

Body Condition at Weaning Affects the Duration of the Postweaning Fast in Gray Seal Pups (*Halichoerus grypus*)

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ABSTRACT

Gray seals (*Halichoerus grypus*) undergo a terrestrial postweaning fast (PWF) that depletes energy reserves acquired during the suckling interval. Plasticity in PWF duration may ensure that pups of variable body condition depart for sea with adequate energy reserves. To test this hypothesis, we examined body condition of 30 gray seal pups at weaning and monitored their PWF duration. On average, fat accounted for $47.3\% \pm 0.7\%$ of their 53.2 ± 1.3 -kg weaning mass. Although fasting duration averaged 21 ± 1.1 d ($n = 28$), there was considerable variation in fasting duration (9 to >31 d) and the resulting age when pups departed to sea (26 to >49 d). Percent fat at weaning (38.6%–54.6%) was positively correlated with fasting duration ($n = 28$, $r = 0.376$, $P = 0.0489$). In contrast, total body gross energy (735.3–1,447.4 MJ) and body mass (39.0–66.0 kg) were not correlated with fasting duration. Thus, body composition, not overall body reserves, predicted fasting duration, but the effect was weak, indicating that other factors also account for the observed variation in fasting duration. We speculate that pups with greater percent fat more effectively utilized lipid and conserved protein while meeting metabolic costs throughout the PWF. As a result, fatter pups extended the PWF duration, which may be critical for development of diving physiology and may have facilitated their survivorship to age 1.

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Introduction

In mammals and birds alike, the probability of survival for all age classes is influenced by body condition, and this effect is seen most clearly in neonates and juveniles (Coulson et al. 1997; Reed and Plante 1997). In terrestrial mammals, juvenile survival is positively correlated with body size at weaning (Van Ballenberghe and Mech 1975; Guinness et al. 1978; Wauters et al. 1993), and the same is true for several seal species (Baker and Fowler 1992; McMahan et al. 2000a, 2003; Hall et al. 2001). Because first-year survival is among the most important density-dependent demographic parameters (Sinclair 1996; McMahan et al. 2005), understanding factors that may affect first-year survival is central to understanding population dynamics of a species (Hall et al. 2001).

Phocid seal pups accumulate essential body reserves during the suckling interval. For example, northern elephant (*Mirounga angustirostris*) and gray seal (*Halichoerus grypus*) pups triple their birth mass, with concomitant increases in body fat from approximately 4%–5% near birth to 28%–48% fat at weaning (Rea and Costa 1992; Iverson et al. 1993). Pinnipeds store these lipids in a blubber layer. The blubber layer serves as both the primary thermal barrier and the major energy reserve during periods without food, such as during the postweaning fast (PWF; Worthy and Lavigne 1987; Reilly 1991; Carlini et al. 2001; Noren et al. 2003) and first independent foraging trip, which initially can be unsuccessful (Muelbert and Bowen 1993; Muelbert et al. 2003). An excessive reduction in the blubber layer during fasting could compromise its insulative value; thus, the balance between blubber as energy and as an insulator (Worthy and Lavigne 1987; Nordøy and Blix 1991) may dictate the survival of an animal (Noren and Mangel 2004).

Periods of food deprivation historically have been divided into three phases categorized by the specific fuels catabolized for energy. Phase I is characterized by the utilization and exhaustion of glycogen reserves and is followed by phase II, the mobilization of stored lipids as the body switches to fat oxidation and reduces protein catabolism. Phases I and II enable preferential sparing of protein. Thus, animals with life-history patterns that include extended periods of fasting ideally end the fast before phase III (terminal starvation) begins because by this stage, 30% to 50% of the body protein has been wasted. As a result, phase III can lead to lethal levels of catabolism of critical protein sources, such as cardiac muscle (for review, see Castellini and Rea 1992).

Pinnipeds are adapted to fasting and conserve lean body mass during fasting by primarily relying on lipid catabolism, with the result that protein contribution to energy expenditure is low (2%–9%; Pernia et al. 1980; Reilly 1991; Adams and Costa 1993; Nordøy et al. 1993; Arnould et al. 2001). The ability to spare protein in penguins and mammals, including seals, is affected by adiposity at the onset of fasting (Goodman et al. 1980; Cherel et al. 1992; Houser and Costa 2003; Noren et al. 2003). Thus, fasting tolerance should be correlated with prefast body condition. This has been shown in elephant seal (*M. angustirostris* and *Mirounga leonina*) pups, where lighter, leaner pups had shorter fasting durations than heavier, fatter pups (Arnbom et al. 1993; Kretzmann et al. 1993; Carlini et al. 2001; Noren et al. 2003). Plasticity in the duration of the PWF permitted small elephant seal pups to depart early for their first trip to sea to ensure adequate body energy reserves for survival (Noren et al. 2003). However, there are trade-offs associated with leaving the beach prematurely because physiological changes occur throughout the PWF, such as the development of diving physiology (Thorson 1993). As a result, pups that prematurely terminate their PWF may not be proficient divers.

