Impact of Body Reserves on Energy Expenditure, Water Flux, and Mating Success in Breeding Male Northern Elephant Seals

Daniel E. Crocker[1,*]
Dorian S. Houser[2]
Paul M. Webb[3]

[1]Department of Biology, Sonoma State University, Rohnert Park, California 94928; [2]National Marine Mammal Foundation, San Diego, California 92106; [3]Department of Biology, Roger Williams University, Bristol, Rhode Island 02809

ABSTRACT

In capital breeders, individual differences in body size and condition can impact mating effort and success. In addition to the collateral advantages of large body size in competition, large nutrient reserves may offer advantages in endurance rivalry and enable the high rates of energy expenditure associated with mating success. We examined the impacts of body reserves and dominance rank on energy expenditure, water flux, mating success, and breeding tenure in the adult male northern elephant seal, a polygynous, capital breeder. Adult males expended energy at a rate of 195 ± 49 MJ d^{-1}, which is equivalent to 3.1 times the standard metabolic rate predicted by Kleiber's equation. Despite high rates of energy expenditure and a long fasting duration, males spared lean tissue effectively, deriving a mean of 7% of their metabolism from protein catabolism. Body composition had a strong impact on the ability to spare lean tissue during breeding. When controlling for body size, energy expenditure, depletion of blubber reserves, and water efflux were significantly greater in alpha males than in subordinate males. Large body size was associated with increased reproductive effort, tenure on shore, dominance rank, and reproductive success. Terrestrial locomotion and topography appeared to strongly influence energy expenditure. Comparisons with conspecific females suggest greater total seasonal reproductive effort in male northern elephant seals when controlling for the effects of body mass. In polygynous capital breeding systems, male effort may be strongly influenced by physiological state and exceed that of females.

* Corresponding author; e-mail: crocker@sonoma.edu.

Introduction

Within polygynous mating systems, much of the variation in individual mating success is related to the ability of males to defend access to females (Clutton-Brock 1989). In addition to ecological factors that influence female clumping and defensibility in time and space (Emlen and Oring 1977), differences in male competitive ability may be directly influenced by male physical condition at the time of breeding. Variation in male physical condition may arise because of ontogeny, genetic differences, developmental stress, or hormone action (Moore et al. 1998; Lindstrom 1999; Festa-Bianchet et al. 2004). In some polygynous mating systems, body size and condition are likely to be important state variables that influence reproductive success. Body size can influence male reproductive success through its effect on dominance status (e.g., Haley et al. 1994), mate choice (e.g., Brown 1990), territory quality (e.g., Howard 1978), maintenance of tenure (e.g., Anderson and Fedak 1985), and choice of mating tactics (e.g., Lidgard et al. 2005). In capital breeders, where reproductive expenditure is limited by nutrient reserves at the onset of breeding, individual differences in both long-term and recent foraging success can impact mating effort and success through cumulative effects on growth, body size, and condition. In addition to the collateral advantages of large body size in competitive interactions, large nutrient reserves may offer advantages in endurance rivalry (Arnould and Duck 1997; Judge and Brooks 2001) and enable the high rates of energy expenditure associated with mating success (Vehrencamp et al. 1989; Deutsch et al. 1990; Judge and Brooks 2001; Yoccoz et al. 2002; Galimberti et al. 2007). Males with smaller nutrient reserves may be forced to adapt alternative, less successful strategies (Lidgard et al. 2005) or exhibit reduced mating effort.

Northern elephant seals, *Mirounga angustirostris*, are ideal for investigating the energetics of reproductive effort (RE) in a polygynous mammal. They are sexually size dimorphic, with adult males being two to eight times heavier than females (Deutsch et al. 1994). The males present during the breeding period are 8–14-yr-old adults and 5–7-yr-old subadults, which are sexually mature but still growing. Males compete for position in a dominance hierarchy used to control access to estrous females (Le Boeuf 1974; Haley et al. 1994) while also fasting from food and water, losing ~36% of their arrival body mass over a 3-mo period (Deutsch et al. 1994). Previous studies on male northern elephant seals have revealed positive associations between body size, dominance rank, and mating success (Deutsch et al. 1990); however, factors other than body size accounted for 56%–84% of the variation in dominance rank (Haley et al. 1994). Investigations of male southern elephant seals suggest similar positive effects of body size on harem

position, tenure, and mating success (Modig 1996; Galimberti et al. 2007).

