

# Reproductive effort of male northern elephant seals: estimates from mass loss

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Received October 2, 1989

DEUTSCH, C. J., HALEY, M. P., and LE BOEUF, B. J. 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. *Can. J. Zool.* **68**: 2580–2593.

The energetic component of reproductive effort of male northern elephant seals, *Mirounga angustirostris*, was estimated from mass loss over the breeding season and correlated with dominance rank and age. Fifty-four unrestrained bulls were weighed on a platform scale by luring them with a model of a female seal or moving them with a tarpaulin and using playback of male aggressive vocalizations. Adult males weighed up to 2300 kg upon arrival at the breeding rookery. Mean rate of mass loss during the breeding season was  $7.1 \pm 1.5$  (SD) and  $4.6 \pm 0.8$  kg per day for 17 adults and 13 subadults, respectively. Rate of mass loss was positively correlated with body size (mass or length) for both age-classes. Mass-specific rate of mass loss did not differ between age-classes but increased with increasing dominance rank among adult males. Reproductive effort, expressed as percentage of body mass lost over the 3-month breeding season, was greater for high-ranking bulls (mean 41.4%) than for low-ranking adults (33.8%), but was not related to age-class or body size. High-ranking males experienced higher mating success and expended more energy than subordinate males. Comparison with a previous study on conspecific females indicates that mass-specific energetic investment in reproduction is similar for both sexes, despite marked sex differences in reproductive strategy and duration of effort.

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La composante énergétique de l'effort reproducteur des Éléphants de mer *Mirounga angustirostris* mâles a été estimée par évaluation de la perte de masse durant la saison de reproduction et la corrélation entre cette composante et le rang social et l'âge a été déterminée. Cinquante-quatre mâles en liberté ont été pesés sur une balance plate-forme où ils avaient été attirés au moyen d'un modèle de femelle ou déplacés avec une bâche en leur faisant entendre des enregistrements de cris agressifs d'autres mâles. Les mâles adultes pesaient jusqu'à 2300 kg à leur arrivée à la rookerie. Le taux moyen ( $\pm$  écart type) de perte de masse au cours de la saison de reproduction était de  $7,1 (\pm 1,5)$  kg par jour chez 17 adultes et de  $4,6 (\pm 0,8)$  kg par jour chez 13 subadultes. Le taux de perte de masse était en corrélation positive avec la taille du corps (masse ou longueur) au sein des deux classes d'âge. Le taux de perte spécifique à la masse ne différait pas chez les deux classes d'âge, mais augmentait avec le rang de dominance chez les mâles adultes. L'effort reproducteur, exprimé en pourcentage de la masse perdue au cours des 3 mois de la saison de reproduction, était plus grand chez les mâles de rang élevé dans la hiérarchie (moyenne 41,4%) que chez les mâles de rang peu élevé (33,8%), mais n'était relié ni à la classe d'âge, ni à la taille du corps. Les mâles de statut élevé avaient plus de succès auprès des femelles et dépensaient plus d'énergie que les mâles subordonnés. Ces résultats, ajoutés à ceux d'une étude antérieure sur les femelles conspécifiques, indiquent que l'énergie spécifique à la masse investie dans la reproduction est semblable chez les deux sexes, en dépit de différences très marquées dans la stratégie de reproduction et la durée de l'effort reproducteur.

[Traduit par la revue]

## Introduction

The concept of reproductive effort (RE), defined as the proportion of available resources (time and energy) that an organism devotes to reproduction over a specified period of time (Gadgil and Bossert 1970; Hirschfield and Tinkle 1975), plays a key role in life-history theory because investment in current reproduction is thought to occur at the expense of the parent's future fecundity or survival (Williams 1966a; Gadgil and Bossert 1970; Pianka 1976). The pattern of RE in males, and the selective forces molding this pattern, are likely to be quite different from those of females in polygynous species (Warner 1980) because reproductive success of females is usually limited by energetic considerations, whereas that of males is constrained principally by access to fertile females (Trivers 1972). Clearly, RE theory must address the sexes separately, especially in polygynous animals (Stearns 1976; Warner 1980). Yet most theoretical life-history models have been developed with females in mind (Stearns 1976), and most empirical studies on RE have also focused on females (Tinkle 1969; Ballinger and Clark 1973; Tinkle and Hadley 1975; Smith 1976; Ballinger 1977; Millar 1977; Andrews 1979; Robbins and Robbins 1979; Baltz 1980; Hirschfield 1980; Stenseth and Framsted 1980;

Galef 1983; Clutton-Brock 1984; Stewart 1986, 1987), or on both sexes of monogamous species (Bryant 1979, 1988; Pugesek 1981, 1983; Beissenger 1987; Brunton 1988a, 1988b). Studies on the effort males in polygynous societies invest in reproduction are relatively rare (Mac Nally 1981; Thornhill 1981; Anderson and Fedak 1985; Maher and Byers 1987; Kenagy et al. 1989; Vehrencamp et al. 1989).

The strong bias toward females in studies on the energetics of mammalian reproduction (Loudon and Racey 1987; Gittleman and Thompson 1988) exists for at least two reasons. First, ecologists and agricultural scientists interested in determining the energetic constraints on population growth rate or on domestic animal productivity have studied female reproduction because the reproductive output of females sets the limits of population change (Cole 1954). Secondly, maternal investment can be readily quantified, in terms of neonatal litter mass or energy value (e.g., Cabana et al. 1982; Kovacs and Lavigne 1986), and milk energy transferred from the mother to the young (e.g., Ortiz et al. 1984; Gittleman and Oftedal 1987; Oftedal et al. 1987), whereas male mating effort (*sensu* Low 1978) is difficult to measure.

The aims of this study were to estimate the energetic component of reproductive effort in males of a highly polygynous mammal, the northern elephant seal (*Mirounga angustirostris*), to examine the relationships of male RE to dominance rank and age, and to compare RE between the sexes. Elephant

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TABLE 1. Sample sizes for number of weights, number of males weighed, and number of males reweighed, by age-class and year of weighing

Age-class	Year	No. of weights	No. of males weighed	No. of males reweighed
Adults	1987–1988	42	23	15
	1988–1989	5	3	2
Subadults	1987–1988	46	29	13
Total		93	54	29

NOTE: The discrepancy between the total number of males weighed and the sum of adult and subadult males is due to the fact that one male (KZ4) was weighed as a subadult in 1987–1988 and as an adult in 1988–1989; he is therefore included in both age categories, but only once in the total number of males.

seals are ideal subjects for studying RE because adults fast and remain on land during the breeding season, relying on stored energy reserves, mainly in the blubber. Weight loss can therefore be used as an index of reproductive energy expenditure (Fedak and Anderson 1987). The northern elephant seal is highly sexually dimorphic; adult females weigh from 250 to 710 kg (Costa et al. 1986; Le Boeuf et al. 1988, 1989; B. J. Le Boeuf and D. P. Costa, unpublished data) and adult males have been estimated to weigh up to 2700 kg (Le Boeuf 1981). However, there are no published data on weights of physically mature bulls. Adult males actively compete for high dominance status and attempt to mate with estrous cows while fasting for approximately 3 months (Le Boeuf 1974). Many bulls appear gaunt and physically exhausted by the time they return to sea at the end of the breeding season. We weighed male seals and used percentage of body mass lost over the breeding season as our measure of the energetic component of RE.

We test two hypotheses regarding the level of reproductive effort in male elephant seals. The first hypothesis is that RE is positively correlated with age. Some life-history models predict that RE increases with age in iteroparous species as the number of expected future offspring (i.e., residual reproductive value) declines (Williams 1966a, 1966b; Gadgil and Bossert 1970; Pianka and Parker 1975; Pianka 1976); others predict that this relationship holds only under certain environmental or demographic conditions (e.g., low extrinsic adult mortality rate, low rate of population increase) (Hirschfield and Tinkle 1975; Charlesworth and León 1976). In this study, males were categorized into age-classes to distinguish gross changes in male RE with age.

