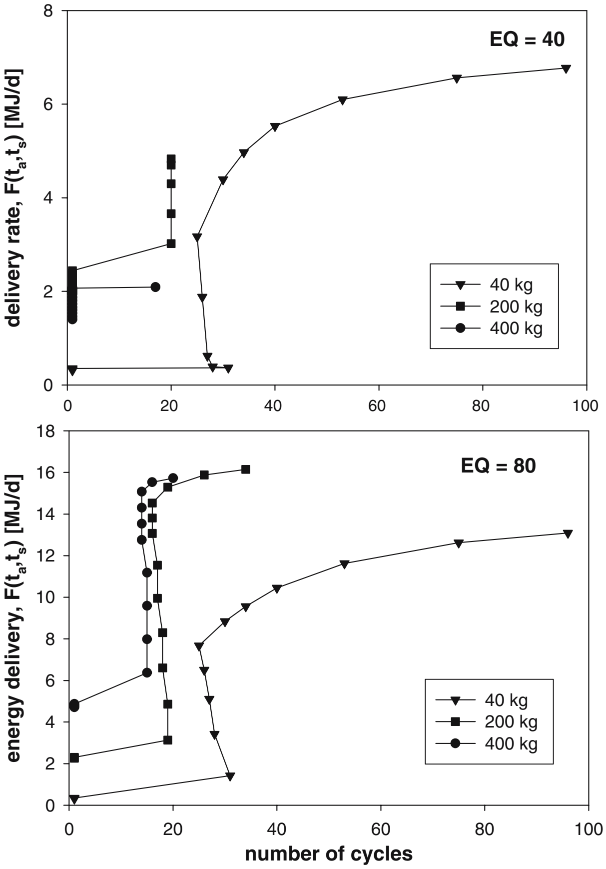

Fig. 7 Rate of energy delivery to shore as a function of the number of cycles at low (EQ=40) and intermediate (EQ=80) environmental quality. Travel time was varied from 0.1 to 10 days

Range of accessible solutions with body size

Figure 8 shows that the minimal environmental quality required for achieving a positive energy income solution increases with body size (right ordinate). For a given environment with low quality (EQ=40), larger animals must switch to a yearly cycle at shorter travel times to achieve a positive energy delivery. At higher environmental quality (EQ=90), the yearly cycle becomes optimal only at long travel times. Under those conditions, the smallest and the largest females (from 300 kg upwards) begin to switch to a yearly cycle as the optimal solution before medium-sized animals. Again, the yearly cycle is most probably not a solution that allows sufficient energy delivery to shore for the smallest animals.

Robustness of the model predictions

Allometric relationships are important ingredients in our model. While some of these relationships were directly derived from empirical data, others had to be inferred in a more indirect way. This holds, in particular, for the parameters characterizing the allometric relationships for the aerobic dive limit, ADL, the rate of energy delivery to the pup, β, and the rate of energy storage, γ. To check the robustness of our predictions, we increased and decreased the parameters involved in the equations for ADL, β, and γ by 50% and compared the results with those obtained for our standard parameter settings. Varying the ADL-relationship in this way changes the effect of body size on foraging efficiency and, thereby, influences time at sea. When ADL increases more steeply with body size, time at sea is

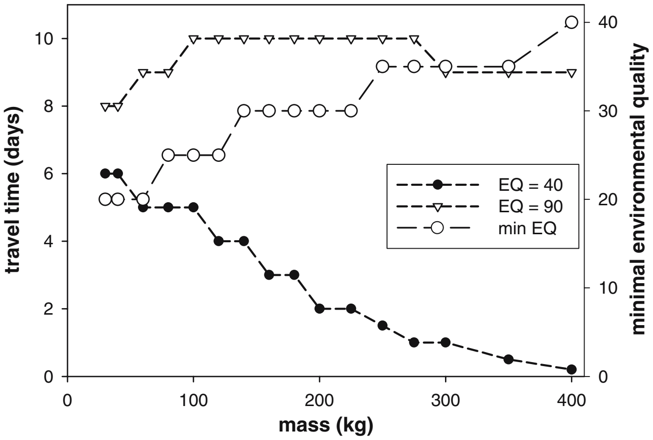

Fig. 8 Travel times at which the 1-year-cycle solution becomes optimal for animals of different mass for two environmental qualities (*left ordinate*). Also shown is the minimal environmental quality at which animals of different mass can find an optimal solution yielding a positive energy income (*right ordinate*)

reduced, allowing larger animals to operate at lower environmental qualities. For a given environmental quality, larger animals can deliver more energy to shore. A decrease of the parameters of the ADL-relationship has the opposite effect. Qualitatively, however, the system behaves very much the same as under standard parameter conditions. The same holds for a change in the allometric relationships for β and γ. Changing the relation between the rate of energy delivery and body size has an obvious effect on time ashore, but does not affect our results qualitatively. Finally, changing the relation between the rate of energy storage and body size shortens or increases time at sea and increases or decreases delivery to shore per unit time, but again does not change our qualitative conclusions.