Early arrival and long tenure duration may influence mating success in elephant seals because of impacts of prior residence on interaction outcomes (Haley 1994). Furthermore, large nutrient reserves may permit increased commitment of energy to RE by impacting both the rate and the duration of RE. For animals that fast during breeding, metabolic strategies that preserve vital organs and body protein reserves may be critical to breeding tenure (Castellini and Rea 1992). Studies of energy expenditure in lactating female elephant seals suggest strong impacts of state variables on RE (Crocker et al. 2001) and an impact of body composition on protein sparing during breeding (Crocker et al. 1998). Similar investigations in fasting weaned pups suggest that body size and composition affect protein sparing and fasting duration (Noren et al. 2003). The degree of protein catabolism influences urinary water loss and the ability to maintain water balance without drinking through metabolic water production. The quality of state variables may similarly impact sustainable levels of energy expenditure and tenure in breeding adult males.

In this study, the relationships between male body size and composition, energy expenditure, water flux, and mating success were investigated in male northern elephant seals. We predicted that RE, measured as energy expenditure, would increase with dominance rank and copulatory success. The impact of body reserves on protein sparing and water economy were examined to better understand any potential role these factors play in constraining male effort or tenure.

Methods

Study Site and Study Animals

All animal handling procedures were approved by the University of California–Santa Cruz Chancellor's Animal Research Committee, and work was conducted under National Marine Fisheries Service Marine Mammal permit 836. Twenty-one adult male seals from Año Nuevo State Reserve, California, were studied during the winter breeding season. The study was conducted at the northern part of the rookery, where three distinct harems (H1, H2, and H3) were geographically separated from the rest of the colony. Individual animals were considered to be adults on the basis of body mass and the development of secondary sexual characteristics (Le Boeuf 1974; Deutsch et al. 1990). Individuals were identified by preexisting flipper tags and dye marks (Lady Clairol, Stamford, CT).

Field Procedures

Males were sampled twice during the breeding season: in January and again in late February or early March. Adult males were lured onto a platform truck scale (± 5 kg; Senstek, Saskatoon, Saskatchewan) by using a plaster model of an adult female elephant seal (Deutsch et al. 1994). Repeated weights of males measured on the same day were within 1% of each other.

When weighed successfully, each male was given an intramuscular injection of 185–296 MBq ^3H_2O in 12 mL of sterile saline to determine total body water (TBW) and body composition. Syringes were gravimetrically calibrated to accurately determine injection volume. Animals were allowed to equilibrate over night (12–16 h). Equilibration times for intramuscular isotope injections in adult male elephant seals are not known, but since water turnover rates are so low and errors due to lack of equilibration are very high, we opted to wait overnight to ensure equilibration. On the basis of water flux measurements, the error in specific activity from waiting 12 h past equilibration would be <0.4%, which is well below our measurement precision. After equilibration, the animal was sedated with 0.3 mg kg^{-1} of tiletamine HCl and zolazepam HCl (Telazol, Fort Dodge Animal Health, Fort Dodge, IA). Blood samples (20 mL) were obtained from the extradural vein, collected into a serum tube, and placed on ice until they were returned to the lab (typically within 6 h). Samples were obtained at the beginning and the end of each procedure ($\sim$30 min apart) and compared to confirm equilibration of the isotope. Blood samples were centrifuged for 15 min (1,500 g at 4°C), and the serum was collected and frozen at -70°C for later analyses. The procedure was repeated late in the breeding season, except that adult males were immobilized immediately after weighing. Blood samples for the measurement of the clearance of the initial isotope injection were taken, and a second dose of ^3H_2O was administered to measure TBW and body composition. The animal was allowed to equilibrate for 12–16 h before being immobilized for a final blood collection.

Body Composition, Water Flux, and Energy Expenditure

TBW and body composition were estimated using isotopic dilution of ^3H. The activity of ^3H in each serum sample was measured in triplicate, using 100-μL aliquots of serum and the freeze-capture method (Ortiz et al. 1978). Samples were counted in 10 mL of Ecolite scintillation cocktail, using a Beckmann LS3801 scintillation counter. The activity of an injectate standard was measured in triplicate at the same time as the samples. Dilution space was determined as the activity of injected isotope divided by the activity of the postequilibration sample. Background activity from the initial isotope injection was subtracted from the postequilibration specific activity for the late breeding measurements. TBW was estimated from the dilution space, using the equation of Bowen and Iverson (1998). Fat mass was determined from TBW, using the following equation:

$$M_F = M_T - 1.37 TBW, \qquad (1)$$

(Iverson et al. 1993), where M_F is the fat mass of the seal and M_T is the total body mass (both in kg). Daily water influx and efflux were calculated according to the procedure of Nagy and Costa (1980).