The second hypothesis is that RE is positively correlated with dominance rank in male elephant seals and in other species exhibiting male dominance polygyny. In such highly polygynous species, intense male competition for high social status and copulations results in high variance in male mating success, a small proportion of the males performing most of the mating (e.g., Le Boeuf 1974; Clutton-Brock et al. 1982; Le Boeuf and Reiter 1988). Male dominance rank is highly correlated with mating success in *Mirounga* (Le Boeuf and Peterson 1969; Le Boeuf 1974; McCann 1981; Le Boeuf and Reiter 1988). An expected consequence of these high stakes is that potentially successful males should expend great amounts of time and energy, and take great risks, to achieve and maintain the high rank or territorial status necessary for mating, perhaps even at the expense of body maintenance. Males unsuccessful in competition might be expected to invest less in reproduction (Warner 1980), allocating energy to maintenance and growth or reserving it for future breeding attempts (Calow 1979). Alterna-

tively, such males could adopt noncompetitive mating strategies in an attempt to circumvent the monopoly (Alcock 1979; Thornhill 1981; Hogg 1984; Howard 1984). Our specific prediction was that the energetic cost of reproduction (measured as mass-specific mass loss per day and over the season) would increase with dominance rank, the highest-ranking bulls experiencing the greatest rates of mass loss.

We address the following specific questions: (1) How much do sexually mature northern elephant seal males weigh? (2) What is their rate of mass loss during the reproductive period? (3) What proportion of a male's mass is lost over the entire breeding season, and how does this compare with the mass loss of conspecific females? (4) What factors (e.g., age, dominance rank) affect rate of mass loss and total mass loss in breeding male elephant seals, and what is their relative importance?

## Methods

The study was conducted on the mainland of Año Nuevo, California, during the 1987–1988 and 1988–1989 winter breeding seasons. During these years, about 350 male and 1000 female northern elephant seals bred on the mainland, distributed among 11–13 harems. Male elephant seals were individually identified by means of plastic numbered tags placed in the interdigital webbing of the hind flippers (Le Boeuf and Peterson 1969), and names or numbers on their pelage marked with a mixture of Wellite cream bleach (Wella Corp., Englewood, New Jersey) and 30% peroxide. Subadult and adult males were distinguished by overall body length and development of secondary sexual characteristics (neck shield and proboscis) (Le Boeuf 1974; Cox 1983). Subadult bulls, approximately 5–8 years old, are sexually mature but physically and socially immature. Adult bulls can range from 8 to 14 years of age (Le Boeuf and Reiter 1988), and show full development of the pendulous nose and rugose neck shield. Age classification was based solely on the above morphological characteristics, which correlate positively with age (Le Boeuf 1974; Clinton 1990).

A total of 93 weights was obtained on 54 male elephant seals during the weighing periods (31 December 1987 to 13 March 1988, 11–21 December 1988, and 2–4 March 1989) (Table 1). The sample of 29 bulls weighed more than once over the breeding season encompassed a wide range of weights, ages (estimated 5–13+ years), and dominance ranks (low-ranking to alpha status). Six males were weighed three times each and one was weighed four times in the 1987–1988 season; one of these bulls was weighed twice again in the 1988–1989 season. Only males whose serial weighings were at least 1 week apart were included in the reweighed sample.

## Weighing apparatus

The scale (Senstek, Inc., Saskatoon, Sask., Canada) consisted of three parts: (1) a platform; (2) two weigh bars, containing load cells, that supported the platform; and (3) cables from the weigh bars to an electronic display. The platform was made of aircraft-strength alumi-



FIG. 1. A subadult male crosses the scale to approach the female model. The playback equipment is situated to the right of the scale. The person reading the weight from the LCD is hidden behind the willows.

num, weighed 145 kg, and measured 4.9 m long  $\times$  1.2 m wide  $\times$  0.13 m high (Fig. 1). It was painted brown and tan to blend in with the sandy substrate. Two removable aluminum "wings" measuring 1.2 m long  $\times$  0.3 m wide were attached to increase the width of the scale in the area occupied by the seal's pectoral flippers. The platform was supported at each end by one 0.8 m long steel weigh bar placed on a 1.2 m  $\times$  1.2 m  $\times$  2 cm sheet of plywood. Each weigh bar contained two load cells which measured the stress on the bars and sent electronic signals via a 23 m long cable to a battery-powered liquid crystal display (LCD), where the weight was read. The scale was accurate to  $\pm 0.25\%$ , or about 5 kg. Repeated weights of males on the same or consecutive days were within 4.5 kg of each other.

#### *Weighing procedure*

The scale was typically placed 40–80 m from large harems in sites bounded closely by dunes or willow thickets, which acted as a natural containment or funnel. All but two weights on one subadult male were obtained without chemical immobilization. A variety of techniques was employed to get the male onto the scale. Bulls were lured onto the scale with a life-size model of a female elephant seal and recordings of vocalizations given by females being mounted (Fig. 1). The rear end of the model was moved from side to side in synchrony with the vocalizations, to simulate the behavior of a female responding to a mount (Le Boeuf 1972). Males up to 50 m away were attracted by the playback of the female vocalizations, and then approached the model as

it was pulled at the end of the scale. Occasionally, males mounted or displayed other sexual behaviors (e.g., neck slam) toward the model female. The model was constructed of urethane pour foam on a blank surfboard base; the exterior was fiberglassed and painted. The size and measurements for the model were patterned on a female at the end of lactation (i.e., in estrus). The playback system included a tape recorder, two amplifiers in series, a noise filter, and a speaker mounted in a metal weatherproof casing. The system was powered by two NiCad 6-V rechargeable batteries.

Males that were not attracted to the model, or that were too distant (e.g., up to 100 m away), were moved by two to four persons waving a tarpaulin, banging on a plywood board, or playing loud male threat vocalizations through the speaker system described above. Sometimes we set up wooden snow fences (1.2 m high and 15 m long) to act as a funnel as we moved a male toward the scale. We often used this technique to move a male to the base of the scale, where the subject came to rest and often slept; after about 30 min, the male was awakened by playing the female vocalization and moving the model across his field of view at the opposite end of the scale. This caused the male to cross the scale of his own volition, which was a considerably more successful method of obtaining an accurate reading than forcing him across the scale.

The seal had to be completely stopped on the scale for 5–10 s to obtain an accurate reading. A male lured onto the platform could usually be stopped by having a person step in front of him. Males that

we moved onto the scale were stopped by raising a remotely operated snow fence at the foot of the scale. A pair of headset transceivers was used to communicate the weight displayed on the LCD to the person who could see whether the seal was completely on the scale.

We obtained accurate weights (i.e., within 9 kg) on 42% (86/206) of our attempts to weigh males in the 1987–1988 season. Weights with poorer reliability were obtained when the seal moved off the scale before the reading had stabilized, or had a portion of its body off the platform. We typically obtained one to three good weights per day. Initially we attempted to weigh any male near the scale, choosing adults in preference to subadults. Near the end of each season we concentrated on weighing previously weighed males to obtain data on mass loss.

One young subadult male (PQ), estimated to have been 5 years old, was immobilized and weighed 13 days after his arrival and again 46 days later at the end of the breeding season. The animal was immobilized with a mixture of ketamine hydrochloride, diazepam, and atropine sulfate, using protocol and dosages similar to those for conspecific females (Briggs et al. 1975; Costa et al. 1986), and was then rolled onto the platform scale for weighing. PQ departed the rookery within hours of recovering from the anesthesia after the second capture. Since his departure was apparently hastened by the handling, this data point was excluded from the statistical analyses of duration of stay on the rookery and total percentage of body mass lost over the breeding season.

#### *Length measurements*

After an animal was weighed, it was photographed from a distance of about 6 m at a 90° angle to the body axis, with a 4 m long ruled surveying pole held over the seal's back. Lengths were determined from photographs of males lying straight on their ventrum. Standard length was difficult to measure precisely from photographs, and therefore length measurements were taken from the base of the proboscis to the base of the hind flipper. Repeat measurements of length at different times in the season were consistent, generally within 2% of each other (mean difference 1.65%).

#### *Activity level, dominance rank, and mating success*

We measured indices of activity, dominance, and mating success: potential variables correlated with mass loss. The proximity of males to harems indicates the effort made to compete for females and is a general correlate of activity (C. J. Deutsch, unpublished data). The proximity of each marked male to harems was recorded daily throughout the breeding season, using the following categories: (1) in a harem; (2) on the periphery of a harem (within 5 m); (3) near a harem (within 6–50 m); and (4) away from harems (>50 m away). These data were expressed as percentages of the total number of daily observations of the male during the time period between that male's first and last weights.