Like elephant seal pups, gray seal pups exhibit variable PWF durations (Reilly 1991) during which physiological traits for diving develop (Noren et al. 2005). Yet Reilly (1991) suggested that, unlike the PWF duration of elephant seal pups, which is predicted by pup body condition at weaning (Carlini et al. 2001; Noren et al. 2003), the PWF duration of gray seal pups was not correlated with body condition at weaning (mass, percent body fat, or total body gross energy [TBGE]). The difference in results across studies could reflect species-specific differences or may be an artifact of differences in sample size and the resulting range of variability represented in the sample. Carlini et al. (2001) and Noren et al. (2003) studied large samples, whereas Reilly (1991) examined only eight individuals. In light of these studies, we reexamined the relationship between body condition at weaning and fasting duration in gray seal pups. We also considered the trade-off between shortening the PWF to conserve the body energy reserve and prolonging the PWF for development of diving physiology, and we speculated how the amount of body fat at weaning may impact first-year survival.

Material and Methods

Field Site and Animals

All experimental protocols used in this research were approved by the Smithsonian Institution Conservation and Research Center's Institutional Animal Care and Use Committee. Permission to import and possess seal samples was granted through National Marine Mammal Laboratory permit 782–1697. The study was conducted at Sable Island, Nova Scotia, Canada (43°55'N, 60°00'W) during the pupping season (December 2002–February 2003). Eighty gray seal (*Halichoerus grypus*) mother-pup pairs with known parturition dates were marked with dye, and a numbered tag (Jumbo Rototag, Dalton, UK)

was placed in the hind flipper of each pup. These pairs were observed once a day to determine the date of weaning, as indicated by the mother's immediate departure from the island. Of these pups, 30 (15 males and 15 females) with normal suckling periods (≥ 14 d) were chosen for this study to examine body condition at weaning, duration of the PWF, and movement during the fast. Ten additional pups (five males and five females) were chosen for a concurrent study and were weighed at 0, 12, and 24 d postweaning to estimate the change in body mass during the PWF; constraints of the concurrent study precluded measurement of body condition in these pups.

Capture and Measurements

Pups were captured in hand-held nets and sedated with 0.03–0.05 mL kg⁻¹ of diazepam administered via the extradural vein (McMahon et al. 2000b; Noren et al. 2005), using a sterile 3.5-in 18-gauge spinal needle (Terumo). Once the pup was sedated, standard dorsal body length and axillary girth were measured, and body mass to the nearest 0.1 kg was measured using a Salter scale. To determine background isotope levels, an initial 10-mL blood sample was taken as described above and collected in a serum separator tube (Vacutainer). To measure body composition, each pup received an intravenous injection of tritiated water (³H₂O; approximately 5 mL of 0.1 mCi mL⁻¹); the absolute amount of tracer injected was determined by gravimetric calibration of the syringes used for isotope administration. Blood samples (10 mL) were taken at 1.5 and 2 h postinjection to determine ³H₂O concentration and to ensure that equilibration had occurred. All blood samples were immediately placed in a cooler until processed at the field laboratory 1–3 h later.

At the field laboratory, all blood samples were spun at 1,000 rpm for 25 min with a desktop centrifuge. The serum was decanted into airtight 15-mL tubes (Corning) and stored at –30°C. The frozen blood samples were transported to Dalhousie University, Halifax, Nova Scotia, where further analyses were performed within 1 mo of collection.

Duration of the Postweaning Fast

Before release, each of the 30 pups was fitted with a small radio transmitter (13.5 g, 13-mm diameter × 48-mm length; model MM140; Advanced Telemetry Systems, Isanti, MN) that was attached to the pelage using 5-min epoxy. This method of attachment ensured that the transmitter would be shed by the time of molting, approximately 16 mo later. Pups were held for approximately 3 h to complete all isotope measurements and fitting of the radio transmitter. Once released, pups were not disturbed, to avoid inducing premature departure from the beach. The departure date, which marked the end of the terrestrial PWF period, was defined as the date each pup's radio frequency was no longer heard at the rookery, indicating that the pup was in the ocean. Transmitter frequencies of all pups, even ones that were recorded as having departed, were mon-