Daily energy expenditure (DEE) was estimated from mass and body composition changes. The energy produced through nutrient catabolism was calculated assuming protein or lipid lost by the male and was 17.99 and 39.33 kJ g^{-1}, respectively

Table 1: Tenure on shore and mean rate of copulations, agonistic behaviors, and movement during the measurement period

	Alpha males ($n = 3$)	Beta males ($n = 5$)	Gamma males ($n = 4$)	Peripheral males ($n = 6$)
Tenure on shore (mean d $\pm$ SD)[a]	96.7 $\pm$ 6.5[A]	91.5 $\pm$ 3.1[A,B]	88.0 $\pm$ 5.8[B,C]	82.0 $\pm$ 2.9[C]
Copulation	.09	.01	.00	.00
Head lift/rear[a]	2.36[A]	1.67[B]	1.24[B]	.23[C]
Trumpet[a]	2.96[A]	1.23[B]	1.07[B]	.65[C]
Moving threat/submission	2.24	2.16	1.99	2.13
Movement (mean m h^{-1} $\pm$ SD)	24.3 $\pm$ 9.0	27.8 $\pm$ 3.1	19.4 $\pm$ 2.7	NA

Note. Data are mean number per hour per male, unless otherwise indicated. Means shown for sexual and agonistic behavior were weighted by observation duration. Different superscript uppercase letters denote significant differences from post hoc comparisons (Tukey's HSD: $P < 0.05$). NA, not applicable.

[a] Significantly different between ranks (ANOVA: $P < 0.05$).

(Costa 1987). Fat loss was assessed directly from changes in fat mass. The remainder of mass loss was assumed to be lean tissue, composed of 27% protein (Pace and Rathbun 1945).

Behavioral Observations

Observers were stationed at the location of each harem, and animals were observed for 5–8 h each day during daylight hours throughout the measurement period, for a total of 793 h of observation. Dominance rank was determined from the outcome of agonistic interactions between males (e.g., fights, vocal threats, or posturing). All interactions in which one male retreated from another were recorded, excluding interactions between peripheral males located >50 m away from a harem. Agonistic encounters between males were recorded as a head lift/rear, trumpet, moving threat/submission, or fight (Le Boeuf 1974; Deutsch 1990). Dominance hierarchies were constructed, and males were assigned daily ranks as alpha, beta, gamma, or peripheral for each harem, on the basis of a dominant-subordinate matrix. All changes in dominance rank ($n = 6$) occurred during the first 2 wk of the study. These animals were assigned a rank that they held for the remainder of the breeding season. Copulatory success was measured as the estimated number of females inseminated (ENFI; Le Boeuf 1974; Le Boeuf and Reiter 1988; Deutsch et al. 1990, 1994; Haley 1994; Haley et al. 1994; Galimberti et al. 2000, 2002, 2007; Fabiani et al. 2004; Sanvito et al. 2007). ENFI was calculated as the number of successful copulations with individual marked females that were observed for a male in a breeding area, divided by the total number of copulations between all study males and individual marked females observed in the area and multiplied by the total number of females in the area. Multiple copulations by a given male with the same female were not counted. Copulations were considered to be successful when intromission lasted for a minimum of 90 s (Le Boeuf 1974). The ENFI metric slightly overestimates true fertilization success (Hoelzel et al. 1999), but it is a simple way of using observed copulations with marked females to estimate mating success for the entire harem. Duration of stay (tenure) on the rookery was determined as the number of days from arrival to departure. Males

were marked immediately on arrival to the study site, but they may have hauled out previously at other areas. Changes in daily harem location of males were used to estimate the number of movements between harems. Within harems, movements of >5 m were recorded.

Data Analysis

Comparisons between dominance ranks were made using ANOVA. Post hoc comparisons were made using Tukey's HSD. To control for differences in body mass when energy expenditure and water flux were compared, an ANCOVA with body mass (average of initial and final sample) as a covariate was used. Statistics were performed using SAS, version 9, with a significance level of $P < 0.05$. Means are presented as ± 1 SD.

Results

Breeding Behavior

Three males left the study area during the measurement period and were not included in subsequent analyses. For the remaining 18 subjects, the mean measurement interval between captures was 44.1 ± 6.1 d, or 50% of the average time spent on shore (89 ± 7 d). Tenure varied significantly between dominance ranks (table 1; $F_{3, 17} = 6.9$, $P < 0.01$), with alpha and beta males spending more time on shore than gamma or peripheral males (Tukey's HSD: $P < 0.05$). Tenure increased significantly with initial body mass ($F_{1, 17} = 25.0$, $r^2 = 0.52$, $P < 0.01$). Over the study period, 85, 118, and 44 females bred in harems H1, H2, and H3, respectively. The mean proportion of females that were marked and observed daily throughout the breeding season at each harem site was $47\% \pm 3\%$. All marked females were observed copulating with a study male. Of the 237 copulations recorded, 114 were between a unique male and female pair. At two harems, equally ranked males held positions at opposite sides of the group. These males were never observed to interact with one another and were both assigned the same rank. Thus, there were two beta ranks assigned at H1 and two beta and two gamma ranks assigned at H2. Peripheral males