Dominance rank of adult bulls was determined from the outcome of fights and other agonistic interactions among males (Le Boeuf and Peterson 1969; Sandegren 1976; Cox 1981). A dominance index for each adult male was calculated using the Bradley–Terry (BT) model from the method of paired comparisons (Boyd and Silk 1983), based on 4745 dominance interactions in the 1987–1988 season. This index is a cardinal measure of rank which is normally distributed. The rank order of males produced by the objective BT method was in close agreement with the more subjective ranking of males based on a conventional dominant–subordinate matrix. Furthermore, it had the advantage of providing a single rookery-wide index, so that males that were never seen to interact could be compared.

Male mating success was measured as the estimated number of females inseminated (ENFI) (Le Boeuf 1974). ENFI was calculated as the number of copulations by a male in a harem divided by the total number of copulations observed in the harem, multiplied by the total number of females in the harem, and summed for each harem in which the male copulated.

#### *Data analysis*

Only weights accurate to within 9 kg were used in the data analyses, except for those of six males for which one of the two serial weights had

an error of  $\pm 14$ –23 kg. Since the time interval between successive weighings was long in each case, the error in rate of mass loss was small (0.3–0.7 kg/day).

In the analysis of factors affecting rate of mass loss, only the 1987–1988 data were used because it is inappropriate to combine BT dominance indices calculated for separate seasons. Since body size affects the absolute energy requirements for maintenance metabolism (Schmidt-Nielsen 1984), we used partial correlation analyses to control for size in order to examine the effects of other variables (e.g., dominance rank) on the rate of mass loss. Since the dates of the initial weighings varied greatly among males in 1988 (7 January to 23 February), body mass was standardized using estimated mass on 12 February 1988. This date was chosen because most serial weighings crossed it or were close to it (Fig. 3); thus, estimated body mass was accurate and comparable across males, and reflected the male's weight during the peak mating period. Mass on 12 February was estimated by either linear interpolation between weights or linear extrapolation from the nearest weight, based on that individual's rate of mass loss. (Qualitatively and statistically similar results were obtained for all analyses when initial mass or mean mass over weighing interval was used instead of mass on 12 February.) Photographic measurements of length were used as a crude index of the animal's lean body mass (Anderson and Fedak 1985), and as a second means of assessing the effect of size on mass loss.

Body mass at arrival, mass at departure, and total percentage of arrival mass lost over the breeding season were estimated for a subset of the weighed males ( $N = 19$  in 1987–1988,  $N = 2$  in 1988–1989) for which we had the following data: date of arrival (to within 8 days); date of departure; and rate of mass loss calculated from two weights taken over 1 week apart. For these calculations we assumed a constant rate of mass loss throughout the time ashore, and used these individual rates to extrapolate back to the arrival date and forward to the departure date.

Probabilities for test statistics were one-tailed when hypotheses were tested relating (i) rate or total mass loss to dominance, age, body size, or proximity to harem, and (ii) percent mass lost per day or per season to dominance, age, or proximity to harem; two-tailed tests are noted in the text. Percentage data were transformed using an arcsine square root transformation to meet the assumptions of normality and homogeneity of variances for parametric statistical tests (Sokal and Rohlf 1981). The level of significance was set at  $\alpha = 0.05$  for all statistical tests.

## **Results**

### *Weights*

Forty-seven weights obtained on 26 adult male elephant seals during the breeding season ranged from 914 to 2087 kg; 46 weights obtained on 29 subadult males ranged from 531 to 1270 kg. Mean mass for each age-class was not calculated from the raw data because the measurements were taken at various times over the season and are therefore not comparable.

Body mass upon the seal's arrival at the rookery, estimated for 13 adult males weighed two or more times, ranged from 1432 to 2265 kg, with a mean of 1704 kg; the estimated body mass of eight subadult males ranged from 727 to 1483 kg upon arrival, with a mean of 1178 kg (Fig. 2). These ranges in mass are representative of the smallest and largest animals of each age-class present on the rookery.

The largest male elephant seal in our sample (GB276), being one of the most massive bulls on the Año Nuevo rookery in 1988–1989, weighed 2087 ( $\pm 18$ ) kg on 11 December 1988. He was at least 13 years old and had been an alpha male for 5 of the 6 years of his known history. Based on his rate of mass loss over the season, we estimate that this male weighed 2265 ( $\pm 43$ ) kg when he first appeared on the rookery in late November.

The only male weighed in 2 successive years (KZ4) doubled his mass over the 9-month period between breeding seasons! We estimate that he weighed 713 kg at departure from the

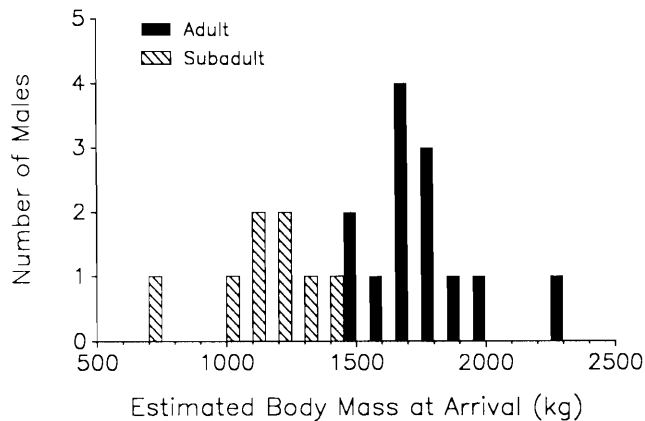


FIG. 2. Estimated body mass upon arrival at the breeding rookery for 13 adult males and 8 subadult males weighed 2 or more times. Note that there is some overlap in arrival body mass of adults and subadults in the 1400–1500 kg range.

rookery in March 1988 as a large subadult (approximately 7–8 years old), and 1432 kg when he returned to the rookery in November 1988 as a small adult. KZ4's estimated arrival mass in November 1987 was 1167 kg, so he increased his mass by about 23% over a 12-month period (from arrival to arrival).

#### Rate of mass loss

Body mass changes of 29 males weighed two or more times are illustrated in Fig. 3A. Measured mass loss ranged from 45 to 821 kg, over intervals of 9–83 days (mean 32.7 days) (Fig. 4). Mean rates of mass loss for 17 adults and 13 subadults were  $7.08 \pm 1.54$  (SD) and  $4.55 \pm 0.83$  kg/day, respectively (Student's *t*-test on log-transformed data:  $t = 5.662$ ,  $df = 28$ ,  $P < 0.0001$ ) (Fig. 4). This daily mass loss represented  $0.401 \pm 0.054\%$  of estimated body mass at arrival, and was similar for adults ( $0.406 \pm 0.061\%$ ,  $N = 13$ ) and subadults ( $0.393 \pm 0.044\%$ ,  $N = 8$ ) (Mann–Whitney test:  $U = 60$ ,  $P > 0.10$ ).

Rates of mass loss were virtually constant from one period to the next for the four subadult males weighed three times each (Fig. 3B), suggesting a linear decline in body mass. For three adults the rate of mass loss apparently increased by 14–34% during the last 1–2 weeks of the breeding season (Fig. 3B), a time during which most males were inactive. One of these adult bulls was weighed four times and showed the following changes in mass loss: 8.2 kg/day from 18 January to 2 February; 9.4 kg/day from 2 February to 25 February; and 10.7 kg/day from 25 February to 3 March. This bull departed on 6 March. Higher rates of mass loss at the end of the season may reflect increased utilization of protein as an energy substrate because lean tissue has a lower energy density than adipose tissue. Changes in mass loss rates based on short weighing intervals (e.g., 7 days) must be interpreted with caution, however, because of the potential error associated with each weight.

#### Total mass loss over the breeding season

The estimates of total mass loss over the entire breeding season varied from 198 kg for the smallest subadult to 1049 kg for the largest adult in our sample. Total mass loss was positively correlated with the animal's estimated arrival mass ( $r = 0.84$ ,  $df = 18$ ,  $P < 0.0001$ ). The mean percentage of estimated arrival mass lost by males over the breeding season was  $35.6 \pm 5.7\%$ , and ranged from 25.7 to 46.3%.

