Energy reserve allocation in fasting Northern Elephant Seal Pups: inter-relationships between body condition and fasting duration

D. P. NOREN*†‡ and M. MANGEL§

‡*Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95064, USA, and* §*Department of Applied Mathematics and Statistics, Jack Baskin School of Engineering, University of California Santa Cruz, Santa Cruz, CA 95064, USA*

Summary

1. Organisms are forced to make trade-offs when allocating energy reserves during sustained periods of fasting.

2. For most animals, lipid catabolism is the preferred source of energy to safeguard important protein sources. However, marine mammals also have a compounding pressure to conserve some lipid stores. The main site of lipid storage in these animals is the blubber layer, which is not only an important energy source during fasting, but is also the primary thermal barrier when at sea.

3. To explain how the allocation of protein and lipid reserves during fasting are influenced by body condition (body mass and percentage lipid of total body mass), a dynamic state variable model that takes into account fitness consequences of different allocation strategies was developed.

4. This model was parameterized with respect to conditions faced by weaned Northern Elephant Seal (*Mirounga angustirostris* Gill) pups. It incorporates the independent effects of body mass and protein mass (the two state variables) on survival and the costs of utilizing either lipid or protein during the postweaning fast.

5. Predictions of lipid and protein allocation by the model were not significantly different from measurements on wild seals. Finally, the model showed that body lipid content and fasting duration both influence allocation of energy reserves.

Key-words: Dynamic state variable model, fasting metabolism, individual variation, lipid catabolism, protein catabolism

Functional Ecology (2004) **18**, 233–242

Introduction

Fasting plays a key role throughout the life history of Northern Elephant Seals, *Mirounga angustirostris* Gill. All activities on land (mating, nursing pups and moulting) are accomplished while abstaining from food and water for periods of 1–3 months (Le Boeuf & Laws 1994). Consequently, Northern Elephant Seals are champions of fasting, exhibiting some of the longest natural fasting durations.

These seals undergo their first fast early in their lives. They have a short suckling period of 28 days and are subjected to abrupt weaning (Le Boeuf & Laws 1994); maternal investment is terminated when the mother goes to sea, leaving the pup on the beach. At this point the pup is not capable of foraging on its own and remains on the beach to fast for up to 2·5 months, as it continues to develop and hone its swimming and diving skills (Reiter, Stinson & Le Boeuf 1978; Thorson & Le Boeuf 1994). Upon completion of the fast, the pup then goes to sea where it must forage and survive on its own. Thus, Northern Elephant Seal pups offer a particularly good system to study fasting physiology and behaviour.

The typical mammalian fasting pattern is described by three phases, characterized by specific fuel sources that are catabolized for energy. Glycogen reserves are utilized a few days after food deprivation; glucose (derived from protein) and ketone bodies (products of lipid catabolism) supply energy to the central nervous system, while energy supplied to the rest of the body is provided by the oxidation of lipid (Castellini & Rea

*Present address: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Blvd East, Seattle, WA 98112, USA.

†Author to whom correspondence should be addressed. E-mail: Dawn.Noren@noaa.gov

1992). During Phase I, glycogen reserves are almost completely utilized, and the mobilization of stored lipids is activated, as the body switches to fat oxidation and reduces protein catabolism. Phase II is characterized by increased oxidation of lipids, production of ketone bodies and partial sparing of proteins. Terminal starvation, or Phase III, occurs when 30–50% of body protein has been used for metabolism. At this point, lipid utilization falls, circulating ketones decline, and death can occur if fasting continues (Castellini & Rea 1992). Clearly, the entrance into Phase III terminal starvation is not adaptive for long-term fasting. The most reasonable solution for fasting adapted species would be to prolong Phase II, thereby sparing body protein for as long as possible, and to terminate the fast before the onset of Phase III.

One might assume that animals should avoid catabolizing prime protein sources, specifically cardiac muscle, which is depleted soon after other protein stores become limited in non-fasting adapted species (Goodman *et al*. 1984). However, for many species, large lipid reserves are also important for survival. For example, unlike terrestrial mammals, marine mammals store fat in a blubber layer, which serves as both the primary energy store during fasting periods and the primary thermal barrier in water. Blubber is also important for buoyancy and streamlining in these animals (Webb *et al*. 1998). Thus, the blubber layer is a critical adaptation for both the postweaning fast and the first foraging trip of Northern Elephant Seal pups. Theoretically, reduction of the blubber layer during the postweaning fast could result in a thermal challenge for the pups when they enter the ocean to forage for the first time. This exemplifies two conflicting functions of the blubber layer, an energy source to be utilized and a thermal barrier to be conserved (Nordøy & Blix 1985; Worthy & Lavigne 1987; Ryg, Smith & Øritsland 1988; Markussen, Ryg & Øritsland 1992). The balance of these functions may affect survivorship during the first foraging trip.