Table 2: Body mass, mass loss, body composition, fat loss, protein loss, initial total body water, water flux, and tenure on shore for each dominance rank

	Alpha males (n = 3)	Beta males (n = 5)	Gamma males (n = 4)	Peripheral males (n = 6)
Body mass (kg)[a]	1,768 ± 124[A]	1,576 ± 203[A]	1,485 ± 320[A,B]	1,257 ± 202[B]
Loss (kg d^{-1})[a]	11.1 ± 4.4[A]	9.0 ± 1.2[A,B]	7.2 ± 1.6[A,B]	6.0 ± 1.1[B]
Early body fat (%)	28.8 ± 1.9	28.6 ± 1.7	29.2 ± 2.8	30.7 ± 1.8
Late body fat (%)[a]	16.3 ± 2.3[A]	20.5 ± 1.9[A]	20.1 ± 1.6[A,B]	22.6 ± 2.2[B]
% mass loss from fat	63.2 ± 17.0	54.8 ± 8.4	64.4 ± 9.7	63.7 ± 13.0
% mass loss from protein	8.0 ± 5.1	10.6 ± 2.5	7.7 ± 2.9	7.9 ± 1.5
Body water (kg)[a]	919.3 ± 78.1[A]	822.4 ± 113.4[A]	770.8 ± 188.3[A,B]	637.6 ± 117.7[B]
Water influx (L d^{-1})	11.0 ± 3.4	7.9 ± 1.0	8.5 ± 1.1	6.7 ± .9
Water efflux (L d^{-1})[b]	14.0 ± 1.3[A]	10.8 ± 1.7[B]	10.3 ± 1.7[B]	8.4 ± 1.2[B]

Note. Data are means ± SD. Different superscript uppercase letters denote significant differences from post hoc comparisons (Tukey's HSD: $P < 0.05$).

[a]Significantly different between ranks (ANOVA: $P < 0.05$).

[b]Significantly different between ranks (ANCOVA with mass covariate: $P < 0.05$).

that were excluded from a position of close proximity to the harems occasionally moved between the harems.

ENFI varied significantly between dominance ranks (ANOVA: $F_{3,17} = 22.3$, $P < 0.001$). Of the 247 females in the study area, ENFI calculations suggested that 151 (61%) were inseminated by the three alpha males whereas 60 (24%) were inseminated by the five beta males and 32 (13%) were inseminated by the four gamma males. No peripheral males were observed successfully copulating with a marked female.

Body Mass and Composition

The mean mass of males at initial capture was 1,481 ± 277 kg. Mean mass, mass loss rate, and body composition are shown for each dominance rank in table 1. Initial mass and mass loss rate varied significantly between dominance ranks (ANOVA: $F_{3,17} = 3.9$ and 4.7, $P = 0.03$ and 0.02) but were significantly different only between alpha and peripheral males (Tukey's HSD: $P < 0.05$). When peripheral males were excluded from the analysis, there were no significant differences between ranks (ANOVA: $P > 0.05$). Mean proportion of mass lost over the measurement

period was 23.1% ± 5.8%, or an average loss of 7.8 ± 2.7 kg d^{-1}. There was no relationship between proportional mass loss and initial mass or dominance rank ($P > 0.05$).

Initial fat composition (% fat) was negatively related to initial mass ($F_{1,17} = 26.8$, $r^2 = 0.64$, $P < 0.001$), but it did not vary significantly with dominance rank (ANOVA: $P = 0.37$). Male body fat decreased from 29.5% ± 2.1% to 20.4% ± 2.8% between the first and second measurements. Higher-ranking males experienced a greater percentage of depletion of initial body fat ($F_{3,17} = 6.6$, $P < 0.01$), and consequently, body composition late in breeding was lower in alpha males than in subordinate males ($F_{3,17} = 6.7$, $P < 0.01$; Tukey's HSD: $P < 0.05$). Average mass lost by males was 61.3% ± 11.6% fat, 8.6% ± 3.5% protein, and 30.1% ± 8.1% water.

Water Flux

Initial TBW, water influx rates (WIRs), and water efflux rates (WERs) for each dominance rank are shown in table 2. Mean WIR for all males was 8.1 ± 2.5 L d^{-1} or 4.0 ± 0.8 mL kg^{-1} d^{-1}, and this did not vary with dominance rank (ANCOVA:

Table 3: Daily energy expenditure (DEE) calculated from changes in body mass and composition, estimated number of females inseminated (ENFI), proportional contribution of protein to energy metabolism (EE), and DEE expressed as multiples of predicted standard metabolic rate (SMR) in breeding adult male elephant seals