Precise measurements of total mass loss over the breeding season were obtained for two adult males weighed on 11

December 1988 and again, 83 days later, on 4 March 1989. One was a large alpha bull, GB276, who lost 821 kg over the weighing interval, or an average of 9.9 kg per day. Total mass loss over his 106-day breeding fast was estimated to be 1049 kg, representing 46.3% of his body mass at arrival! GB276 was alpha of the largest harem (about 350 females) on the mainland rookery from 16 December through 6 March, and had the highest mating success on the entire rookery. A low-ranking first-year adult male, KZ4, lost 447 kg over the weighing interval, or an average of 5.4 kg per day. This male lost an estimated total of 538 kg over his 100-day stay on the rookery, representing 37.6% of his arrival mass. Interestingly, KZ4's reproductive effort was approximately the same as in the previous year, when he lost an estimated 38.8% of his arrival mass over the season. KZ4 was not observed to copulate in either year.

#### Variables affecting rate of mass loss

The following variables were postulated to be positively related to the daily rate of mass loss: body size (mass on 12 February and length), age-class, dominance rank, mating success, and activity (proximity to harem). Mass loss per day was positively correlated with body mass ( $r = 0.81$ ,  $df = 26$ ,  $P < 0.0001$ ) (Fig. 5). This relationship was expected, since absolute resting metabolic rate increases with body size (Schmidt-Nielsen 1984; Kleiber 1975). However, the percentage of body mass lost per day was not related to body mass ( $r = 0.05$ ,  $df = 26$ ,  $P > 0.80$ , two-tailed), subadults losing proportionately as much as adults. The variance in the relationship of rate of mass loss to body mass was greater for adult males ( $r = 0.48$ ,  $df = 13$ ,  $P < 0.05$ ) than for subadult males ( $r = 0.72$ ,  $df = 11$ ,  $P < 0.005$ ), as reflected in the scatter of points around the regression line (variance ratio test on residuals, adults vs. subadults:  $F = 3.6604$ ,  $df = 14, 12$ ,  $P < 0.025$ , one-tailed) (Fig. 5).

Analyses using the cube of body length as an index of the seal's lean mass corroborated the above results. Mass loss per day was positively correlated with  $\text{length}^3$  ( $r = 0.82$ ,  $df = 26$ ,  $P < 0.0001$ ) (Fig. 6). The correlation between rate of mass loss and  $\text{length}^3$  was stronger for subadults ( $r = 0.72$ ,  $df = 11$ ,  $P < 0.005$ ) than for adults ( $r = 0.52$ ,  $df = 13$ ,  $P < 0.05$ ).

It is striking that the rate of mass loss for some adults was nearly twice that of other adults of approximately the same body mass (Fig. 5). Differences in dominance rank partially account for this variability; rate of mass loss was significantly correlated with the BT dominance index ( $r = -0.70$ ,  $df = 13$ ,  $P < 0.005$ ) (Fig. 7). However, since dominance index was also correlated with body size (body mass:  $r = -0.47$ ,  $df = 13$ ,  $P < 0.05$ ;  $\text{length}^3$ :  $r = -0.54$ ,  $df = 13$ ,  $P < 0.05$ ), it was necessary to control for the confounding effect of body size on rate of mass loss. A partial correlation analysis suggests that high-ranking males incurred a greater rate of mass loss as a result of their status, independent of body size (partial  $r = -0.61$ ,  $df = 12$ ,  $P = 0.010$ , controlling for body mass on 12 February; partial  $r = -0.58$ ,  $df = 12$ ,  $P = 0.015$ , controlling for  $\text{length}^3$ ). Consequently, the percentage of a male's body mass that was lost per day increased with increasing dominance rank ( $r = -0.49$ ,  $df = 13$ ,  $P < 0.05$ ); two of the three highest values were for bulls that attained alpha status for brief periods.

Adult rate of mass loss was also positively correlated with mating success (ENFI) ( $r = 0.68$ ,  $df = 13$ ,  $P < 0.005$ ); this relationship was significant even when the effects of body size were removed (partial  $r = 0.57$ ,  $df = 12$ ,  $P < 0.025$ , controlling for body mass; partial  $r = 0.53$ ,  $df = 12$ ,  $P < 0.05$ ,

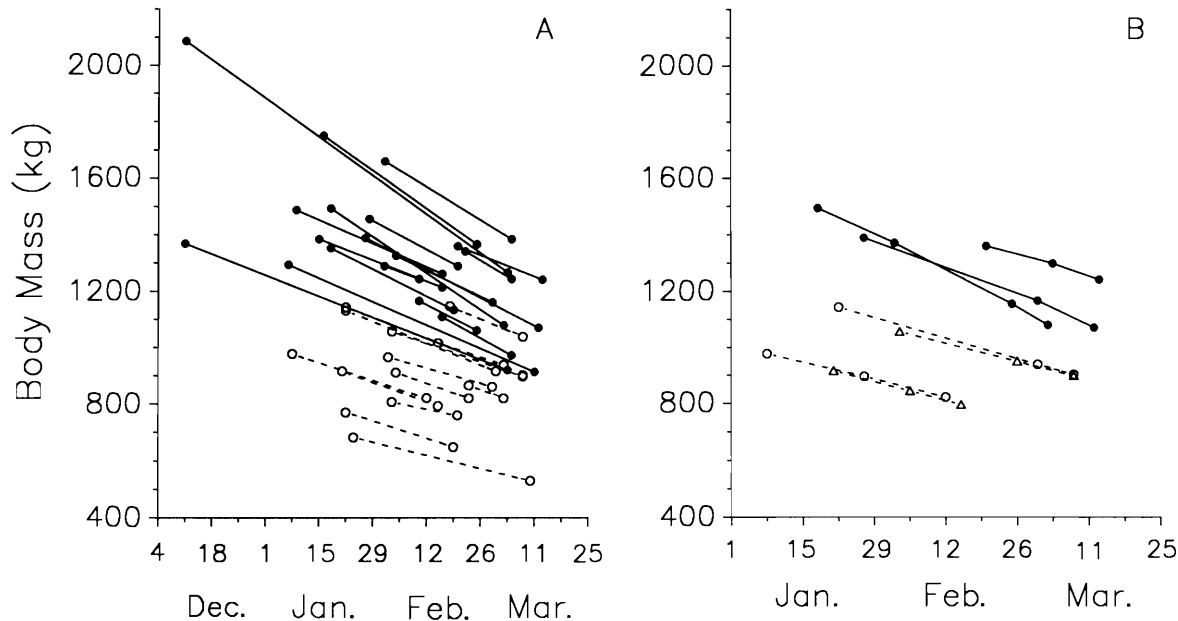


FIG. 3. (A) Body mass changes for 17 adult males (●) and 13 subadult males (○) weighed 2 or more times during the 1987–1988 and 1988–1989 breeding seasons. (Only the first and last weights are shown.) (B) Body mass changes for three adult males (●) and four subadult males (○, △) weighed 3 or more times over the 1987–1988 breeding season, showing the first, intermediate, and final weights. (Two different symbols were used for subadults to distinguish between individuals.)

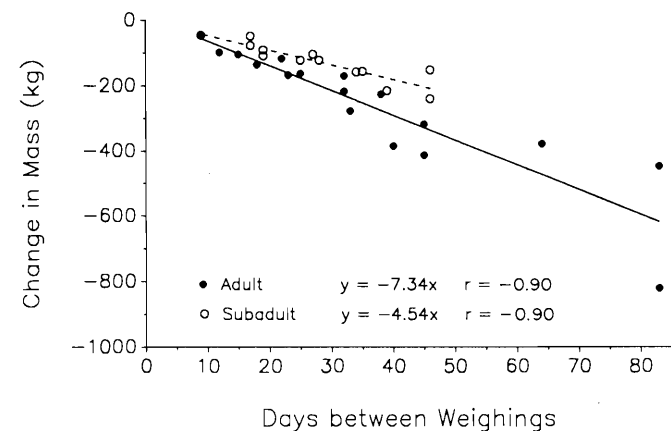


FIG. 4. Mass loss as a function of number of days between weighings for 17 adult males and 13 subadult males. The least-squares regression lines were constrained to go through the origin (Zar 1984), and their slopes are significantly different from each other ( $t = 4.0292$ ,  $df = 28$ ,  $P < 0.0005$ ).

controlling for length<sup>3</sup>). Only the four highest-ranking males in our sample achieved substantial mating success, and three of these exhibited the greatest rates of mass-specific mass loss. There was almost no variation in subadult male mating success (ENFI was zero for all but one male), so this variable could not explain variation in subadult mass loss rate.