For the related Southern Elephant Seal, *Mirounga leonina* (McMahon, Burton & Bester 2000, 2003) and for the Grey Seal (Hall, McConnell & Barker 2001), first year survival is correlated with weaning mass. In contrast, there is no significant relationship between weaning mass and first year survival in Northern Elephant Seal pups (Le Boeuf, Morris & Reiter 1994). Both Southern (Carlini *et al*. 2001) and Northern (Noren 2002a; Noren *et al*. 2003) Elephant Seal pups are weaned with a wide range of body mass and total body lipid content. Unlike Southern Elephant Seals (Carlini *et al*. 2001), body lipid content (% lipid of body mass) is positively correlated with weaning mass in Northern Elephant Seals (Noren 2002a; Noren *et al*. 2003). Consequently, fasting physiology and behaviour that ensure that energetic and thermoregulatory demands are met during the postweaning fast and first foraging trip may be specific to each pup. As a result, patterns of lipid and protein reserve utiliza-

tion and the duration of the postweaning fast may vary among individual Northern Elephant Seals in order to maximize the chance of survival during the first foraging trip.

In this study we modelled how Northern Elephant Seal pups utilize their body energy reserves because we had the best available data for this component of the postweaning fast. To illustrate the role of individual variation in fasting metabolism, we developed a dynamic state variable model (Mangel & Clark 1988; Mangel & Ludwig 1992; Houston & McNamara 1999; Clark & Mangel 2000) that adaptively adjusts allocations of fat and protein to fasting metabolism according to anticipated effects on fitness. We compared performance of the model to predictions based on all energetic needs met by fat oxidation and to data from weaned Northern Elephant Seal pups fasting at Año Nuevo, California (Noren 2002a; Noren *et al*. 2003). We then made novel predictions of the patterns of allocation to be expected for pups representing a wide range of body mass and lipid content for multiple fasting durations.

Materials and methods

STUDY AREA AND SUBJECTS

Data for total body mass, lipid mass and protein mass from 40 weaned Northern Elephant Seal pups, captured twice during the postweaning fast at Año Nuevo, CA, USA in 1999 and 2000 (Noren 2002a; Noren *et al*. 2003) were used for construction of a dynamic state variable model predicting allocation of lipid and protein reserves during the postweaning fast of Northern Elephant Seals (Plastic Allocation Model, PAM). These data were also used to compute an estimate of the actual allocation during the fasting period between field captures for comparison with predictions made by the PAM and a model with all energetic needs met by fat reserves (Fixed Allocation Model, FAM). The complete empirical methods and results of the study on fasting weaned Northern Elephant Seal pups are reported elsewhere (Noren 2002a; Noren *et al*. 2003). Nineteen pups that were captured near the beginning of the postweaning fast but were not successfully re-captured were also entered into the PAM to make predictions for a larger range of body mass and lipid content.

THEORY

We constructed two models to predict body mass and protein content of Northern Elephant Seal pups after fasting periods of various durations. For simplicity, the state of a pup can be characterized by its body mass $B(t)$, lipid mass $L(t)$ or protein mass $P(t)$ at time t and all measured in kg; any two of the three implies the third according to (Table 1):

$$B(t) = L(t) + 3\cdot7P(t), \qquad \text{eqn 1}$$

Table 1. Parameters, interpretations and values in the dynamic state variable model

Parameter	Interpretation	Value
T	Length of the postweaning fast period	(1) Actual duration between captures
		(2) Hypothetical fast durations (32, 65 and 78 days)
$B(t)$	Body mass in kg at time t	
$P(t)$	Protein mass in kg at time t	
$L(t)$	Lipid mass in kg at time t	$B(t) - 3\cdot7P(t)$
$M(t)$	Metabolic rate in MJ at time t	$4\cdot5 + 0\cdot06B(t)$
	Energy provided from lipid mass lost in kg MJ^{-1}	$1/39\cdot3$
	Energy provided from protein mass lost in kg MJ^{-1}	$1/18$
C	Lipid content at time t	$L(t)/B(t)$

where the constant 3·7 accounts for the hydration state of protein. Besides lipid, protein and water, other materials in the body are negligible (<5% of body mass in phocid seals; Worthy & Lavigne 1983; Reilly & Fedak 1990) and are not utilized as major fuels during long-term fasting. Instead, lipid and protein are the main fuels utilized to meet energetic demands, and water is also lost during the catabolism of these tissues in fasting seals (Worthy & Lavigne 1983; Nordøy & Blix 1985; Worthy & Lavigne 1987; Castellini & Rea 1992; Worthy *et al*. 1992; Muelbert & Bowen 1993; Carlini *et al*. 2001; Noren *et al*. 2003). In what follows, we used body mass and protein mass, with lipid mass computed from the other two.

Metabolic demand as a function of body mass was derived from a regression equation that describes the relationship between average body mass and average daily energy from lipid and protein mass lost during the postweaning fast in 40 Northern Elephant Seal pups (see Noren 2002a; Noren *et al*. 2003):

$$M(t) = 4\cdot5 + 0\cdot06B(t), \qquad \text{eqn 2}$$

where $M(t)$ is metabolic rate in MJ day^{-1} and $B(t)$ is body mass in kg at time t. This metabolic need can be met by using a mixture of protein and lipid; in which energy gained from oxidation of lipid and protein are 39·3 and 18·0 MJ kg^{-1}, respectively (Schmidt-Nielsen 1997).

An allocation strategy consists of a sequence $\{a(t)\}$ representing the fraction of metabolic need on day t met by using lipid (so that $a(t)$ ranges between 0 and 1·0). Given a body mass $B(t)$ and protein mass $P(t)$ on day t (lipid mass is computed from equation 1), if allocation $a(t)$ is used to meet metabolic rate computed from equation 2, the dynamics of protein and lipid are:

$$P(t + 1) = P(t) - [1 - a(t)]M(t)/18, \qquad \text{eqn 3}$$

$$L(t + 1) = L(t) - a(t) M(t)/39\cdot3.$$

Body mass $B(t + 1)$ at day $t + 1$ is computed from equation 1.