	Alpha males (n = 3)	Beta males (n = 5)	Gamma males (n = 4)	Peripheral males (n = 6)
DEE (MJ d^{-1})[a]	267 ± 41[A]	209 ± 25[B]	179 ± 33[B,C]	155 ± 13[C]
ENFI[b]	50.4 ± 23.3[A]	13.9 ± 3.0[B]	7.9 ± 2.4[C]	0 ± 0[D]
% EE from protein	6.3 ± 5.6	8.4 ± 2.8	5.4 ± 2.4	5.9 ± 3.7
DEE (Kleiber multiples)[b]	3.9 ± .7[A]	3.2 ± .7[A]	2.8 ± .3[B]	2.8 ± .2[B]

Note. Data are means ± SD. SMR (in MJ d^{-1}) calculated as $0.293 \times (\text{mass})^{0.75}$ (Kleiber 1975). Different superscript uppercase letters denote significant differences from post hoc comparisons (Tukey's HSD: $P < 0.05$).

[a]Significantly different between ranks (ANCOVA with mass covariate: $P < 0.05$).

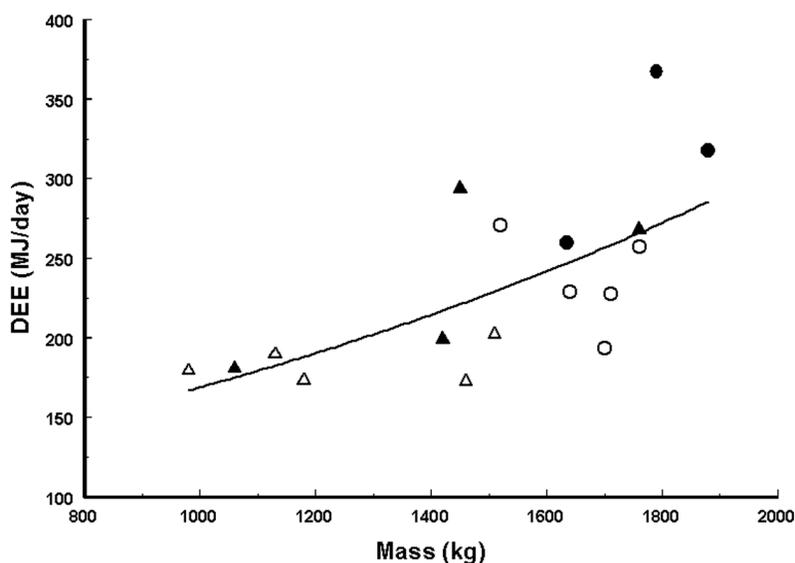[b]Significantly different between ranks (ANOVA: $P < 0.05$).

Figure 1. Relationship between body mass and daily energy expenditure (DEE) over the measurement period. DEEs were calculated from mass and body composition changes. DEE (in MJ d^{-1}) was calculated as $68.5 + e^{(0.0007 \times \text{mass})}$. Filled circles are alpha males; open circles are beta males. Filled triangles are gamma males; open triangles are peripheral males.

$P = 0.25$). Mean WER for all males was 10.4 ± 2.4 L d^{-1} or 4.9 ± 0.9 mL kg^{-1} d^{-1}, and it varied significantly between dominance ranks (ANCOVA: $F_{3,17} = 4.3$, $P = 0.03$), with alpha males having significantly higher rates of efflux than males of the other ranks (Tukey's HSD: $P < 0.05$). WIR varied with DEE ($F_{1,16} = 9.4$, $r^2 = 0.37$, $P < 0.01$). Mass-specific WIR and WER were not significantly related to body mass or composition ($P > 0.05$). WER was not significantly correlated with tenure on shore ($P = 0.38$).

Energy Expenditure

DEEs estimated from changes in mass and body composition and ENFI are shown in table 3. Mean DEE was 195 ± 49 MJ d^{-1}, which was equivalent to 3.1 times the standard metabolic rate (SMR) predicted from Kleiber's equation (Kleiber 1975). DEE increased exponentially with initial mass (fig. 1; $F_{1,16} = 25.1$, $r^2 = 0.57$, $P < 0.01$). When controlling for mass, energy expenditure varied significantly between dominance ranks (ANCOVA: $F_{3,17} = 6.4$, $P < 0.01$), with alpha males exhibiting higher energy expenditure than all other males and beta males exhibiting higher energy expenditure than peripheral males (Tukey's HSD: $P < 0.05$).

ENFI increased significantly with DEE over the breeding period (fig. 2; $F_{1,17} = 17.1$, $r^2 = 0.52$, $P < 0.001$). However, a visual inspection of figure 2 suggests that this was driven largely by differences between ranks. Rates of agonistic interactions or copulations among ranked males during the measurement did not impact DEE ($P = 0.23, 0.74$). Among the ranked males, movement rate was a significant predictor of DEE ($F_{1,12} = 11.2$, $r^2 = 0.53$, $P < 0.01$). On average, the six peripheral males moved between harems 11.6 ± 5.3 times during the measure-

ment period. DEE increased with the number of movements between harems ($F_{1,4} = 9.8$, $r^2 = 0.71$, $P = 0.04$).