The weighed adult males were observed nearly half of the time (during weighing intervals) in or on the periphery of harems ( $46.2 \pm 27.8\%$ ). This index of activity was positively correlated with adult rate of mass loss ( $r = 0.50$ ,  $df = 13$ ,  $P < 0.05$ ), even when body size was held constant (partial  $r = 0.47$ ,  $df = 12$ ,  $P < 0.05$ , controlling for body mass; partial  $r = 0.52$ ,  $df = 12$ ,  $P < 0.05$ , controlling for length<sup>3</sup>). Subadult bulls, on the other hand, spent little time in harems or on harem peripheries ( $11.6 \pm 13.6\%$ ), and this measure was not signifi-

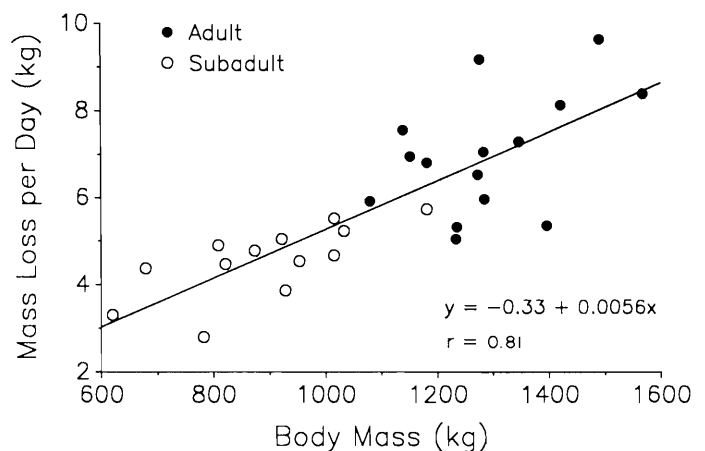


FIG. 5. Relationship between mass loss per day and body mass (on 12 February) for 15 adult males and 13 subadult males in the 1987–1988 breeding season.

cantly correlated with their rate of mass loss ( $r = 0.22$ ,  $df = 11$ ,  $P > 0.20$ ). Moreover, the mass loss rate of subadults was not significantly correlated with time spent in, or within 50 m of, harems ( $61.3 \pm 26.1\%$ ) ( $r = 0.19$ ,  $df = 11$ ,  $P > 0.25$ ). Holding body mass or length<sup>3</sup> constant did not alter these conclusions ( $P > 0.05$  for all partial correlations).

In summary, the daily rate of mass loss was affected by male age-class and body size (mass or length<sup>3</sup>) (Figs. 5 and 6). The mass-specific rate of mass loss, however, was not related to either of the above variables, but showed significant correlations with dominance, mating success, and harem proximity for adult bulls. These three independent variables were intercorrelated ( $r$  values 0.59–0.70), and the effects of this multicollinearity make it difficult to assess their separate contributions to variance in mass loss rate (Neter et al. 1989). But since both mating success and harem proximity depend in large part on

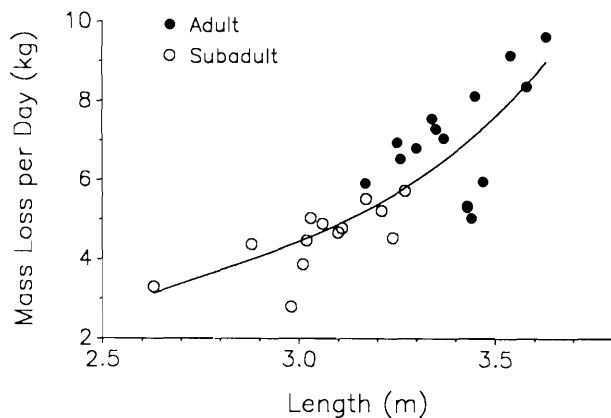


FIG. 6. Relationship between mass loss per day and body length for 15 adult males and 13 subadult males in the 1987–1988 breeding season. Since lean body mass should be proportional to the cube of the length, a third-order regression was performed:  $y = -86.87 + 91.42x - 31.85x^2 + 3.84x^3$  ( $r^2 = 0.68$ ,  $P < 0.0001$ ). The fit was slightly better than that of a linear regression ( $r^2 = 0.64$ ).

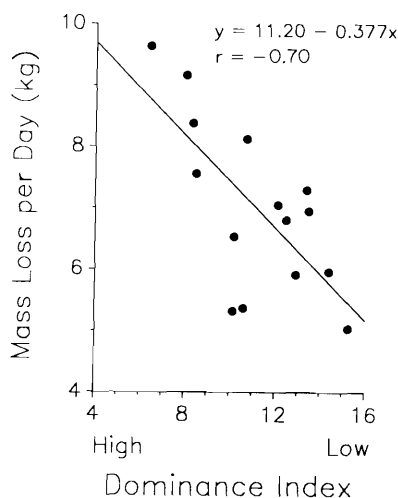


FIG. 7. Relationship between mass loss per day and the Bradley-Terry dominance index for adult males in the 1987–1988 breeding season. Note that low dominance index values indicate high dominance ranks.

dominance rank, and not vice versa, we conclude that dominance was the most important measured variable affecting mass-specific rate of mass loss in adult male elephant seals. The dominance index accounted for a substantial proportion of the variation in mass loss per day, when body mass was held constant (coefficient of partial determination = 0.37,  $P = 0.01$ ). Dominance rank and body mass together accounted for 52% of the variation in adult rate of mass loss ( $F = 6.42$ ,  $df = 2, 12$ ,  $P = 0.013$ ). About half of the variation in subadult male rate of mass loss was explained by body mass ( $r^2 = 0.51$ ,  $F = 11.59$ ,  $df = 1, 11$ ,  $P < 0.01$ ) or length ( $r^2 = 0.51$ ,  $F = 11.13$ ,  $df = 1, 11$ ,  $P < 0.01$ ). No other measured variables were significantly correlated with rate of mass loss among subadult males.

#### Variables affecting total mass loss over the breeding season

Age-class, body size (mass and length), and dominance rank were examined for correlations with total percent mass loss, the energetic component of male reproductive effort. Two proximate factors determined the total proportion of body mass lost

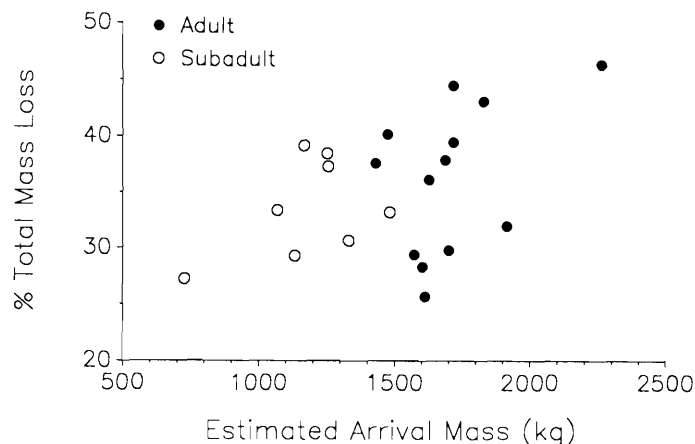


FIG. 8. Percentage of total mass lost over the breeding season as a function of estimated arrival mass for 13 adult males and 8 subadult males ( $r_s = 0.28$ ,  $N = 20$ ,  $P > 0.20$ ). The smallest male was excluded from the statistical analysis (see Methods).

by a male while breeding: the mass-specific rate of mass loss, and the duration of stay on the rookery. Duration of stay varied widely, from 51 to 106 days, and was therefore important in affecting total male RE.

There was no relation between age-class and total percent mass loss: the percentage of estimated arrival mass lost by adults over the breeding fast ( $36.2 \pm 6.6$ ,  $N = 13$ ) was not significantly different from that of subadults ( $34.5 \pm 3.8$ ,  $N = 7$ ) ( $U = 53$ ,  $P > 0.10$ ). Adults tended to be more variable than subadults, however (variance ratio test,  $F = 3.032$ ,  $df = 12, 6$ ,  $0.05 < P < 0.10$ , one-tailed test) (Fig. 8). The mass-specific rate of mass loss did not vary with age-class (see section on Rate of mass loss). Duration of stay was also similar for adults ( $91.0 \pm 14.8$  days) and subadults ( $90.1 \pm 10.0$  days) in this sample ( $t = 0.137$ ,  $df = 18$ ,  $P > 0.40$ ).