itored once a day with a VHF receiver (Advanced Telemetry Systems) until the end of the study. This ensured that none of the pups returned to the island after their initial departure. Visual sightings and locations (GPS 76, Garmin, Olathe, KS) of the pups were recorded at the same time that the transmitter frequencies were monitored, with the exception of three days of bad weather when only transmitter frequencies could be monitored. The interval between movement sightings was approximately 24 h. Purpose-built software (Visual Basic run within an Access database) was used to obtain total movement during the PWF for each pup, and an estimate of average daily movement was determined by dividing total movement by the number of days fasting. PWF duration is defined as the number of days between weaning and departure dates.

Determination of Body Composition

Total free water was collected from aliquots of serum (50 μ L) into scintillation vials by distillation, following the method described in Ortiz et al. (1978). A scintillation cocktail (10 mL; Scintiverse II) was added to each vial, and the tritium activity of each sample was determined using a scintillation counter (LS6000TA, Beckman Coulter, Fullerton, CA). All samples were analyzed in triplicate and run with a standard dilution series.

Total body water (TBW; in kg) was determined for each pup from the activity of the injected isotope in counts per minute (cpm) divided by the specific activity of the equilibration sample (cpm g^{-1}). TBW determinations were corrected for overestimation of body water by the hydrogen isotope dilution method, using the equation of Bowen and Iverson (1998):

$$TBW = 0.003 + (0.968 \times \text{mean dilution space}). \quad (1)$$

The following equations, which were developed for gray seals (Reilly and Fedak 1990), were used to calculate total body fat (TBF; %), total body protein (TBP; %), and TBGE (MJ):

$$\%TBF = 105.1 - (1.47 \times \%TBW), \quad (2)$$

$$\%TBP = (0.42 \times \%TBW) - 4.75. \quad (3)$$

These methods have been used on gray seals and are outlined in detail by Bowen and Iverson (1998) and Mellish et al. (1999).

Statistics

All variables were normally distributed; thus, Student *t*-tests were used to determine whether there were significant differences between male and female gray seal pups in the parameters that were measured. With the exception of average daily movement and total movement during the PWF, variables were similar across sexes, so these data were combined for subsequent analyses. Pearson correlation coefficient and linear regression were used to determine the relationships among variables. Forty days postpartum (DPP) marks the end of the development of hemoglobin (Hb) levels in the blood of gray seal pups at Sable

Island (Noren et al. 2005), and thus, Student *t*-tests were used to compare data from pups that departed the island at fewer than 40 DPP (immature Hb) with data from pups that departed past the age of 40 DPP (mature Hb).

Estimates of mass loss were derived from pups that were repeatedly measured over time. We fitted these data using a linear mixed-effects model with individual seals as the random effect and time as the fixed effect. We compared models with common intercepts and slopes of all individuals with those with different intercepts but common slopes (as suggested by the data; see Fig. 1). Best-fitting models were determined on the basis of lowest small-sample corrected Akaike Information Criterion. This analysis indicated that pups had significantly different intercepts (i.e., weaning mass) but similar rates of mass loss (appendix Table A1). Given the similarity in mass loss across pups, data were combined for mass loss per day, mass-specific mass loss per day, and the proportion of weaning mass lost during the PWF for each of the 10 gray seal pups.

Linear mixed-effects models were fitted in S-Plus 7.0. Jandel Sigma Stat software was used for all other statistical analyses. Means are presented ± 1 SE. Results were significant at $P \leq 0.05$.

Results

Twenty-eight of the 30 pups departed to sea before the end of the study; one male and one female pup remained on the island. The results for PWF duration and age at departure exclude these two pups unless otherwise noted. The suckling duration, PWF duration, age at departure, and body condition at weaning of male and female pups did not differ significantly (Table 1). Thus, data from both sexes were combined for subsequent analyses. Average daily movement during the PWF was significantly less for males (range: 7–115 $m d^{-1}$) than females (range: 7–164 $m d^{-1}$), with the result that males traveled less (range:

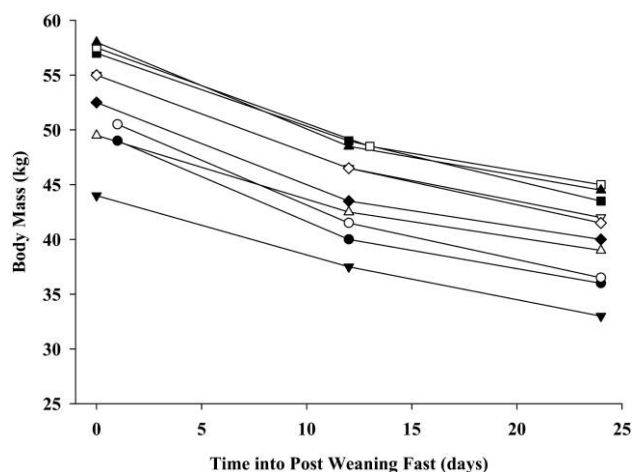


Figure 1. Body mass during the postweaning fast for 10 gray seal pups followed longitudinally. Mass loss within each individual is represented by a unique symbol.