On average, males met $7.0\% \pm 2.7\%$ of their energy expenditure through protein catabolism and 93.0% through fat catabolism. The proportional contribution of protein to energy metabolism was not correlated with body mass ($P = 0.17$) and was not different between dominance ranks (ANOVA: $P = 0.30$). The proportional contribution of protein to energy metabolism decreased significantly with the initial proportion of body fat (fig. 3; $F_{1,17} = 22.6$, $r^2 = 0.55$, $P < 0.001$). The proportional contribution of protein to energy metabolism was not significantly correlated with rate of water efflux ($P = 0.18$) or tenure on the rookery ($P = 0.20$).

Discussion

Despite the long duration of the breeding period and the exclusive use of stored body reserves to meet energetic costs, male elephant seals exhibited high levels of energy expenditure, which averaged 3.1 times the predicted SMR predicted from Kleiber's equation. Body size significantly impacted both DEE and tenure. Mating success in adult male elephant seals varied directly with DEE over the breeding season. Alpha males secured the majority of copulations and exhibited significantly higher rates of DEE than other ranks, with levels of energy expenditure approaching four times the predicted SMR. DEE was also relatively high in unsuccessful males, with peripheral males obtaining no copulations averaging sustained metabolic rates (MRs) approaching three times the predicted SMR. The relationship between DEE and breeding success was largely linear but had considerable variation in energy expenditure among the most successful males.
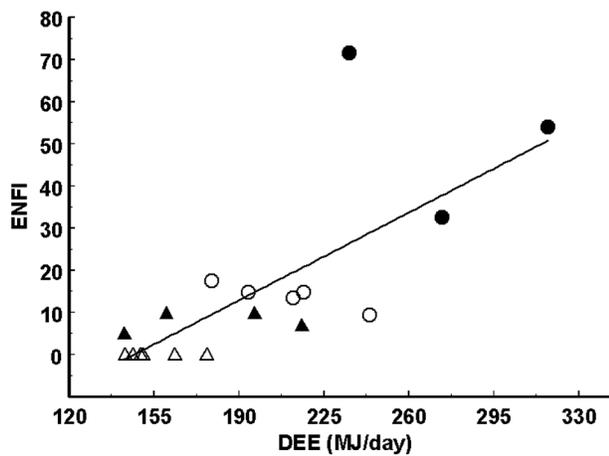
Figure 2. Relationship between energy expenditure (MJ d^{-1}) and estimated number of females inseminated (ENFI). Energy expenditure was calculated from changes in mass and body composition. Body composition was assessed from isotopic dilution. ENFI was calculated on the basis of the proportion of copulations with marked females to harem size. Symbols denote dominance rank as in figure 1.

Large fat reserves were important in maintaining lean tissue during breeding, but in contrast to allometric predictions (Lindstedt and Boyce 1985) and findings in other pinnipeds (e.g., Coltman et al. 1998), fat reserves decreased proportionally with increasing male size. This may reflect limits on rates of energy intake while foraging and trade-offs between somatic growth and fat storage during recovery from breeding. The strong relationship between adipose tissue reserves and protein sparing during fasting is consistent with that reported in a wide variety of species (e.g., Goodman et al. 1980), including lactating female northern elephant seals (Crocker et al. 2001) and fasting weaned pups (Noren et al. 2003). Protein sparing was preserved even though energy expenditure rates were high, a finding that is contrary to the suggestion that reductions in MR may be critical to protein sparing during fasting (Henry et al. 1988).

One important determinant of onshore MR may be the cost of terrestrial locomotion. This is suggested by the relationship between movement rate and DEE in ranked males and between long terrestrial movements and DEE in peripheral males. It is also consistent with the effect of harem topography on energy expenditure among alpha males. Although not significantly different from other ranks, rates of movement were highly variable among alpha males and were apparently strongly influenced by topography. The effect of harem topography on female movement in response to tidal changes is depicted in figure 4. Females in H1 responded to high tides by moving up into a long, steep gully. One beta male assumed a position at the back of the gully, and the alpha male was able to control access to the females primarily through threat vocalizations. The alpha male demonstrated comparatively low rates of energy expenditure and movement (15 m h^{-1}) and high reproductive success, inseminating 72 (85%) of the available females. In contrast, a

large portion of harem H2 moved up into three distinct steep gullies in response to high tides. The alpha male moved back and forth between the gullies, sometimes temporarily ceding a gully to a beta male as the season progressed. This male exhibited the highest rates of movement in the study (34 m h^{-1}) and had the highest MR of all of the males despite comparatively lower copulatory success; he inseminated 54 (46%) of the available females. The third harem, H3, was flattened out against a steep cliff by tidal action. The alpha male of this harem exhibited moderate levels of movement (24 m h^{-1}), energy expenditure, and breeding success, inseminating 32 (73%) of the available females. Thus, in our small sample of harems, topography appeared to strongly influence the ability of males to monopolize access to females, and it affected rates of movement and individual energy expenditure.