The percentage of mass lost over the breeding season was not correlated with either body length ( $r_s = -0.02$ ,  $N = 20$ ,  $P > 0.90$ , two-tailed test) or estimated arrival mass ( $r_s = 0.28$ ,  $N = 20$ ,  $P > 0.20$ , two-tailed test) (Fig. 8).

Dominance rank was correlated with rate of mass loss in adult bulls (Fig. 7) but not with duration of stay on the rookery ( $r = 0.18$ ,  $df = 9$ ,  $P = 0.30$ ). Using only the 1987–1988 data, percentage of mass lost over the season was not significantly correlated with BT dominance index ( $r_s = -0.28$ ,  $N = 11$ ,  $P = 0.20$ ). When data on weighed adult males from both years were pooled, they fell into two distinct dominance categories: four bulls ("high-ranking") were in the upper 30% of the dominance hierarchy, whereas all of the other nine bulls ("low-ranking") for which we had data on total mass loss were in the lower half of the hierarchy. These males likewise showed a bimodal distribution in mating success: mean ENFI of the high-ranking males was 32.3 (range 9–87), and that of the low-ranking adult males was 0.3 (range 0–2). The high-ranking bulls lost a significantly greater percentage of their estimated arrival mass ( $41.4 \pm 6.47$ ) than did the low-ranking adults ( $33.8 \pm 5.48$ ) ( $U = 31$ ,  $n_1 = 4$ ,  $n_2 = 9$ ,  $P < 0.05$ ). In conclusion, total reproductive effort over the breeding season was apparently related to the male's dominance status but not to age-class or body size.

#### Discussion

Male northern elephant seals weighed up to 2300 kg and lost more than one-third of their body mass while breeding at the



Año Nuevo rookery. Maximum body mass was about 400 kg less than had been expected on the basis of anecdotal statements in the literature (Le Boeuf 1981). Most adult bulls did not exceed 2000 kg, however, weighing between 1600 and 1900 kg early in the breeding season. Southern elephant seal bulls (*M. leonina*) grow much larger than male *M. angustirostris*; the greatest weight reported for *M. leonina* is 3692 kg (Ling and Bryden 1981). Females of the two species, on the other hand, average about the same length and mass (Ling and Bryden 1981; Reiter et al. 1981; Costa et al. 1986; Le Boeuf et al. 1988, 1989; McCann et al. 1989).

Our study shows that large pinnipeds can be successfully weighed without chemical or physical restraint. This technique avoids the risks inherent in repeated chemical immobilization of pinnipeds (Hammond and Elsner 1977; Baker and Gatesman 1985; Gales and Burton 1987b; see review by Gales 1989), particularly in *M. angustirostris*; adult males of this species seem to be more sensitive to immobilization with ketamine hydrochloride than females (A. C. Huntley, D. P. Costa, and B. J. Le Boeuf, unpublished data). Adult elephant seals are too large to be physically restrained without drugs, a technique which is useful for some smaller pinnipeds (Gentry and Johnson 1978). In studies on growth and body composition in *M. leonina*, Bryden (1969, 1972) used a bulldozer to tow anesthetized bulls to a hydraulic crane scale; the largest bulls were killed first and then weighed in sections (Bryden 1972). More commonly a tripod is used as a support to hoist immobilized seals weighing up to nearly 2000 kg (Anderson and Fedak 1985, 1987; Costa et al. 1986; Fedak and Anderson 1987; Gales and Burton 1987b). Our method is safer for the animals, and has the further advantage of being less expensive than chemical immobilization.

Elephant seals undergo dramatic seasonal changes in mass and body condition associated with the breeding season and the molt. They fast and spend most or all of their time on land during these periods. Clearly, the effort devoted to reproduction by male *M. angustirostris* is immense: 26–46% of body mass is lost over the breeding season. Male southern elephant seals lose about 25% of their initial mass over the 38-day molt period (Gales and Burton 1987b). Although males of many pinniped species fast for long periods while reproducing (Bartholomew 1970), breeding mass loss in free-ranging males has been measured in few other pinnipeds. Territorial male Antarctic fur seals (*Arctocephalus gazella*) lose an average of about 25% of their starting mass over a 1 month long breeding tenure, but this varies widely (from 4 to 41%) due to variable tenure duration (Boyd and Duck 1991; I. L. Boyd, personal communication). Similarly, northern fur seal bulls (*Callorhinus ursinus*) lose approximately 20–25% of their body weight over their breeding tenure on a territory (R. L. Gentry, personal communication). The gray seal (*Halichoerus grypus*), like the elephant seal, is a polygynous phocid, yet the two species exhibit some interesting differences in the reproductive energetics and behavior of males. Male gray seals lose about 17% of their body mass over the breeding season (calculated from data in Anderson and Fedak 1985), and up to 25% for a long-tenured male (Fedak and Anderson 1987). They lose about 0.9% of their initial body mass per day (calculated from Anderson and Fedak 1985), more than twice the estimated rate experienced by elephant seal bulls. Since male activity budgets of the two species are similar during the mating season (Anderson and Harwood 1985; Boness 1984; Sandegren 1976; Deutsch 1990), the greater mass-specific rate of mass loss in *H. grypus* is probably due in large part to higher metabolic “overhead” (i.e., higher mass-specific maintenance

costs) associated with the smaller size of this species (180–300 kg for adult males). Nevertheless, the total proportion of body mass lost by male gray seals while breeding (17%) is only half that of male northern elephant seals (36%).

This striking difference in reproductive effort between the males of two phocid species with similar breeding systems may be explained by differences in male intrasexual competition and breeding tenure. Gray seal males, unlike elephant seals, arrive after females (Anderson et al. 1975) and do not establish a dominance hierarchy (Boness and James 1979; Anderson and Fedak 1985). Few of the bulls remain on the rookery for the entire 6-week period during which most females come into estrus, though theoretical calculations indicate that they have the energy stores to do so (Anderson and Fedak 1985). In contrast, most mature elephant seal bulls are present several weeks before, during, and for a short while after the 8-week period of female receptivity (Le Boeuf 1974). Thus, the large difference in duration of fasting between species is the important proximate factor accounting for the difference in male reproductive effort. In gray seals the degree of polygyny and the potential reproductive gains to a male in a given year are not as great as they are in elephant seals. Since the life-span of male gray seals is about twice that of male northern elephant seals (Anderson and Fedak 1985; Le Boeuf and Reiter 1988), any trade-off between current and future reproduction should have greater impact in the former species. For male gray seals, the lower reproductive benefits and the potentially higher costs in lost future reproduction seem to have selected for a more conservative, longer-term reproductive strategy relative to that of male elephant seals. This is consistent with the idea that in more polygynous species, males exhibit greater RE and suffer higher mortality than in less polygynous ones (Trivers 1972; Thornhill 1981).

Direct comparisons of the energetic cost of reproduction among species on the basis of mass loss alone is complicated by the fact that the ratio of fat to protein used as the substrate of energy metabolism may vary across taxa (Worthy and Lavigne 1987). Furthermore, relatively few vertebrate species cease feeding entirely during the reproductive period. Nevertheless, males of many other species of polygynous vertebrates lose weight or body condition during the mating season. In anuran amphibians, for instance, males lose from 10% to more than 30% of their body weight over the breeding season (Wells 1978; Mac Nally 1981; Arak 1983). Males of some frog species are apparently unable to stay at breeding ponds throughout the reproductive season because of energetic constraints associated with calling and reduced foraging (Mac Nally 1981; Ryan 1985). Among some freshwater fish species, males lose up to 17% of their body mass while spawning (Mottley 1937; see Bell 1980). Body mass changes while breeding vary considerably across avian species (Ricklefs 1974; Bryant 1988; Cherel et al. 1988). The emperor penguin (*Aptenodytes forsteri*) exhibits the most extreme breeding weight loss among birds, males losing 40% of their body weight over a 4-month period of courtship and incubation during the Antarctic winter (Groscolas 1986).

Few actual measurements of breeding mass loss or energy expenditure have been made in free-living male mammals, however. In many ungulate species, breeding males are in poor condition by the end of the rut because they drastically reduce foraging time while increasing time spent in energy-expensive activities, such as herding females and fighting or chasing males (McCullough 1969; Geist 1971; Jarman 1979; Lott 1979; Clutton-Brock et al. 1982). Red deer stags (*Cervus elaphus*)



lose about 15% of their pre-rut weight over the autumn rut; in so doing, they deplete nearly all of their rump fat and kidney fat reserves, which they do not regain until the following summer (Mitchell et al. 1976).