Discussion

Our model extends the formulation presented by Boyd (1998) and provides a continuous description for pinnipeds of all sizes. Assuming that all processes can be described by appropriate allometric equations, it couples gains at sea with delivery to shore in a mechanistically meaningful way. Modelling maternal provisioning strategy in such a way can explain why small pinnipeds are more likely to provision offspring by attendance cycle strategies and why only larger ones can achieve a complete capital breeding solution. In this respect, our results support Boyd's (1998) conclusion that the yearly cycle in large animals is a consequence of large body size and long travel times. Larger animals need higher food availability to achieve a positive energy balance due to the higher metabolic rate at sea of larger animals. Besides body size, environmental quality and travel time to the foraging areas proved the most influential parameters determining delivery of energy to shore. The time-at-sea constrained solution proved an option over a fairly substantial range of parameters, extending the attendance cycle solution to lower environmental quality and intermediate travel times.

Travel time is the factor which influences most the maternal behavior in our model. Increasing travel time between shore and foraging site influences the range of feasible solutions even more than environmental quality. Increasing travel time above 1 day makes the unconstrained option unachievable for animals of most sizes. With intermediate travel times (about 3 days), time-at-sea-constrained solutions often proved optimal. Only at long travel times did the yearly cycle become better than the time-at-sea-constrained solution. For small animals, the one-cycle solution seems unachievable because storage capacity proves insufficient for fuelling the cost of travel, of maternal metabolism ashore, and sufficient transfer to the pup. We assumed that a 40-kg mother could store about 7 kg of lipids. Even if this were a slight underestimate of maximal body stores, it would constrain small pinnipeds to attendance cycle strategies under most environmental conditions. Moreover, for females of all sizes, the one-cycle solution leads to lower total transfer of resources to the pup. This result of the model is consistent across all body sizes. Even large animals, with their correspondingly larger storage capacity (Lindstedt and Boyce 1985), do not profit from one-cycle solutions unless travel time is long or local environmental quality low. Otherwise, large animals should choose the attendance cycle strategy. This result of the model agrees with the empirical finding (Costa 1993) that all phocid pups are weaned at lower relative body mass (around 30–35% of maternal mass) than otariid pups (in the range of 40–55%). This finding might also explain why smaller phocids follow a capital breeder strategy only at the beginning of lactation (when pup starvation threshold must be particularly low) and later on increasingly switch to a foraging cycle strategy (Boness et al. 1994; Bowen et al. 2001).

In all simulations, time ashore in an attendance cycle situation proved quite insensitive to the parameters and varied least among conditions. This agrees with emprirical observations, where, for example in Subantarctic fur seals (*Arctocephalus tropicalis*), time at sea varies from a mean of 10.8 days during summer to 22.7 days in winter, whereas, time ashore stays the same (3.8 and 3.7 days) (Georges et al. 2000).

Parameter estimates used here are surrounded by considerable uncertainty like, for example, the estimates of the influence of size on metabolic rate at sea and on diving ability as expressed in ADL. How large exactly the differences in environmental quality need to be to explain the switch from an attendance cycle to the one-year cycle with increasing body mass depends on the assumptions about BMR at sea and the scaling of ADL to body size. If large animals, relative to small ones, have lower metabolic rates at sea (in terms of multiples of BMR), as we assumed here, and if, at the same time, they are more efficient foragers due to a higher ADL-effect of size, then the difference between small and large animals in threshold environmental quality needed to reach positive energy balance is reduced. However, the model proves relatively robust to moderate changes in the parameters used and, therefore, the broad conclusions seem valid irrespective of uncertainties in these parameters.

Discrepancies between model results and empirical findings

While the model fits general trends quite well, closer scrutiny reveals a number of discrepancies. Table 2 lists predictions derived from the model (compare empirical values in Table 1).