Alpha males exhibited significantly higher water efflux rates than did subordinates when controlling for body mass. Deutsch (1990) found that the ventilation rates of alpha males were 25% greater than those of low-ranking adults and that the duration of their apneas were significantly shorter. Alpha males vocalized in agonistic encounters at significantly higher rates than did males of any of the other ranks. Since vocalizing requires males to bypass their nasal turbinates, the reduced locomotor costs enabled by vocal interactions may come at an osmoregulatory cost to dominant males via respiratory evaporative water loss. Further, dominance rank has been shown to have a strong impact on skin temperature in elephant seals (Norris et al. 2010), suggesting the potential for increased cutaneous water loss in higher-ranking males. There was no relationship between protein loss and water efflux rate, suggesting that the strong urinary-concentrating ability of elephant seals minimizes impacts of urea production on water economy (Ortiz et al. 2006).

Empirical studies that quantitatively compare male and female RE in polygynous vertebrates are rare (Stearns 1976; War-
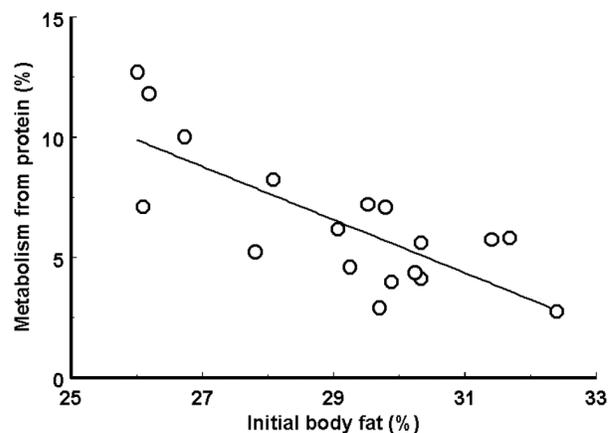

Figure 3. Contribution of protein catabolism to energy metabolism as a function of initial proportion of body fat. Body fat was assessed by isotopic dilution. Protein catabolism was estimated on the basis of proportions of mass loss from lean and lipid compartments. Protein catabolism (%) was calculated as -1.11 (% fat) $+ 38.6$.
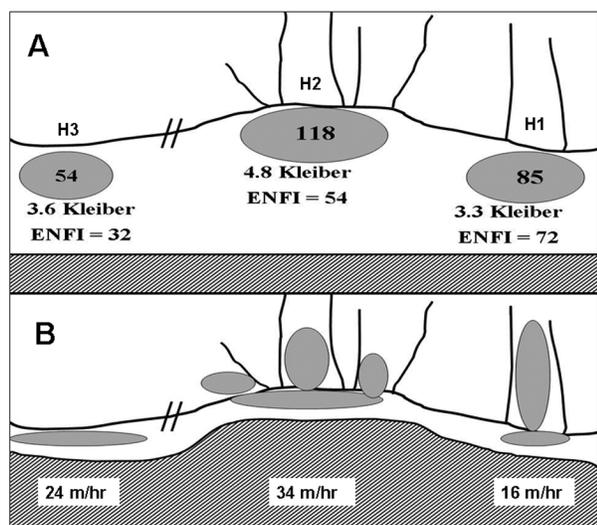
Figure 4. Illustration showing effects of topography and tide changes on female group characteristics. *A*, Harem configurations at low tides. Energy expenditure of alpha males is reported as multiples of the predicted standard metabolic rate from Kleiber's equation (Kleiber 1975). Estimated number of females inseminated (ENFI) was calculated on the basis of proportion of copulations with marked females to harem size. *B*, Change in harem configuration during high tide.

ner 1980; Gittleman and Thompson 1988; Michener and Lockyear 1990; Lane et al. 2010). In most cases, sex differences in energy intake during breeding and in risks associated with reproducing can make direct comparisons of RE between the sexes difficult (Knapton 1984). The temporal separation of foraging and breeding in northern elephant seals allows for the direct energetic comparison of RE, as all energy expenditure above maintenance levels serves a reproductive function. RE in female northern elephant seals is largely devoted to parental care, with an average breeding female expending energy at 5.7 times the SMR predicted from Kleiber's equation, or 3,490 MJ, during breeding (Crocker et al. 2001). Males exhibiting at least some copulatory success in this study averaged 3.3 times the predicted SMR, or 24,770 MJ, during breeding. This comparison ignores gestational effort and maintenance costs of the 6.5-d prepartum residency by females (Crocker et al. 2001). When accounting for these costs using MR and neonate energy content data (Crocker et al. 2001), average female RE increases ~35%, to 4,867 MJ. Note that this estimation excludes the metabolic cost of gestation for females above the energy content of the pup. Little is known about gestational costs in diving phocids, but some studies have suggested metabolic suppression during gestation (e.g., Sparling et al. 2006). When total energy costs over breeding are compared among sexes, using ANCOVA with mass as a covariate, total RE is significantly higher in males than in females ($F_{1,44} = 26.8$, $P < 0.0001$). When combining the data for both sexes, body mass accounts for 94% of the variation in total energy expenditure over breeding.