PLASTIC ALLOCATION MODEL (PAM)

This dynamic state variable model (Clark & Mangel 2000) allows us to determine the optimal allocation of

body reserves (lipid and protein) to meet daily metabolic demands and maximize a measure of fitness. Measurements from pups in the field are taken at specific time intervals and only allow allocation estimates to be averaged for the fasting period between measurements (for example, see Noren 2002a; Noren *et al*. 2003). The dynamic state variable model has the additional feature of allowing for plasticity in allocation levels throughout the fasting duration.

The allocation of body reserves to meet metabolic needs for each day was determined by taking into account the fitness of the pups' present and future body conditions. We defined body condition C as the relative lipid content of each pup:

$$C(t) = L(t)/B(t). \qquad \text{eqn 4}$$

We modelled a fasting period of T days, fixed for each trial type and identical for all pups, except for the trial that tested fasting metabolism for the period of time between field captures.

The fitness proxy of our model is survival during the first foraging trip at sea, which is determined by minimum levels of fat necessary for insulation in the ocean and maximum levels of fat that would not hinder diving in the ocean owing to positive buoyancy. We set the lower critical level of $L(t)/B(t)$ to 0·20 because 2-week-old pups have adipose contents that are approximately 0·25–0·30 (Kretzmann, Costa & Le Boeuf 1993), and pups that are abandoned 2 weeks after birth do not survive to normal weaning age (4 weeks old) unless they are adopted and nursed by a surrogate mother (Le Boeuf, Whiting & Gantt 1972; Reiter, Stinson & Le Boeuf 1978). We set the upper critical level of $L(t)/B(t)$ at 0·65 because there have been no reports of pups having attained that level of lipid content. Furthermore, 45–180 kg pups that are 65% lipid are positively buoyant, with values ranging from 18·2 to 72·9 N (calculated according to methods in Webb *et al*. 1998). Extreme positive buoyancy may prevent pups from diving, consequently inhibiting foraging and making them easy targets for predators, such as Great White Sharks. In addition, critical levels of $B(t)$ and $P(t)$ were set at 48 kg and 7 kg, respectively, which are slightly lower than the lowest measurements made on a pup near the end of the fast (Noren 2002a; Noren *et al*. 2003). We defined fitness as:

$W(b, p, t)$ = maximum probability that a pup survives
to the first feeding at sea,   eqn 5

given that $B(t) = b$ and $P(t) = p$. We set the maximum value of $W(b, p, T)$ at 0·5 because mortality on the beach is low (<1%) for pups weaned in good condition (Reiter, Stinson & Le Boeuf 1978), and the survival rate at sea for pups weaned at 50 kg or greater is 46·0 ± 7·7% (Le Boeuf, Morris & Reiter 1994). Therefore, we set $W(b, p, T)$ = 0·5 for pups with lipid content ($C = L/B$) ranging from 0·28 to 0·50, which is the approximate range of lipid content for weaned pups greater than 50 kg (based on linear regressions of body mass and lipid content at weaning from Noren 2002a; Noren *et al.* 2003). For simplicity, we also assumed that $W(b, p, T)$ for pups with lipid content <0·28 decreases linearly from $W(b, p, T)$ = 0·5 until the lower critical level of lipid content (0·20) is reached, for which $W(b, p, T)$ = 0. Similarly, we assumed that $W(b, p, T)$ for pups with lipid content >0·50 decreases linearly from $W(b, p, T)$ = 0·5 until the upper critical level of lipid content (0·65) is reached, for which $W(b, p, T)$ = 0. Consequently, condition (lipid content) on day T is $C = L(T)/B(T)$; then fitness on that day is $W(b, p, T) = \Phi(b, p)$, where $\Phi(b, p)$ is equal to:

$$0 \quad \text{if} \quad C \le 0\cdot2, \qquad \text{eqn 6}$$

$$6\cdot25C - 1\cdot25 \quad \text{if} \quad 0\cdot2 < C < 0\cdot28,$$

$$0\cdot5 \quad \text{if} \quad 0\cdot28 \le C \le 0\cdot5,$$

$$2\cdot17 - 3\cdot33C \quad \text{if} \quad 0\cdot5 < C < 0\cdot65,$$

$$0 \quad \text{if} \quad C \ge 0\cdot65.$$

That is, at the end of the fasting period, the pup is either alive or dead, depending upon whether its fat is below the minimum or above the maximum critical levels for its mass. At any time previous, the challenge to the animal is to use resources so as to maximize the chance of survival.

In the model, for days previous to T, $W(b, p, t)$ satisfies the equation of dynamic programming determined as follows. First, set $m = 4\cdot5 + 0\cdot06b$, $p'(a) = p - (1 - a)ml/18$, $l'(a) = (b - 3\cdot7p) - am/39\cdot3$ and $b'(a) = l'(a) + 3\cdot7p'(a)$. Second, set

$$W(b, p, t) = \max_a W[b'(a), p'(a), t + 1], \qquad \text{eqn 7}$$

where $\max_a$ denotes that the value of a chosen maximizes $W[b'(a), p'(a), t + 1]$. This procedure is solved backwards and generates the optimal allocation sequence $\{a^*(t)\}$ and optimal survival probability.