#### *Energetic cost of dominance*

Priority of access to estrous females in many polygynous mammals is determined largely by a male's dominance status (Le Boeuf and Peterson 1969; Geist 1971; Le Boeuf 1974; Lott 1979; Packer 1979; Gibson and Guinness 1980a, McCann 1981; Samuels et al. 1984; for review and exceptions see Dewsbury 1982 and Fedigan 1983). We have shown that for northern elephant seals the sexual benefits of high social rank were obtained at the expense of greater daily energetic costs; the rate of mass loss in adult males increased with increasing dominance rank, independent of body size.

Data on activity budgets, ventilation rates, and time spent in energy-conserving sleep apnea suggest that the greater daily energy expenditure of high-ranking bulls may have been due to a higher level of activity and possibly an elevated resting metabolic rate (Deutsch et al. 1989; Deutsch 1990). High dominance status is apparently associated with an elevated level of resting metabolism in some birds (Røskft et al. 1986; Hogstad 1987) and small domestic mammals (Myrcha and Szwkowska 1969; Bray and Bell 1984). Though daytime resting metabolic rates of deer mice (*Peromyscus maniculatus*) maintained in a captive breeding colony do not vary with dominance status, the daily energy expenditure of dominant male mice is significantly higher than that of cohabiting subordinate males because the dominant mice are more active during the night (Farr and Andrews 1978). In the polygynous oriole, *Cacicus cela*, large dominant males lose weight over the breeding period due to decreased foraging time and high activity levels while consorting successive mates (Robinson 1986). The effect of this weight loss is to dramatically lower the male's position in the dominance hierarchy, and therefore to depress his subsequent mating success.

High dominance rank in male northern elephant seals seemed to be associated with greater total reproductive effort, but the relationship was not clear-cut. The percentage of arrival mass lost over the entire breeding season by the highest-ranking males was significantly greater than that lost by the lower-ranking males. The alpha bull of a large harem lost nearly one-half of his body weight over the season, whereas subordinate bulls lost an average of one-third of their weight. Yet the correlation between percent mass loss over the 1988 season and BT dominance index was not significant. A possible explanation for these conflicting results is that the relationship between total RE and dominance rank may be nonlinear, and thus a linear correlation may be an inappropriate analysis. Although there is a dominance hierarchy among the subordinate adult males, they can be considered "functionally equivalent" in rank because they are excluded from most breeding activity in the harems by the alpha bull and the other high-ranking males. Perhaps only the highest-ranking males gain additional copulations by investing such a large proportion of their energy stores in reproduction. If so, one might expect a step function: total RE increasing with social rank only for bulls high enough in the dominance hierarchy to achieve some mating success. This view is supported by the observation that total percent mass loss was over 40% for three of the four high-ranking males but reached this level for only one of the nine subordinate adults.

Among large wild mammals there is indirect evidence for an energetic cost of dominance or territory possession in the

ungulates. As in elephant seals, males of many ungulate species experience a net negative energy balance during the breeding season, and this deficit may be accentuated in the most dominant or sexually active males. Male impala (*Aepyceros malampus*) holding territories used most often by hinds suffer the most rapid decline in body condition, as measured by a subjective, visual index, and are then displaced by males in better condition (Jarman 1979). In red deer, successful breeders tend to be in poorer condition after the rut, as indicated by date of antler casting in spring, than unsuccessful stags (Gibson and Guinness 1980b). The largest gray seal bulls achieve the highest rates of copulation and lose mass at rates greater than predicted on the basis of metabolic needs (Anderson and Fedak 1985). These studies indicate that there is an energetic cost associated with being a sexually successful male. The results from our study on northern elephant seals provide strong support for this point: high dominance rank enhanced mating success but entailed an elevated rate of mass loss. Moreover, the data suggest that the cumulative effect of this added daily energetic cost was a greater RE (percent mass loss) over the breeding season for the highest-ranking bulls.

#### *Reproductive effort and age*

Although theoretical work has predicted the presence of age-specific patterns in reproductive effort (Williams 1966b; Gadgil and Bossert 1970; Pianka and Parker 1975; Pianka 1976; Charlesworth and León 1976), age (over 5 years) was not found to be an important variable affecting the energetic component of RE of male northern elephant seals in this study. This statement is supported by the following points: (i) the mean percentage of body mass lost per day did not vary with age-class or size; (ii) the total percentage of body mass lost over the breeding season did not vary with age-class or size; and (iii) one male, KZ4, exhibited approximately the same mass-specific rate of mass loss and total percent mass loss as a subadult and as a 1st-year adult the following year. At this gross level of resolution, age had no obvious effect on reproductive effort.

These results are in contrast with those of other studies supporting the prediction that RE increases with age (Pugesek 1981, 1983; Maher and Byers 1987; Clutton-Brock 1984). Female harp seals (*Phoca groenlandica*), on the other hand, show a decline in RE with age (Stewart 1986). Subadult male elephant seals achieve only a small fraction of the total copulations, and the vast majority do not succeed in mating at all (Le Boeuf 1974; Le Boeuf and Reiter 1988). We expected RE of younger males to be less than that of mature bulls, reasoning that males in highly polygynous species should devote energy to reproduction only if they have a chance of mating successfully (Warner 1980). Why then do subadults lose one-third of their body mass in a typically fruitless attempt to breed, when they could be channelling this energy to growth or reserving it for future, potentially more successful breeding seasons? Perhaps this level of mass loss does not incur a cost in terms of reduced survival at sea (Tuomi et al. 1983; but see Cox 1983). However, a reduction in growth resulting from the long breeding fast seems likely, and small size at adulthood reduces survival and lifetime reproductive success (Clinton 1990). The large energetic investment in mating effort by subadult males may reflect the important role of experience in developing the fighting and sexual skills necessary for success in reproductive competition as an adult (Cox 1983).

#### *Sexual differences in reproductive effort*

In contrast to theory on relative parental investment (Trivers 1972), the question of which sex expends more effort in

TABLE 2. Body mass, rate of mass loss, total mass loss, and duration of stay on the rookery for adult male and adult female northern elephant seals during the breeding season

	Body mass,* kg	Mass loss per day		Mass loss over season		Duration of stay, days
		kg	% body mass*	kg	% body mass*	
Male	1704 ± 213 (13)	7.08 ± 1.54 (17)	0.41 ± 0.06 (13)	622.0 ± 171.5 (13)	36.2 ± 6.6 (13)	91.0 ± 14.8 (13)
Female†	497 ± 69 (14)	7.17 ± 0.96 (14)	1.45 ± 0.12 (14)	181.3 ± 31.9 (14)	36.3 ± 2.6 (14)	25.2 ± 2.5 (14)

NOTE: Values are given as mean ± SD, with sample size in parentheses. Data for females are from Costa et al. (1986) and D. P. Costa and B. J. Le Boeuf (unpublished).

\*Estimated body mass at arrival (males) or parturition (females).

†Values for females are based solely on the lactation period and have been recalculated to make them comparable to the male data. Specifically, estimated postpartum body mass on the day of parturition, calculated by using the individual female's rate of mass loss during lactation to extrapolate from the day of first weighing back to the parturition date, is used instead of mass at first weighing to calculate percent mass lost per day and over the entire lactation period. This method gives lower values of percent mass lost over lactation than does using mass at first weighing.

reproducing has not been developed theoretically and empirical data are scanty (Alexander and Borgia 1979; Warner 1980). In the lizard *Uta stansburiana*, annual reproductive effort of females is twice as great as that of males (Nagy 1983). Ryan (1985) found that female túngara frogs (*Physalaemus pustulosus*) expend substantially more energy in reproduction than males, and he speculated that this sexual disparity may be the rule among vertebrates. However, since male túngara frogs apparently spend less time foraging during the breeding season than females, interpretation of relative RE by the sexes is confounded by differences in energy intake. Beissenger (1987) determined that cumulative breeding energy expenditure of male snail kites (*Rostrhamus sociabilis*) slightly exceeds that of females throughout the period of biparental care. However, female energy investment in the eggs was not included in his study, making sexual comparisons in this monogamous species incomplete. In another monogamous bird, the killdeer (*Charadrius vociferus*), males spend more time than females in both mating activities and parental duties (Brunton 1988a). Reproductive energy expenditure during a successful nesting attempt is equal for the sexes, but cumulative energy investment in RE over the entire breeding season was significantly higher for females (Brunton 1988b). Annual energy requirements are nearly identical for adult male and female golden-mantled ground squirrels (*Spermophilus saturatus*), but energy allocation to reproduction by females far exceeds that by males (Kenagy et al. 1989). Female gray seals lose 38% of their body mass over the 18-day lactation period (calculated from data in Fedak and Anderson 1982), which is over twice that lost by the average conspecific male (17%). This index of RE for seals includes energy expended in maintenance metabolism over the breeding fast, and is therefore not directly comparable to studies in which only energy expended in reproduction per se is measured (e.g., Nagy 1983; Ryan 1985).