163–2,655 m) than females (range: 94–3,839 m) during the PWF (Table 1); these data were not combined for subsequent analyses.

Percent body fat increased significantly with body mass at weaning (Fig. 2). As expected, body mass decreased throughout the PWF (Fig. 1). The rates for body mass loss per day and mass-specific body mass loss per day during the PWF ranged from 0.4 to 0.6 kg d⁻¹ (mean 0.5 ± 0.02 kg d⁻¹; *n* = 10) and 8.8–12.1 g d⁻¹ kg⁻¹ (10.1 ± 0.3 g d⁻¹ kg⁻¹; *n* = 10), respectively. This resulted in a 21.2%–27.7% loss of weaning mass after 24 d of fasting (mean: 24.1% ± 0.6%; *n* = 10). Although both body mass and TBGE at weaning were not correlated with PWF duration (body mass: *n* = 28, *r* = 0.168, *P* = 0.394; TBGE: *n* = 28, *r* = 0.244, *P* = 0.211), percent body fat at weaning was positively (although weakly) correlated with the PWF duration (Fig. 3). Movement per day was not correlated with PWF duration for males (*n* = 14, *r* = 0.044, *P* = 0.880) nor females (*n* = 14, *r* = 0.238, *P* = 0.413). Age at departure was positively correlated with fasting duration (Fig. 4).

The comparison of pups that departed the rookery at <40 DPP and those that departed at >40 DPP indicated that suckling duration was similar across groups, as was body length, axillary girth, body mass, and TBGE at weaning (Table 2). However, in comparison to pups departing at >40 DPP (mature Hb), pups departing at <40 DPP (immature Hb) had a significantly lower percentage of body fat at weaning and a shorter PWF

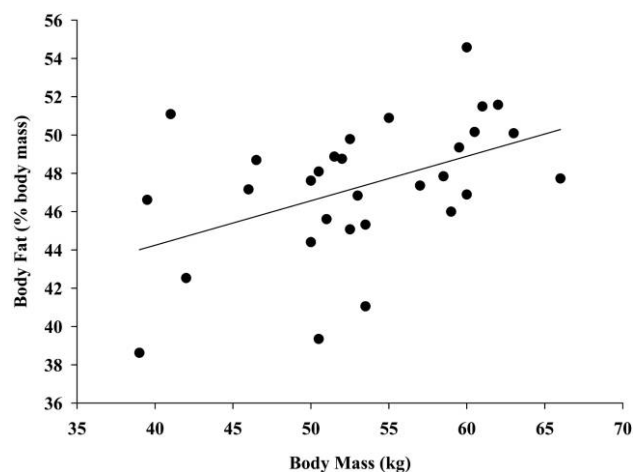


Figure 2. Percent body fat in relation to body mass for newly weaned gray seal pups. Body fat at weaning is positively correlated with body mass, according to percent body fat = 0.2 × body mass + 34.9, where body mass is in kilograms (*n* = 30, *r*² = 0.213, *F* = 7.562, *P* = 0.010).

duration (Table 2). Average daily movements and total movements during the PWF were similar across groups in both males and females (Table 2).

Table 1: Suckling duration, body condition at weaning, average daily movement, total movement, duration of the postweaning fast (PWF), and age at departure of gray seal pups