Throughout, time ashore proved difficult to fit as it varied least with changing model circumstances. Only drastic changes in milk transfer rate influence maternal time ashore noticeably. Extreme rates of specific energy transfer would enable quick unloading of maternal reserves by the pup. Such an effect probably describes the exceptional case of the hooded seal where pups are weaned after only 4 days of nursing (Bowen et al. 1985). As this is highly efficient because it enables maximum transfer of reserves to the pup while the energy used up by maternal metabolism on shore is kept minimal, one would expect

Table 2 Model predictions for a few pinniped species

Species	Mass (kg)	Time ashore t_a (days)	Time at sea t_s (days)	Environmental quality
Otariids				
Galápagos fur seal	29	1.5	2.0	100
Antarctic fur seal	39	2.9	4.3	140
Northern fur seal	41	2.9	7.0	57.5
Juan Fernandez fur seal	48	3.2	11.3[b]	42.5
Subantarctic fur seal	50	3.6	11.4[b]	57.5
Steller sea lion	200	3.1	1.4	1000
Phocids		Time ashore	Travel time, t_t	Environmental quality
Harbor seal[a]	85	11.1	2.5	30
Harp seal	140	12.0	6	30
Grey seal	190	15.3	2	35
Weddell seal[a]	450	26.5	6	70
Southern elephant seal	525	24.0	7	57.5

Compare with empirical values in Table 1. Abbreviations refer to variables in the model. For otariids travel time—as the most influential parameter—was taken from observed values (Table 1). Subsequently, EQ was changed systematically to search for those values of time at sea and time ashore that best approximate the observed values. For phocids, time ashore was taken as the fixed value and travel time and EQ varied to provide the closest possible fit

[a] As expected, time ashore for Harbor seals and Weddell seals fits poorly, as these two species are known to feed during lactation

[b] t_s-constrained solution

that rates of transfer should always evolve to maximal values. This obviously has not happened in most pinnipeds and other mammals. There will be a cost to the fast transfer of reserves from mother to pup: One possible trade-off prohibiting such an adaptation of pup intake rate could lie in an increased metabolic rate of a highly active intestine, thus, inacceptably increasing costs to the pup during fasting intervals. Also, pups with extremely high specific intake rates will necessarily suffer a reduced ability to assimilate maternal resources (especially protein) for use in structural growth. This is supported by the observation that among all seals, the hooded seal, with its extremely short lactation period of only four days, has the highest relative lean body mass at birth and the lowest milk protein content (Oftedal et al. 1988), i.e., transfer after birth concerns lipids and hardly any structural growth is possible from birth to weaning. Thus, the patterning of milk flow may be important for the development of the pup, particularly with respect to protein transfer and growth of lean body mass, and not only total delivery to shore, as assumed here.

In contrast to the range over which we found the time-at-sea-constrained solution to be optimal, it seems the exception rather than the rule in real pinnipeds. Even though we do not have experimental measures of starvation thresholds, it is clear from observations on abandoned Galápagos fur seal pups that newborn pups will usually succumb after about 10–14 days without food (Trillmich, personal observation). Only the Juan Fernandez (*A. philippii*) (Francis et al. 1998) and the Subantarctic fur seal (*A. tropicalis*) (Georges and Guinet 2000) might follow the solution where maternal time at sea is constrained by pup fasting capacity (Table 2). Such a strategy produces lower delivery to shore than unconstrained multiple cycles, and appears risky if mother's return always cuts close to the starvation threshold of the pup. Simultaneously, it maximizes the cost of pup maintenance metabolism even if pup metabolism is curbed by specific adaptations to prolonged fasting periods, like reduced activity or maintenance of increased lipid reserves (Beauplet et al. 2003; Arnould et al. 2003). Furthermore, our analysis does not consider the risk of starvation to the mother under conditions of stochastic food returns. This may also influence maternal provisioning strategies as shown by Dall and Boyd (2002).

Model predictions deviate most from empirical observations for the Steller sea lion (*Eumetopias jubatus*). We have to assume extremely high environmental quality to approximate the observed time budget (Table 2). Of course, there is quite some uncertainty in the empirical data as well. For an apparently simple measurement like body mass, different authors provide widely differing means: Schulz and Bowen (2004) report mean body mass of Steller sea lion females as 275 kg, whereas, Calkins et al. (1998) report a mean of about 200 kg for fully adult females (estimated from Fig. 5 in Calkins et al. 1998). Similar variance surrounds estimates of travel time and time ashore. Nevertheless, the large discrepancy in the Steller sea lion values suggests that this species is following a different strategy. Steller sea lions do not follow the lipid storage allometry, which we assumed. They are relatively lean, with female body lipid content estimated at between 5 and 14% only (Pitcher et al. 2000), in strong contrast to the much fatter fur seals (about 25%; Costa and Trillmich 1988) and especially the phocids where lipid reserves are greater than 30% and may go up to 47% (Bowen et al. 2001; Beck et al. 1993).

