Moult energetics of the northern elephant seal (*Mirounga angustirostris*)

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(With 1 figure in the text)

Northern elephant seals, *Mirounga angustirostris*, undergo an annual moult during which they shed all of their pelage and underlying epidermis. Moulting takes place on land and lasts a mean of 32.0 ± 6.6 days. During this time the mean mass loss of adult females was 24.7 ± 6.1%. Mean body composition at arrival (25.6 ± 4.8% fat) did not differ significantly from that at departure (24.9 ± 3.2% fat). Fat catabolism accounted for 93.6% of derived energy and 41% of mass lost. Approximately 3.5% of total mass loss was associated with the shedding of the pelage and epidermis. Moulting female northern elephant seals express an average daily metabolic rate of 2.0 ± 0.6 times that predicted for adult terrestrial mammals. This energy demand was met by losing 3.0 kg d−1 of total body mass. These energy expenditures suggest that, similar to data for harbour seals, the moult period is a time of relatively low energy expenditure.

Introduction

The northern elephant seal (*Mirounga angustirostris*) is a large, sexually dimorphic phocid seal that breeds at several locations along the Californian and Mexican coastlines. Each spring, between April and June, adult female elephant seals return to the rookeries for their annual moult. Elephant seals spend the majority of their time on the beach while moulting, so it is relatively straightforward to monitor the time course and progress of the process.

Moulting in pinnipeds commences around the eyes, ears, anus and penile opening and then proceeds along the ventral midline and from both the anterior and posterior dorsal midline areas (Stutz, 1967). The moult then spreads over the body surface, eventually replacing the entire pelage (Stutz, 1967; Worthy, Rose & Stormshak, 1987). Northern elephant seals follow this same basic

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moult pattern. However, unlike any other mammals, members of the tribe Monachini (northern and southern elephant seals, *Mirounga leonina*, and monk seals, *Monachus sp.*) exhibit an unusual moult wherein the hairs are shed along with large sheets of cornified epidermis through which the club hairs penetrate (Ling, 1970; Worthy et al., 1987). Owing to the structure of the stratum corneum, elephant seals and monk seals are basically encased in a continuous sheet of keratin, which breaks loose from the underlying tissue during the annual moult (Ling, 1965). All other pinnipeds shed their hairs individually (Ling, 1970).

Most previous studies of moulting in pinnipeds have addressed the progression and timing of moult or its histology (e.g. Scheffer, 1962; Ling, 1965, 1966, 1968; Ling & Thomas, 1967; Stutz, 1967; Ronald et al., 1970; Ling & Button, 1975; Fay, 1982; Thompson & Rothery, 1987). Studies of metabolic or endocrinological changes have been limited to the harbour seal, *Phoca vitulina* (Riviere, Englehardt & Solomon, 1977; Ashwell-Erickson & Elsner, 1981; Ashwell-Erickson et al., 1986). The data of Ashwell-Erikson et al. (1986) suggest that the moult is energetically inexpensive and that basal metabolism is depressed during a time period when the seals are fasting (Ashwell-Erickson et al., 1986). Northern elephant seals also fast, and spend considerable periods of time sleeping on the beach, during the approximately four week duration of their moult. It is unclear whether the suggestion of a depressed metabolism can be extended to northern elephant seals, given that they are not only replacing all their hair, but also their epidermis.

Elephant seal metabolism has been well documented during the lactation period (Le Boeuf & Ortiz, 1977; Ortiz, Le Boeuf & Costa, 1984; Costa et al., 1986). Lactation is a period during which the female mobilizes large quantities of energy for transfer to the pup as well as to maintain her own metabolism. Data are also accumulating on the behaviour and energetics of this species while it is feeding at sea (Le Boeuf et al., 1986, 1988, 1989). During both of these time periods, however, seals are either physically or metabolically active and therefore data cannot be extrapolated to the moult period.

Our objectives were two-fold. First, to document the body compositional changes that occur during the moult and therefore to determine which body components are acting as substrates to meet metabolic and anabolic requirements. Secondly, to determine the energy cost of the unusual form of moult observed in this species.

**Materials and methods**

**Subjects and field procedures**

Eight adult female northern elephant seals were immobilized using ketamine-Valium (Costa et al., 1986) on each of 2 occasions. The first occasion was within 2–3 days of their arrival at Año Nuevo, California, the second was at the end of the moult approximately 4 weeks later. In addition to the 8 seals which were sampled twice, 5 seals were sampled on arrival on the beach and 2 seals were sampled at the end of their moult immediately prior to departure. This latter subset of 7 animals was used only in the calculation of body composition.

Some of these animals had been used in studies documenting the lactation and at-sea energetics of the species (Le Boeuf et al., 1986, 1988, 1989; Costa et al., 1986). The time course of the moult and behaviour of the previously sampled animals was similar to that of other females on the beach.