Characteristic	Male <i>n</i> = 15	Female <i>n</i> = 15	Male vs. Female Statistics	Overall Mean <i>n</i> = 30	Overall Range <i>n</i> = 30
Suckling duration (d)	19 ± .3	18 ± .3	df = 28, <i>t</i> = .852, <i>P</i> = .401	19 ± .2	16–22
Length (cm)	108.8 ± 1.7	106.8 ± 1.4	df = 28, <i>t</i> = .907, <i>P</i> = .372	107.8 ± 1.1	95.0–120.0
Axillary girth (cm)	108.3 ± 1.3	108.1 ± 1.7	df = 28, <i>t</i> = .0941, <i>P</i> = .926	108.2 ± 1.0	96.0–120.5
Body mass (kg)	51.5 ± 1.8	54.9 ± 1.8	df = 28, <i>t</i> = 1.353, <i>P</i> = .187	53.2 ± 1.3	39.0–66.0
Body fat (%)	46.3 ± 1.0	48.3 ± .8	df = 28, <i>t</i> = 1.530, <i>P</i> = .137	47.3 ± .66	38.6–54.6
TBGE (MJ)	1,104.8 ± 46.7	1,214.4 ± 49.1	df = 28, <i>t</i> = 1.617, <i>P</i> = .117	1,159.6 ± 34.8	735.3–1,447.4
Average daily movement (m d ⁻¹) ^a	47.73 ± 8.87	78.30 ± 11.90	df = 28, <i>t</i> = 2.059, <i>P</i> = .049	N/A	N/A
Total movement (m) ^a	954.05 ± 196.11	1,730.89 ± 290.26	df = 28, <i>t</i> = 2.218, <i>P</i> = .035	N/A	N/A
PWF duration (d)	20 ± 1.5 (<i>n</i> = 14)	22 ± 1.6 (<i>n</i> = 14)	df = 26, <i>t</i> = .688, <i>P</i> = .498	21 ± 1.1	9 to >31
Age at departure (DPP)	39 ± 1.4 (<i>n</i> = 14)	40 ± 1.6 (<i>n</i> = 14)	df = 26, <i>t</i> = .497, <i>P</i> = .623	40 ± 1.1	26 to >49

Note. Values are means ± SE. DPP = days postpartum; TBGE = total body gross energy.

^a Denotes characteristics that are significantly different between male and female pups.

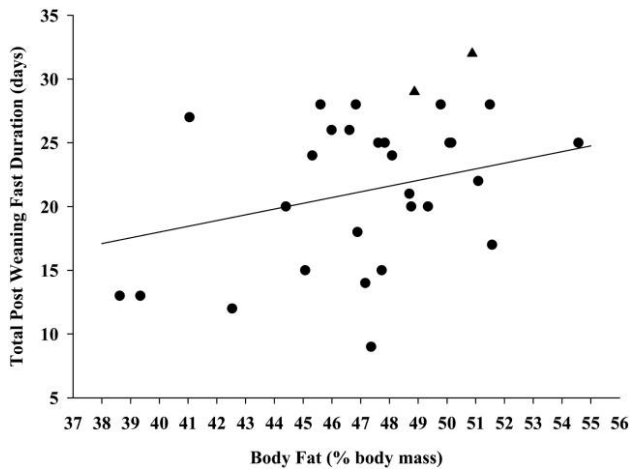


Figure 3. Total duration of the postweaning fast in relation to percent body fat at weaning. Postweaning fast (PWF) duration is significantly but weakly correlated with body fat at weaning, according to PWF duration (days) = $0.6 \times \text{body fat} - 6.6$, where body fat is represented as a percentage of body mass ($n = 28$, $r^2 = 0.141$, $F = 4.271$, $P = 0.0489$; *line*). The two pups that had not departed the rookery at the end of the study (denoted by *triangles*) were not included in the correlation reported above. If we assume that these pups left the day following the end of the study, the correlation is stronger, according to PWF duration (days) = $0.7 \times \text{body fat} - 11.4$ ($n = 30$, $r^2 = 0.175$, $F = 5.935$, $P = 0.021$).

Discussion

To survive the transition to nutritional independence, the body reserves of newly weaned phocid pups must support energy expenditure throughout the duration of the PWF and during initial foraging attempts, which are likely to be unsuccessful. The mean daily energy expenditure based on changes in body composition for phocid pups fasting on land ranges from 9.8 to 23.6 MJ (Reilly 1991; Carlini et al. 2001; Noren et al. 2003). To meet these energetic needs, pups lose 0.4–1.1 kg d^{-1} during the PWF (Reilly 1991; Carlini et al. 2001; Noren et al. 2003; Fig. 1). As a consequence, gray seal pups lose an average $24.1\% \pm 0.6\%$ of their weaning mass after 24 d of fasting (this study), and northern elephant seal pups lose an average $28.4\% \pm 0.4\%$ of their weaning mass after 50–57 d of fasting (Noren et al. 2003). Lipid reserves are crucial because they provide the majority of the energy that sustains fasting pups (Worthy and Lavigne 1987; Reilly 1991; Carlini et al. 2001; Noren et al. 2003). For example, lipid catabolism provides $93.9\% \pm 1.5\%$ of the energy used during the PWF of gray seals (Reilly 1991). Consequently, the overall quantity of lipid in the body declines throughout the PWF (Worthy and Lavigne 1987; Reilly 1991; Carlini et al. 2001; Noren et al. 2003).