Once the optimal decisions were computed, we used a forward iteration (Clark & Mangel 2000) to predict allocations for the 59 pups whose body mass and protein mass were determined at the beginning of the postweaning fast. The forward iteration allows us to predict individual allocations and individual mass dynamics.

FIXED ALLOCATION MODEL (FAM)

An alternative model is that the allocation of protein and lipid reserves is fixed and identical for all pups, regardless of body composition. For example, 100% of energetic requirements are met by fat oxidation only, as has been suggested by a previous study (Ortiz, Costa & Le Boeuf 1978). Since metabolic need, equation 2, includes lost protein energy that was not used to meet daily energetic requirements, but was incorporated into new pelage during the postweaning moult, which begins at weaning or shortly thereafter (Reiter, Stinson & Le Boeuf 1978), we adjusted the fat allocation level to account for protein energy utilized (approximately 12% of total energy lost during the fast, Noren 2002a; Noren *et al.* 2003) during the 1–3-week moulting process (Reiter, Stinson & Le Boeuf 1978). Consequently, in this model, $a(t)$ = 0·88 for all values of t, $B(t)$ and $P(t)$. In this case, the dynamics of body mass can be computed directly from equations 1–3.

ACTUAL ALLOCATIONS FOR THE COMPARISON BETWEEN MODELS AND DATA

We compared predictions of the PAM and FAM with actual allocations calculated from data collected on wild pups at Año Nuevo. For every pup, allocation was estimated from the individual's loss of body mass and change in body composition measured in the field. Average allocation was calculated as energy from the oxidation of total lipid mass lost between field measurements divided by the sum of energy from the oxidation of total lipid and total protein mass lost between field measurements (see Noren 2002a; Noren *et al.* 2003).

For the comparison of model predictions with field results, we assumed that if predictions from a model were congruent with field measurements, then we understand the allocation process. Specifically, if predictions from the FAM were comparable to field measurements, then allocation of energy reserves in fasting elephant seals is virtually identical for all individuals. Alternatively, if predictions from the PAM were more similar to field measurements, then allocation of energy reserves is variable between individuals and probably driven by the proportion of body fat reserves. Otherwise, if predictions from either model did not match measurements taken in the field, then important components are missing from the model.

Results

PREDICTED ALLOCATIONS AND BODY SIZE TRAJECTORIES FOR THE PLASTIC MODEL

Field measurements are time consuming and consequently limit sampling intervals and the number of
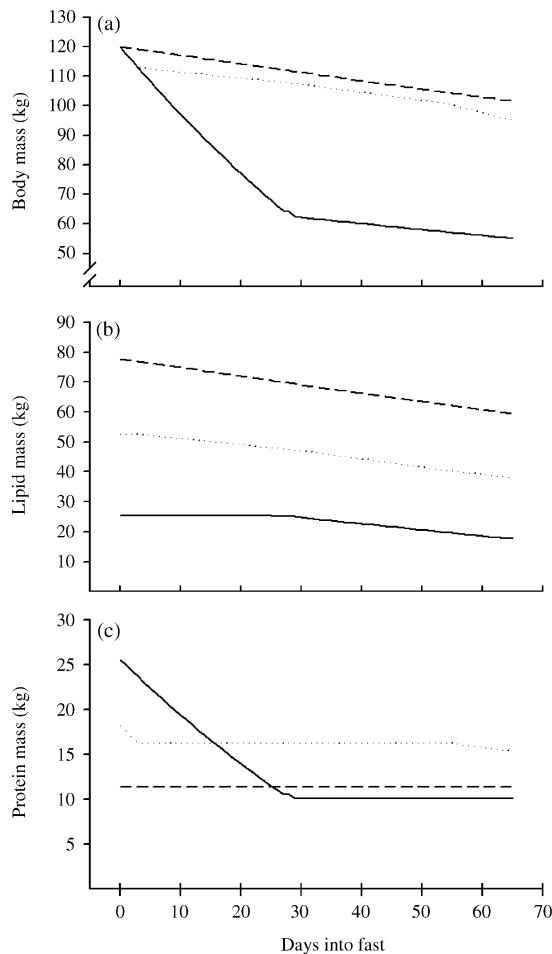
Fig. 1. Daily body mass (a), lipid mass (b) and protein mass (c) predicted for three Northern Elephant Seal pups by the Plastic Allocation Model for a 65-day fast. Daily levels are predicted for three 120-kg pups weaned with 21·1% lipid content (solid line), 43·9% lipid content (dotted line), and 64·9% lipid content (dashed line).

Fig. 2. Allocation of lipid energy to energy expended for fasting Northern Elephant Seal pups. The mean allocation + SEM of 40 pups during the interval between weaning and the second capture calculated from actual field measurements, predicted by the Fixed Allocation Model, and predicted by the Plastic Allocation Model are presented. Allocations significantly different from those calculated from field measurements are denoted by *. The sums of squares of the difference between the allocation calculated from field measurements and that predicted for each individual is 0·29 for the FAM and 0·09 for the PAM.

pups that can be studied. In contrast, models are able to predict how body energy reserves are utilized each day of the fast for a large number of pups, representing a large range of body conditions. Unlike the Fixed Allocation Model, the state-variable Plastic Allocation Model adjusts allocation levels for pups daily, based on current body mass and fat content. To illustrate the utility of the state-variable model, we summarize predicted body size trajectories for three 120-kg pups with distinct lipid contents (percentage lipid mass of total body mass) fasting for 65 days (Fig. 1). From these comparisons, we can see that there is considerable individual variation in the way that the animals are predicted to use lipid and protein stores (Fig. 1b,c).