The RE of male pinnipeds has received considerable attention compared with that of other mammals (Anderson and Fedak 1985; Boyd and Duck 1991; Bartsh et al. 1992; Deutsch et al. 1994; Kovacs et al. 1996; Coltman et al. 1998; Lidgard et al. 2005). Coltman et al. (1998) used published energetic and mass loss data to calculate a scaling relationship of 0.77 for mass
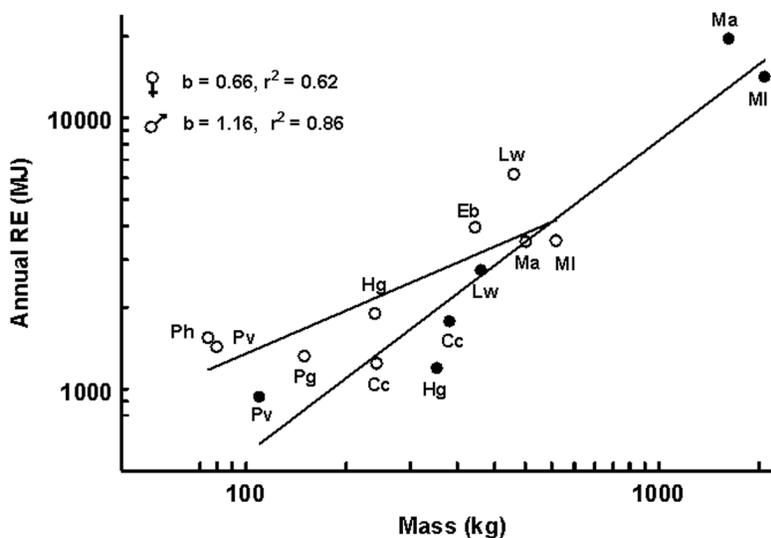

Figure 5. Allometric comparison of annual reproductive effort (RE) in phocid seals. Open circles are females; filled circles are males. Pg, *Phoca groenlandica*; Pv, *Phoca vitulina*; Ph, *Phoca hispida*; Cc, *Cystophora cristata*; Hg, *Halichoerus grypus*; Lw, *Leptonychotes weddelli*; Ma, *Mirounga angustirostris*; Ml, *Mirounga leonina*. Data are from Anderson and Fedak (1985), Arnbom et al. (1997), Bartsh et al. (1992), Bowen et al. (1992), Coltman et al. (1998), Crocker et al. (2001), Galimberti et al. (2007), Kovacs and Lavigne (1992), Kovacs et al. (1996), Testa et al. (1989), and this study.

and breeding energy expenditure among male pinnipeds. This calculation used a standard energetic value for mass loss for several species that assumed that mass lost was 100% adipose tissue. In order to extend our sex comparison to other phocids, we repeated this analysis using the available data for mean RE in male and female phocid seals. Where body composition data were not available, we assumed that mass lost was composed of 90% adipose tissue and 10% lean tissue. Inclusion of the data from this study and a recent study on southern elephant seals suggested a significantly greater scaling exponent for RE in male seals than in female seals (fig. 5). This analysis also suggested that at low body sizes, females have greater annual RE. When the effect of body size is removed, average breeding MR in northern elephant seals is similar to that of other male pinnipeds. However, alpha males that achieved the majority of copulatory success had sustained MRs that were considerably greater than that predicted by the scaling relationship, suggesting that high individual effort may be required to maximize success in this system.

Our data provide strong evidence of the effects of state variables on reproductive effort and success in a polygynous male capital breeder. Large body size was associated with increased reproductive effort, tenure on shore, dominance rank, and reproductive success. Body composition significantly impacted the ability to spare lean body tissue during breeding, although this did not appear to directly impact tenure. The apparent influence of topography demonstrates the role that environmental variables can have in influencing the energetic cost of a given breeding strategy. The relatively high rates of energy expenditure exhibited by smaller, unsuccessful males suggests the importance of gaining early breeding experience and the potential strong impacts of annual foraging success on recovery and subsequent effort. Our data suggest that in capital breeding systems where high rates of effort are necessary for success, male effort may be strongly influenced by physiological state and may exceed that of females.

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