Given the importance of lipids in fueling metabolism during the PWF, indices of body condition at weaning should be associated with fasting tolerance. Reilly (1991) indicated that body condition (mass, percent fat, and TBGE) at weaning in gray seals was not correlated with PWF duration. However, results of this study indicated that the proportion of fat at

weaning in gray seal pups is positively (although weakly) correlated with the duration of the PWF (Fig. 3); this concurs with the correlation shown previously for northern elephant seal pups (Noren et al. 2003). However, in contrast to the correlation of weaning mass and PWF duration found for elephant seal pups (Carlini et al. 2001; Noren et al. 2003), weaning mass of gray seal pups was unrelated to the duration of the PWF. The difference in results across these studies may be an artifact of sample size and the resulting magnitude of the range of body conditions examined. For example, Reilly (1991) examined only eight animals, which may not have included individuals at the extremes of body condition because a greater sample size would have yielded a greater range of body conditions. In contrast, the 30-pup sample of this study and the 60-pup sample of Noren et al. (2003) provided large ranges of body conditions, where the largest animal had a mass of 1.7 times (this study) and 2.3 times (Noren et al. 2003) that of the mass of the smallest animals. Similarly, the fattest animals had a percent lipid of 1.4 times and 1.5 times the percent lipid of the skinniest animals in this and the Noren et al. (2003) studies, respectively. Thus, evidence indicates that smaller and leaner phocid seal pups fast for shorter durations (Carlini et al. 2001; Noren et al. 2003; Fig. 3) and depart for sea at a younger age than larger, fatter pups (Table 2; Fig. 4).

Both our study and that of Noren et al. (2003) indicate that relative fat stores, not total fat stores, influence fasting ability. Variation in energy utilization patterns across individuals may explain this result. In seals, other mammalian species, and birds, relatively fat individuals achieve and maintain a lower rate of

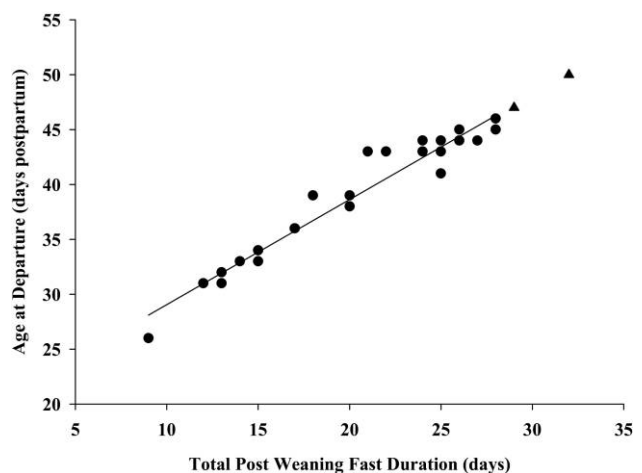


Figure 4. Age at departure in relation to the total duration of the postweaning fast (PWF). Age at departure is correlated to PWF, according to age at departure = $1 \times \text{fasting duration} + 19$, where age at departure and fasting duration are both in days ($n = 28$, $r^2 = 0.947$, $F = 464.456$, $P < 0.001$; *line*). The two pups that had not departed the rookery at the end of the study (denoted by *triangles*) were not included in the correlation reported above. If we assume that these pups left the day following the end of study, the correlation is stronger, according to age at departure = $1 \times \text{fasting duration} + 20$ ($n = 30$, $r^2 = 0.955$, $F = 590.676$, $P < 0.001$).

Table 2: Suckling duration, body condition at weaning, average daily movement, total movement, postweaning fast (PWF) duration, and age at departure of gray seal pups <40 d postpartum (DPP) at departure and >40 DPP at departure (40 DPP marks the end of Hb development in gray seals)