COMPARISONS OF MODEL PERFORMANCE WITH FIELD MEASUREMENTS FOR RECAPTURED PUPS

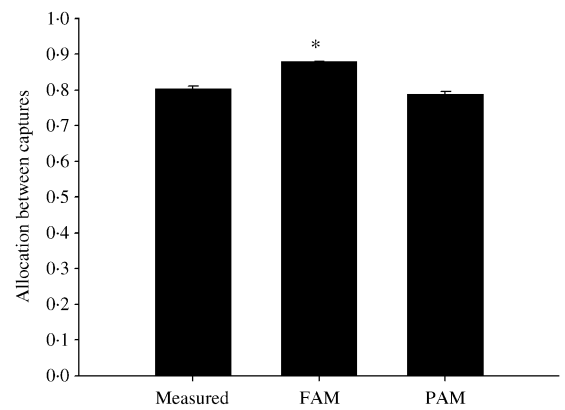To determine which model provides the most accurate prediction of allocation levels during a fast, we

compared allocation levels from the two models for the fasting duration between weaning and the second capture with actual allocations calculated from field data. Actual average allocations (mean: 0·80 ± 0·01 SEM) were significantly less than the allocation of 0·88 (i.e. all energetic needs met by fat catabolism) from the FAM (Mann–Whitney Rank Sum Test: $t = 2360·00$, $P < 0·001$; Fig. 2). For comparison between allocations predicted by the PAM and those calculated from field measurements, we determined average allocation between captures from the model's predictions of final body mass and changes in body composition, as was done for field data. Average allocation levels calculated from predictions of the PAM (mean: 0·79 ± 0·01 SEM) were not significantly different ($t = −1·49$, $P = 0·14$, power = 0·18) than actual average allocation levels calculated from field measurements (Fig. 2).

Although the PAM was fairly precise in predicting allocation levels, there was individual variation in the similarity between allocation levels calculated from field data and predicted by the PAM (Fig. 3). For 27 of the 40 pups, average allocation levels from the PAM were within 0·01–0·05 of those from field data; for 11 pups, allocation levels from the PAM fell within 0·06–0·08 of values from field data. The largest over-estimation of allocation predicted by the PAM was 0·10, and the largest under-estimation was 0·11; each was found for only one pup (Fig. 3). The symmetry of points about the 1 : 1 relationship line in Fig. 3 suggests that predictions made by the PAM were not directionally biased. Furthermore, despite the presence of individual variation, the results suggest that allocation levels predicted by the PAM were not inaccurate for any particular range of weaning body mass (Fig. 4a) or percentage lipid
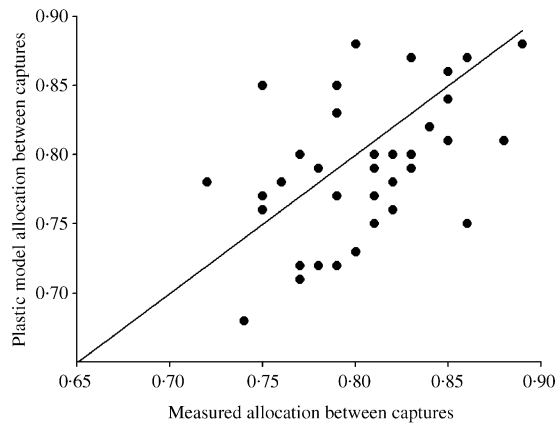
Fig. 3. Allocation of lipid energy to energy expended for fasting Northern Elephant Seal pups predicted by the Plastic Allocation Model in relation to those calculated from field measurements of the same individuals. Allocation levels of 40 pups during the fasting interval between weaning and the second capture and a line of equality are presented.
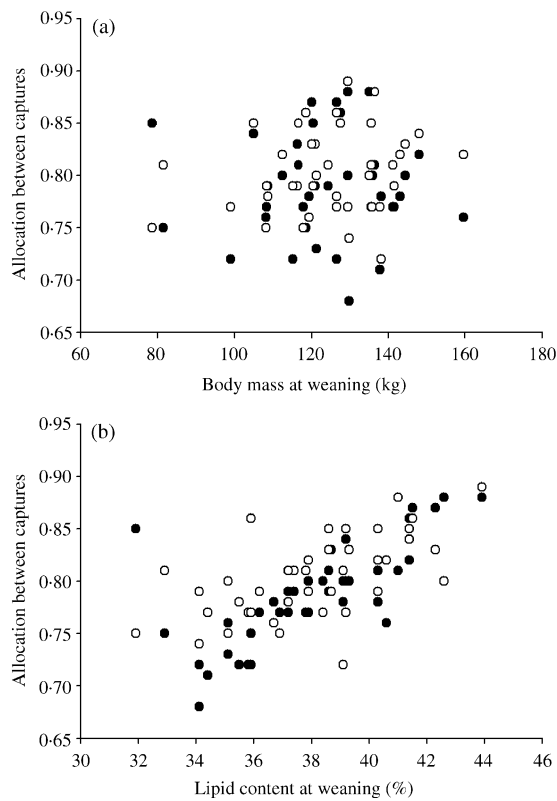

Fig. 4. Allocation of lipid energy to energy expended for fasting Northern Elephant Seal pups predicted by the Plastic Allocation Model and calculated from field measurements in relation to body mass at weaning (a) and lipid content at weaning (b) Allocation levels predicted by the PAM (closed circles) and calculated from field measurements (open circles) for 40 pups during the fasting interval between weaning and the second capture are presented.