In the northern elephant seal, adult males lose a similar percentage of their body mass as females (36%) over the course of the breeding season, despite the great sexual disparity in body size and duration of reproductive effort (Table 2). The two sexes also lose approximately the same absolute mass per day (Table 2). However, on a mass-specific basis, rate of mass loss in lactating females is over 3 times that in males (Table 2), reflecting the more intense maternal effort concentrated into a shorter time span. A value for total percent mass loss for females which is strictly comparable to that of males should include the mass lost during the time from arrival to parturition (approximately 6.5 days (Le Boeuf et al. 1972)). Assuming daily mass

TABLE 3. Mean energy expenditure per day and per breeding season for adult male and adult female northern elephant seals, expressed in absolute (MJ) and mass-specific (MJ/kg) terms

	Rate of energy expenditure		Total breeding energy expenditure	
	MJ/day	MJ/kg-day*	MJ/season	MJ/kg-season*
Male	223 (17)	0.157 (13)	19560 (13)	14.0 (13)
Female	163 (6)	0.391 (6)	4330 (6)	10.3 (6)

NOTE: To convert mass loss into energy expenditure for males, we made the following assumptions: (i) energy densities of pure fat and pure protein are 39.33 and 17.99 MJ/kg, respectively (Schmidt-Nielsen 1975); (ii) adipose tissue is 90% fat and 10% water (Pace and Rathbun 1945; Ortiz et al. 1978), and lean tissue is 27% protein and 73% water, by mass (Pace and Rathbun 1945; Hamilton 1949); (iii) the animal's state of hydration remains constant over the fast, for which there is evidence in fasting weaned elephant seal pups (Ortiz et al. 1978); and (iv) fat catabolism contributes 98% of the overall energy and protein catabolism contributes the remaining 2% (Pernia et al. 1980). The resulting composition of catabolized tissue is 87% adipose and 13% lean tissue by mass, yielding an energy density of 31.45 MJ/kg of mass lost. Energy expenditure for females is based solely on the lactation period. Data for females are from Costa et al. (1986). Sample size is in parentheses.

\*Estimated mean mass over the breeding season was used in the calculations of mass-specific energy expenditure.

loss during the prepartum fasting period to be the same as the mass loss attributed to the female's maintenance metabolism during the lactation period (0.0047 kg/kg of parturition mass per day) (B. J. Le Boeuf and D. P. Costa, unpublished data), females lose an average of 38.3% of their arrival mass (excluding mass of fetus and placenta) over the 32-day breeding fast, slightly more than most males. The similarity in the proportion of body mass lost by males and females while breeding suggests that both sexes may terminate their reproductive effort upon depleting their energy reserves to similar relative levels.

To compare the overall energy expenditure of the sexes during the breeding season, we converted our mass loss figures to energetic equivalents (Table 3). We assume that fat metabolism provided 98% of the males' energy during the breeding fast and that protein catabolism contributed the remaining 2%. This is consistent with data for fasting weaned elephant seal pups (Pernia et al. 1980), and maintenance metabolism measured in lactating female northern elephant seals (Costa et al. 1986). Adult bulls expended about 4 times as much energy over the season as nursing females, but on a mass-specific basis total

breeding energy expenditure was only about 40% greater in males (Table 3). Including the energy expended during the 6.5-day prepartum period on the rookery, estimated by the female's daily maintenance metabolism during lactation (Costa et al. 1986), total breeding energy expenditure and mass-specific energy expenditure of females are increased by about 10%, to 4760 MJ and 11.3 MJ/kg, respectively. However, this measure of reproductive effort for females does not include the energetic costs of gestation (i.e., fetus, placenta, and heat increment of gestation), which amount to 20–25% of the estimated total reproductive costs in gray and harp seals (Anderson and Fedak 1987; Stewart and Lavigne 1984), and about 18–25% in other large mammals with precocial young (ungulates, Oftedal 1985). If these gestation costs are added to a female's energy expenditure during lactation, total RE is roughly similar between sexes (about 13–14 MJ/kg of mean body mass).

Variance in reproductive success in polygynous species is higher in males than in females (Payne 1979; see Clutton-Brock 1988), and we hypothesized that this difference should be mirrored by a higher variance in RE among males than among females. This follows because the level of male effort should be affected by social status (i.e., dominance rank or territory possession) which varies widely, whereas variation in female RE is constrained by energetic considerations. Males that attain a high dominance rank or a high-quality territory should expend great amounts of energy to take advantage of their position and copulate with as many females as possible; subordinate males, with little chance of mating no matter how hard they try, should allocate some energy to growth or reserve some for future breeding attempts. Male pinnipeds can adjust the effort they devote to mating by varying activity level and duration of stay on the rookery. Females, on the other hand, have less scope for varying their reproductive effort, because the minimum amount of maternal investment required to successfully raise a pup represents a substantial proportion of the female's energy reserves (Fedak and Anderson 1982; Stewart 1986; Costa et al. 1986). Using percent mass loss over the breeding season as our measure of RE, males were significantly more variable than females (variance ratio test,  $F = 6.585$ ,  $df = 12, 13$ ,  $P < 0.001$ ). Likewise, the coefficient of variation of percent mass lost per day was 1.8 times greater in males than in females. This supports the prediction that males are more variable than females in their daily and total RE, though the contribution of measurement error to variation was probably more important for males than for females.

With the possible exception of large whales (Brodie 1975; Slijper 1979), male elephant seals surpass all other mammals in their ability to fast for long periods while actively breeding. This capacity for long fasts is facilitated by their large body size (Young 1976; Lindstedt and Boyce 1985), thick layer of blubber, which can compose 30–50% of total body mass (Bryden 1972; Ortiz et al. 1978; Costa et al. 1986; Gales and Burton 1987a), behavioral and physiological mechanisms of water and energy conservation (Bartholomew 1954; Huntley et al. 1984; Huntley 1987), and an apparently rich food supply and catholic diet (Condit and Le Boeuf 1984, Antonelis et al. 1987), which allow rapid recovery of lost body mass (Le Boeuf et al. 1988, 1989). The combination of these traits enables this highly polygynous mammal to invest a great energetic effort in reproduction.

### Acknowledgements

We extend our heartfelt thanks to the many students and

colleagues who assisted us with weighing and behavioral observation in the field; in particular, we acknowledge Joan Leidenthal, Mary Hart, Atina Casas, Geni Fox, and Selina Gleason. We thank Drs. Anthony Huntley and Daniel Costa for the capture and immobilization of a subadult male; the personnel at Año Nuevo State Park for their cooperation in the field; Dr. Anthony Huntley for his efforts in obtaining the scale and in helping us modify it; Dr. Susan Shane for graciously loaning C.J.D. her garage for the construction of the female model; Walter Clinton for writing the computer program used to calculate dominance indices; and staff at the UCSC Electronics Shop and at Senstek, Inc., who were helpful in providing instructions in the repair of the scale. We also thank Dr. Daniel Costa for allowing us to cite some of his unpublished data, and Callan Duck and Dr. Ian Boyd for providing us with a preview of their paper in press. Dr. Sheila Anderson, Dr. Daryl Boness, Dr. Claudio Campagna, Walter Clinton, Dr. Daniel Costa, Dr. James Estes, Chris Otis, and Dr. Graham Worthy commented on and greatly improved early drafts of the manuscript. Drs. Marshall Sylvan, James Estes, and William Rice provided valuable statistical advice. Finally, we are grateful to Chris Deutsch and Chris Otis for their continued support, tolerance, and encouragement throughout the project. This work was part of a Ph.D. dissertation in biology at the University of California, Santa Cruz, by C. Deutsch. The research was funded in part by National Science Foundation grant No. BSR-8117024 to B.J.L., and grants to C.J.D. and M.P.H. from the Biology Board of Studies and the Institute of Marine Sciences at UCSC.

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