Aspects of the dynamics of pup growth and development to independence are not addressed in our model, and this as well as our lack of attention to the increase in pup size over the lactation period may lead to deviations from empirical facts. We also ignored that pup starvation threshold must increase as the pup grows. Including the costs and benefits to the pup (its growth strategy) in the model should help to clarify advantages and disadvantages of the different strategies.

Optimality criteria

By restricting the model—for the time being—to maternal steady state, we have ignored that in subpolar otariids maternal mass may change over the lactation period (Boyd et al. 1997). Following Boyd (1998), our model uses a fitness criterion that only considers immediate benefits of maternal strategy, namely, energy delivery to the pup per unit time. This fitness criterion lacks a life history perspective and does not allow for trade-offs in terms of maternal survival or future fertility. We are fully aware of this limitation, and the discrepancies between model predictions and empirical findings mentioned above indicate that the model needs to be extended in terms of maternal reproductive value. It is known for several species that lactation leads to life history costs through reduced fertility in the next reproductive cycle (Trillmich 1986, 1990; Boyd et al. 1995; Sydeman and Nur 1994). To exclude a long-term life history perspective from the model might cause part of the discrepancies mentioned.

To explain the behavior of medium sized animals in the range of 200 kg, we need to build more detail into the model. Besides introducing a broader life history perspective, such modifications should also consider the pup as an active player in this game. Obviously, pups are not passive vessels into which maternal care is being pumped, but are under selection for an optimal growth strategy and storage dynamic themselves. Mother–offspring conflict might, therefore, also influence the solutions observed in nature. A combined mother and offspring life history perspective might allow conclusions, for example, why Steller sea lions store little lipid and follow the otariid pattern whereas equally large phocid seals maintain major lipid stores and evolved towards using the capital breeder strategy. Such discrepancies appear to point to physiological adaptations in pinniped lactation strategies, which are not directly related to energetic constraints as a consequence of size as suggested by Boyd (1998).

Concluding remarks

Frequently, the optimality approach has been accused of adaptive story-telling (Gould and Lewontin 1979). This criticism implies that models can be adjusted to the point where everything eventually fits. Modelling important aspects of a life history strategy for a whole group of animals avoids this trap. Deriving quantitative predictions from an explicit model for a larger group of animals, as we have done in this study for one aspect of pinniped life history, submits the model to a much harder, empirical test. Our attempt here serves as an example of the potential and the limits of such an approach. On one hand, we show that using relatively simple allometric considerations we can widen the scope of the optimality model qualitatively and quantitatively to a broader group of animals. On the other hand, the model has become quite complex even though we restricted ourselves to a simple optimality criterion (delivery of energy ashore) which while intuitively appealing does not include life history trade-offs. Such a simplification is not unusual in this research area, even though it has been shown (Houston and McNamara 1999) that energetic considerations can at best serve as a proxy to the real currency—reproductive value. Ideally, the model should be re-evaluated using reproductive value as the fitness criterion, an approach necessitating the inclusion of life history trade-offs. In addition, as pointed out above, a comprehensive model should also include the pup's perspective and, thereby, parent–offspring conflict between mother and pup.

Although superior in principle, a more comprehensive and refined modelling approach would have to face serious problems. The resulting models would become complex to the extent that the advantages of the optimality approach (elegance, heuristic value, and reduction of complex trade-offs to simple cost-benefit considerations) would largely disappear. Even more importantly, explicit modelling of the life-history nexus would necessarily shift the focus to aspects that vary qualitatively from species to species (e.g., mating system, sex differences, and differences in physiology and ecology). Such differences can no longer be captured by simple allometric equations, making it difficult, if not impossible, to apply the same optimality model to a broad class of organisms.

This highlights a general dilemma: in principle, a complete realization of the optimality approach based on the best available fitness criterion, reproductive value, is by far the most desirable option. There is little doubt that this should be the preferred choice in conceptual "toy models". In practical applications, however, such an approach is only applicable to individual species, as it relies on ecological and life history details that cannot easily be extrapolated from one species to the next. In such a limited context, the question again arises whether this does not end in adaptive story-telling as the model can be adjusted until it fits. It was just for this reason why we, and others, advocate the use of systematic inter-specific comparisons. To escape the dilemma indicated above, we can only hope that, despite of their theoretical limitations, simple energy considerations in combination with simple allometric relationships will turn out to be useful guiding principles for the understanding of allocation decisions in natural populations. Thus, the optimality approach may indeed be most useful when it makes qualitative and quantitative predictions in interspecific comparisons. However, the limitations mentioned above indicate that such modelling will be much more complex than perhaps expected a few years ago.

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