Characteristic	Pups <40 DPP at Departure (<i>n</i> = 12 unless Otherwise Noted)	Pups >40 DPP at Departure (<i>n</i> = 18 unless Otherwise Noted)	Statistics
Suckling duration (d)	19 ± .3	18 ± .3	df = 28, <i>t</i> = .460, <i>P</i> = .649
Length (cm)	109.9 ± 1.7	106.4 ± 1.3	df = 28, <i>t</i> = 1.659, <i>P</i> = .108
Axillary girth (cm)	107.5 ± 2.0	108.8 ± 1.1	df = 28, <i>t</i> = .599, <i>P</i> = .554
Body mass (kg)	53.0 ± 2.4	53.3 ± 1.5	df = 28, <i>t</i> = .0978, <i>P</i> = .923
Body fat (%) ^a	45.7 ± 1.1	48.4 ± .7	df = 28, <i>t</i> = 2.080, <i>P</i> = .047
TBGE (MJ)	1,131.9 ± 65.3	1,178.1 ± 39.5	df = 28, <i>t</i> = .643, <i>P</i> = .525
Average daily movement (m day ⁻¹):			
Male	48 ± 13.1 (<i>n</i> = 7)	47 ± 12.9 (<i>n</i> = 8)	df = 13, <i>t</i> = .0310, <i>P</i> = .976
Female	80 ± 28.5 (<i>n</i> = 5)	77 ± 12.2 (<i>n</i> = 10)	df = 13, <i>t</i> = .144, <i>P</i> = .887
Total movement (m):			
Male	704 ± 219.8 (<i>n</i> = 7)	1,172 ± 305.6 (<i>n</i> = 8)	df = 13, <i>t</i> = 1.210, <i>P</i> = .248
Female	1,256 ± 548.1 (<i>n</i> = 5)	1,968 ± 333.2 (<i>n</i> = 10)	df = 13, <i>t</i> = 1.172, <i>P</i> = .262
PWF duration (d) ^a	16 ± 1.0	25 ± .5 (<i>n</i> = 16)	df = 26, <i>t</i> = 9.269, <i>P</i> <.001
Age at departure (d) ^a	34 ± 1.1	44 ± .3 (<i>n</i> = 16)	df = 26, <i>t</i> = 9.258, <i>P</i> <.001

Note. Values are means ± SE. TBGE = total body gross energy.

^a Denotes characteristics that are significantly different between pups that departed at <40 DPP and pups that departed at >40 DPP.

protein catabolism than leaner individuals (Goodman et al. 1980, 1984; Øritsland et al. 1985; Robin et al. 1988; Atkinson et al. 1996; Hilderbrand et al. 2000; Carlini et al. 2001; Crocker et al. 2001; Houser and Costa 2003; Noren et al. 2003). As a result, pups that are weaned with low body mass and low percent lipid exhibit relatively high protein catabolism and proportionately greater body mass loss than heavier, fatter pups (Noren et al. 2003). The greater mass-specific mass loss rates measured in lighter, leaner pups during periods of fast and food limitation (Carlini et al. 2001; Houser and Costa 2003; Muelbert et al. 2003; Noren et al. 2003) are a consequence of the relatively higher catabolism of protein-yielding tissues (e.g., muscle), which have approximately one-eighth the energetic density of adipose tissue (Noren et al. 2003). Given the greater proportion of lipid stores and more efficient utilization of lipid and conservation of protein during abstinence from food, fatter animals can tolerate longer fasts than their leaner counterparts.

Another common theme among phocids is that pups exhibit extended fasting periods by having low rates of energy expenditure (Worthy and Lavigne 1987; Reilly 1991; Carlini et al. 2001; Noren et al. 2003). To maintain low rates of energy expenditure, pups should minimize daily movement throughout the PWF. Across pups, the distance moved per day was generally small (range: 7–164 m d⁻¹), and movement patterns of fat pups

with protracted fasts and lean pups with brief fasts were similar (Table 2). It is probably advantageous for both groups to minimize daily movement. Lean pups undoubtedly need to minimize daily energy expenditure to conserve body reserves, while fatter pups need to minimize daily energy expenditure to safeguard the energy reserves that will carry them through their prolonged fast. Admittedly, our index of movement was rather coarse, and more frequent sampling of movement throughout the day may have yielded different results. Therefore, future studies should investigate the relationship between total daily movement and energy utilization during the PWF.

Ultimately, seal pups must terminate the fast to safeguard the blubber layer, conserve protein stores, and avoid entrance into phase III fasting, which could be lethal. The physiological cues that signal the termination of the fast are still not fully understood, in part because the interdependencies between metabolites complicate the determination of causative and reactive factors (Houser and Costa 2003). Nonetheless, seals appear to end their natural fasts before increased protein utilization is necessary (Castellini and Rea 1992), despite an ability to increase protein catabolism when extreme fasting limits are tested (Worthy and Lavigne 1987; Nordøy and Blix 1991). Thus, there may be a mass loss threshold (Wilkinson and Bester 1990) or a critical body composition level (Ortiz et al. 2001; Noren et