Fig. 5. Body tissue mass measured for the second capture in the field and predicted by two models. Mean values + SEM of lean tissue mass (a) protein mass (b) and lipid mass (c) are presented for 40 pups measured in the field and predicted for the same pups by the Fixed Allocation Model and Plastic Allocation Model. Values significantly different from field measurements are denoted by *.

content (Fig. 4b). Finally, percentage lipid content at weaning was correlated with calculated allocations from field data ($r = 0.60$, $P < 0.001$, Fig. 4b) and PAM predictions ($r = 0.73$, $P < 0.001$, Fig. 4b). In contrast, weaning mass was not correlated with allocation levels (field
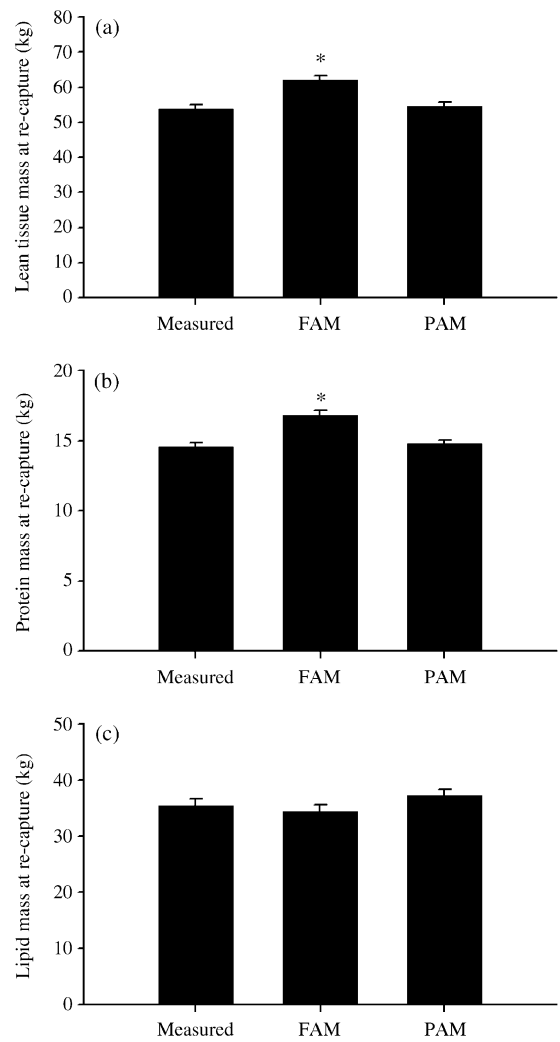
data: $P > 0.05$, power = 0.24; PAM: $P > 0.05$, power = 0.03; Fig. 4a).

To determine which model performs the best in predicting body condition at the end of a fast, we compared body condition (lean mass, protein mass, lipid mass, body mass and lipid content) predicted by the two models with those measured in the field at the time of the second capture. Predictions made by the PAM for lean tissue mass and protein mass did not differ from field measurements (Fig. 5a,b; lean mass: $t = -0.52$, $P = 0.61$, power = 0.05; protein mass: $t = -0.53$, $P = 0.60$, power = 0.05). In contrast, lean tissue and protein levels predicted by the FAM were significantly greater than those measured in the field (Fig. 5a,b; lean mass: $t = -5.06$, $P < 0.001$; protein mass: $t = -5.08$, $P < 0.001$). Lipid mass measured in the field did not differ from levels predicted by the PAM (Fig. 5c; $t = -1.09$, $P = 0.28$, power = 0.07) or the FAM (Fig. 5c; $t = 0.70$, $P = 0.49$,
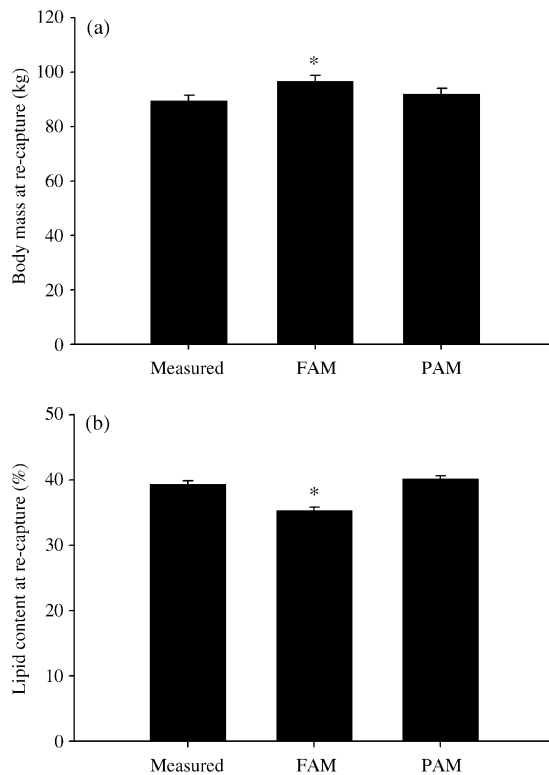
Fig. 7. Predicted average allocation of lipid energy to daily energy expended for fasting northern elephant seal pups predicted by the Plastic Allocation Model for multiple fasting durations. Mean values + SEM are presented for 59 pups that were measured at weaning in the field.