al. 2003; Noren and Mangel 2004) that cues pups to initiate foraging. Considering the importance of blubber for thermo-regulation, a pinniped pup with 45% of its body mass remaining as blubber at the end of the fast may still be limited in lipids that can be catabolized for energy (Castellini and Rea 1992). Estimated fat reserves at the end of the PWF for the pups in this study ranged from 33% to 52% of body mass (mean $43\% \pm 0.9\%$), assuming an average mass loss of 0.5 kg d^{-1} (this study) comprising 64% fat remaining (Reilly 1991). Admittedly, the use of an average mass loss rate and an average lipid contribution value can provide only a rough indication of body condition at the termination of the PWF. Nevertheless, these estimates are similar to field measurements of elephant seal pups nearing the end of their PWF (32%–46% fat; Noren et al. 2003).

Although phocid seal pups must terminate the terrestrial PWF to conserve body reserves, it is advantageous to extend their time on land until two physiological development stages are complete. First, pups must shed their natal pelage (lanugo), which can take several weeks after weaning (Bowen et al. 2003). Second, pups must develop the physiology to permit effective diving, a necessary component of foraging (Thorson 1993; Noren et al. 2005). Lean northern elephant seal pups, which fasted for 5–6 wk, departed for sea with an estimated 69% of adult mass-specific oxygen stores, compared to 78% for fat pups, which fasted for 10–11 wk (calculated from PWF durations from Noren et al. 2003 and oxygen stores from Thorson 1993). Similarly, lean gray seal pups that fasted for only $16 \pm 1.0 \text{ d}$ (Table 2) departed for sea with an estimated 61% of adult mass-specific oxygen stores; this compares with 68% of adult mass-specific oxygen stores for fatter gray seal pups that departed for sea after a $26 \pm 0.6\text{-d}$ fast (Table 2). The mass-specific oxygen stores of weaned gray seals was calculated from a linear regression based on the raw data from the 15–43-DPP weaned pups in Noren et al.'s study (2005), where oxygen stores ($\text{mL O}_2 \text{ kg}^{-1}$) are calculated as $26.23 + 0.48 \times \text{DPP}$ ($n = 27$, $r^2 = 0.624$, $F = 41.435$, $P < 0.001$). As a consequence, the youngest (26 DPP) gray seal pup to depart had a calculated aerobic dive limit (cADL) of 3.3 min, nearly a minute shorter than that of the oldest (50 DPP) gray seal pup to depart (4 min). The cADL of weaned gray seal pups was calculated from a linear regression based on the raw data from the 15–43-DPP weaned pups in Noren et al.'s study (2005), where $\text{cADL} = 2.76 + 0.04 \times \text{DPP}$ ($n = 27$, $r^2 = 0.511$, $F = 26.084$, $P < 0.001$). Although all seal pups forage with limited diving capabilities (Kooyman et al. 1983; Lydersen and Hamill 1993; Thorson 1993; Lydersen et al. 1994; Burns and Castellini 1996; Burns 1999), pups that must terminate the PWF early to conserve body reserves may be especially disadvantaged. Differences in diving capabilities of southern elephant seal pups have been attributed to body condition at weaning; lighter pups dove shallower and for shorter durations than heavy pups (Hindell et al. 1999).

These findings improve our understanding of the challenges faced by young pinniped pups. Pups that are weaned when

relatively lean terminate their PWF early and depart for sea earlier in their physiological development compared with fat pups. Since diving physiology develops throughout the entire PWF, lighter, leaner pups are probably less proficient divers during their first foraging trip compared to heavier, fatter pups. Consequently, leaner pups are presumably at greater risk than fatter pups during times of decreased prey availability, as evident by observations of catastrophic losses of immature pinnipeds (Trillmich et al. 1991) and reproductive failure in marine mammals (Pitcher et al. 1998; Craig and Ragen 1999) during periods of limited prey availability. Although we found evidence for the effect of percent fat on the duration of the PWF, much of the variability (~86%) remains unexplained. We speculate that other variables, such as individual differences in development, energy metabolism, behavior, and the site of parturition/weaning, may also affect the duration of the postweaning fast, but these variables remain to be investigated.

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Appendix

Table A1: Model fits to longitudinal mass loss data from 10 gray seal pups from 0 to 20 d postweaning

Model	Description	K	AIC_c	ΔAIC_c	w_i
2	Different intercepts, common slope	4	144.9	0	.552
3	Different intercepts, different slopes	6	150.3	5.4	.420
1	Different intercepts	3	205.2	60.3	.027

Note. K = number of parameters, AIC_c = corrected small-sample Akaike Information Criterion, w_i = Akaike weights.

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