Fig. 6. Body mass and body condition measured for the second capture in the field and predicted by two models. Mean values + SEM of body mass (a) and percentage lipid content (b) are presented for 40 pups measured in the field and predicted for the same pups by the Fixed Allocation Model and Plastic Allocation Model. Values significantly different from field measurements are denoted by *.

power = 0·05). Predictions made by the PAM for total body mass and percentage lipid content did not differ from values measured in the field (Fig. 6; body mass: $t = -0·84$, $P = 0·40$, power = 0·05; lipid content: $t = -1·18$, $P = 0·24$, power = 0·09). However, the FAM predicted greater total body mass and lower lipid content than actual field measurements (Fig. 6; body mass: $t = -2·39$, $P = 0·02$; lipid content: $t = 5·51$, $P < 0·001$).

Because allocation and body condition levels predicted by the FAM differed from field measurements the most, we conclude that this is an inappropriate model for fasting weaned Northern Elephant Seal pups. Consequently, the remainder of the results focuses on the PAM.

PLASTIC MODEL PERFORMANCE FOR DIFFERENT FASTING DURATIONS

To evaluate model performance for different fasting durations, we compared predictions of allocation and body condition for 59 pups whose body condition at weaning was measured. We present results for multiple fasting periods (Fig. 7), including the minimum (32 days), the mean (65 days) and the maximum (78 days) fasting durations observed in the field (Noren 2002a; Noren *et al.* 2003). It is evident that the PAM
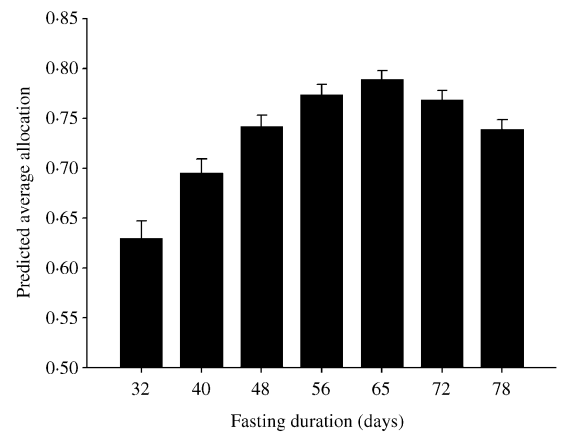
predicts allocation of body energy reserves to change with fasting duration (Fig. 7).

Discussion

The results show that the PAM is an accurate tool for predicting allocation of energy reserves and changes in body condition during the postweaning fast for Northern Elephant Seals weaned with a wide range of body condition. Differences in body condition, specifically lipid content, result in distinct predictions for allocation of energy reserves by the PAM. We find that besides lipid content, fasting duration is also important in determining allocation of energy reserves during the postweaning fast.

The PAM predicted fat oxidation to satisfy the majority of energy requirements during the postweaning fast, as has been shown previously in wild Northern Elephant Seal pups (Ortiz *et al.* 1978; Costa & Ortiz 1982; Castellini, Costa & Huntley 1987; Houser & Costa 2001). However, in contrast to previous studies that measured urine output (Adams & Costa 1993) and urea turnover (Pernia, Hill & Ortiz 1980; Houser & Costa 2001), the model predicts that protein utilization is more than a negligible fraction of total metabolism during the postweaning fast, ranging from 12 to 32%. Higher levels of protein utilization predicted by the model could be attributed to the different methodology used to estimate metabolism and the period of data collection in the field. Unlike previous studies, energetic requirements for the model were estimated from mass loss and changes in body composition with the first set of measurements taken soon after weaning. The postweaning moult begins at weaning or shortly thereafter, and the process takes 1–3 weeks to complete (Reiter, Stinson & Le Boeuf 1978). Consequently, the equation used to estimate energetic requirements for the model includes a portion of measured protein mass that is utilized for new hair growth during the

moult (approximately 60% of lost protein mass, Noren 2002a; Noren *et al*. 2003) and not for satisfying energy demands during the fast. As a result of this relatively high energetic demand, the model predicts higher levels of protein utilization than has been found previously (Pernia *et al*. 1980; Adams & Costa 1993; Houser & Costa 2001). Similarly, greater muscle protein utilization occurs during the moulting fast of King Penguins than during the non-moulting fast (Cherel, Leloup & Le Maho 1988). If we did not incorporate the energetic value of lost protein mass from both daily energy expenditure and the moulting process, accurate predictions of body mass and energy reserve content after fasting would not be possible. Because the moult occurs during the first few weeks after weaning, we would expect pups to exhibit the greatest relative utilization of protein reserves early in the fast. The highest levels of protein catabolism predicted by the model are early in the fast (Fig. 7).

The model also predicts that the utilization of fat and protein during the postweaning fast of Northern Elephant Seals is variable and depends on body condition (i.e. proportion of lipid and lean tissue) and duration of the fasting period. Equivalent results have been found previously. Fatter lactating female Northern Elephant Seals (Crocker *et al*. 2001) and weaned Northern (Noren 2002a; Noren *et al*. 2003) and Southern Elephant Seal pups (Carlini *et al*. 2001) lose proportionally more fat than thinner counterparts during fasting. The reverse is also true. Lactating adult female Northern Elephant Seals with lower percentages of adipose tissue (Crocker *et al*. 1998) and lean Grey Seal pups (Øritsland *et al*. 1985) maintain higher rates of protein utilization during a fast. Similarly, for other mammalian species and birds, individuals that are relatively fat at the beginning of a fast are able to achieve and maintain a lower rate of protein catabolism than leaner individuals (Goodman *et al*. 1980; Robin *et al*. 1988; Atkinson, Nelson & Ramsay 1996; and Hilderbrand *et al*. 2000). Finally, for lactating adult female Northern Elephant Seals, levels of protein catabolism increase with longer fasting durations (Crocker *et al*. 1998). The PAM also predicts that leaner Northern Elephant Seal pups utilize more protein reserves than fatter pups and that, generally, levels of protein catabolism increase for fasting periods greater than 65 days (the mean fasting duration). Lower allocation levels indicate both.

The PAM determines energy reserve allocation patterns in a manner that maintains body lipid content for adequate insulation and appropriate buoyancy. We did not integrate any physiological mechanisms involved in mammalian fasting metabolism in the PAM. Instead, patterns of fat and protein utilization were predicted based on fitness values associated with specific ratios of lipid and protein content in the body. The high level of accuracy of predictions by the model suggests that mechanisms involved in fasting have an adaptive functional role that is linked to the seals' eco-logy. In fact, differences in the ratio of blubber to core (protein and/or diffuse fat) tissue catabolism are attributed to the thermal demands of the environment in which seals fast (Worthy & Lavigne 1987). Sparing lipid reserves by catabolizing some lean tissue safeguards the insulating role of blubber; this may be especially important for Northern Elephant Seal pups that are weaned with relatively low lipid content. Upon termination of the fast, pups must have sufficient lipid stores for thermoregulation during their first foraging trip at sea because body condition influences thermoregulatory abilities of phocids in water (Irving & Hart 1957).

Allocations predicted by the PAM for multiple fasting durations follow a pattern similar to the three phases of fasting exhibited by other mammals, although the time span for Northern Elephant Seals is substantially longer. The predicted allocation pattern for fasting durations ranging from 32 to 78 days is: (1) mainly lipid reserve utilization but also a substantial level of protein reserve utilization for short fasting durations, (2) increased utilization of lipid reserves and decreased utilization of protein reserves for longer fasting durations and (3) decreased utilization of lipid reserves and increased utilization of protein reserves for fasting durations longer than the average of 65 days. Two other studies have found evidence of increased protein catabolism at the limit of fasting in Grey (Nordøy & Blix 1991) and Harp (Worthy & Lavigne 1983) Seals.

The focus of this model was related only to the trade-offs associated with utilizing lipid reserves to meet energetic demands during the postweaning fast while maintaining lipid stores at levels that provide adequate thermal insulation and appropriate buoyancy during the first foraging trip. There are certainly trade-offs associated with utilizing protein stores that were not incorporated into the model. Recognizing that depletion of protein stores leads to death, a minimum critical level of protein was incorporated into the PAM, but specific trade-offs associated with utilizing protein stores were not. Trade-offs associated with utilizing lipid and protein stores are probably both related to body condition at weaning. For example, the duration of fasting in obese rats is limited by lethal depletion of body proteins; while in lean rats, the duration of fasting is limited by lipid availability (Cherel *et al*. 1992). Even so, our model is very successful.

From the allocation patterns predicted above, it is clear that even fasting adapted animals cannot continually maintain fasting without eventually entering destructive Phase III. The obvious extension of this model is to determine how long these seal pups fast on land before entering the water to forage for the first time. Northern Elephant Seal pups are not capable of swimming and diving immediately after weaning, and thus require a period of development on land before initiating their first foraging trip (Thorson & Le Boeuf 1994). In fact, diving capabilities continue to develop during the first foraging trip and throughout the first

year of life (Thorson & Le Boeuf 1994). It is logical to assume that the duration of the postweaning fast may depend on body mass and lipid content at weaning (Noren 2002a; Noren *et al*. 2003), the rate at which energy reserves are utilized during the fast (Wilkinson & Bester 1990; Noren 2002a; Noren *et al*. 2003), the time it takes to reach a lower weight threshold (approximately 70% of weaning mass in Northern and Southern Elephant Seals; Wilkinson & Bester 1990), and the state of diving development. Other factors that could contribute to the departure of weaned seals from the beach are environmental temperature on the beach or oceanic conditions (Reiter, Stinson & Le Boeuf 1978). All pups leave Año Nuevo by mid-May when air temperatures become warmer (D. P. Noren unpublished observation). Pups may reduce total metabolic costs if they initiate the first foraging trip when air temperatures are warm, since metabolic rates measured in 20·9 °C air (approximate ambient air temperature on the beach at Año Nuevo) are higher than those measured in 3·8 °C water (approximate water temperature at depth in Monterey Bay, California, USA; Noren 2002a,b). Future research to determine other physiological or environmental factors that may contribute to dictating fasting duration is required to develop a model that predicts postweaning fasting duration in Northern Elephant Seal pups.

Acknowledgements

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