At the beginning of the moult, females were given an intravenous injection of 2–3 mCi of tritiated water and held for the 3 h equilibration period (Costa et al., 1986). During the equilibration period, total body mass was measured by suspending the animal from a hanging scale accurate to within ±2 kg (Costa et al., 1986). Additionally, blubber depths were measured using an ultrasound device accurate to within ±0.5 mm
(Scanoprobe II, Scanco, Ithaca, New York) at dorsal, lateral and ventral sites around girth rings located at the neck, axilla, umbilicus and pelvis. Total body length and the distance between the tip of the tail and each of these rings was also measured. Females were then marked individually, tagged and allowed to go free.

Approximately 25-40 days later, when the animals had completed their moult and were ready to go to sea, they were recaptured, drugged and the above procedure was repeated. The only deviation from the initial protocol was that a presample of blood was obtained to allow for the determination of residual tritiated water specific activity for calculation of water and energy flux during the moult period (Ortiz, Costa & Le Boeuf, 1978). A second tritiated water equilibration was performed to reassess total body water (TBW) volume.

Sample analysis and calculations

Water was distilled from blood samples (Ortiz et al., 1978; Costa et al., 1986; Costa, 1987) and specific activity determined in triplicate by scintillation spectrometry of 100 μl of distilled water in 10 ml of Betaphase cocktail (Westchem, San Diego, CA). TBW volume was determined from the dilution of tritium in the body (Foy & Schneiden, 1960), corrected for the approximately 4% overestimate in TBW (Crum, Williams & Nagy, 1985; Reilly & Fedak, 1989). Using TBW volume, fat-free mass (FFM) was calculated assuming an average hydration state of 73% (Pace & Rathbun, 1945; Ortiz et al., 1978). Fat mass was calculated as the difference between total body mass and FFM.

Blubber volume was estimated using the method of Gales & Burton (1987), wherein a series of interlocking truncated cones are used to convert length, girth and blubber depth data to a blubber volume. This volume is converted to mass assuming a blubber density of 0.94 g cm⁻³ (Gales & Burton, 1987; G. A. J. Worthy, unpubl. data). This technique presumes that subcutaneous fat stored in the flippers is insignificant.

Available data for northern elephant seals suggests that moulting animals do not feed and we assumed this was the case in our calculations. Metabolic rates of moulting, fasting females were calculated from measurements of water influx rates, assuming that the body water pool was linearly changing (Nagy & Costa, 1980, as modified from Lifson & McClintock, 1966). In fasting, non-drinking animals, such as elephant seals, metabolic water production is the primary component of water influx and is therefore an index of metabolism (Ortiz et al., 1978; Costa, 1987). Estimation of water influx was performed as in Costa et al. (1986). Water production was converted to proportions of catabolized fat and FFM and, thereby, the energy produced (Costa, 1987).

Results

Upon arrival at the beach, the FFM of adult female northern elephant seals was 74.4 ± 4.8% of total mass with fat mass accounting for the remaining 25.6% of total mass (n = 13) (Fig. 1). After 32.0 ± 6.6 days of fasting during the moult, FFM comprised 72.6 ± 3.4% of total mass and fat accounted for the remaining 27.4% (n = 10) (Fig. 1). Body composition on arrival did not differ significantly from composition at departure (t-test, d.f. = 20, P > 0.05), despite having lost a mean of 24.9 ± 3.2% of starting mass at a rate of 3.0 ± 0.3 kg d⁻¹ (Table I). Composition data indicate that 33.6 ± 12.3% of catabolized tissue was fat (Table I). TBW volume did not change significantly over the course of the fast, accounting for 56.2 ± 2.5% of total mass at the beginning and 55.4 ± 1.9% at the end of the fast (Table I).

Blubber mass, calculated from blubber depth and girth data, accounted for 26.2 ± 3.2% (n = 7) of total mass at the beginning of the moult and 25.9 ± 3.4% (n = 6) at the end, an insignificant difference. Moreover, these fat masses were not significantly different from values for total body fat derived from tritiated water (t-test, d.f. = 11, P > 0.05). Body fat estimates derived from tritiated water differed by only 0.1 ± 2.4% from those calculated from blubber depth and girth measurements.
Fig. 1. Mass and relative proportions of fat, dry matter (protein) and water in pre-moult and post-moult adult female northern elephant seals.

<table>
<thead>
<tr>
<th>Seal</th>
<th>Pre-moult Mass (kg)</th>
<th>Pre-moult Water (%)</th>
<th>Pre-moult Fat (%)</th>
<th>Pre-moult FFM (%)</th>
<th>Post-moult Mass (kg)</th>
<th>Post-moult Water (%)</th>
<th>Post-moult Fat (%)</th>
<th>Post-moult FFM (%)</th>
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¹ FFM - fat-free mass
² DOTF was measured in 1986 and 1988
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**Table II**

Water flux values and calculated energy production for fasting, moulting northern elephant seal females. Seals are listed in order of increasing mass.

<table>
<thead>
<tr>
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<td>2.6</td>
<td>0.54</td>
<td>22.4</td>
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<tr>
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<td>360</td>
<td>278</td>
<td>82</td>
<td>210.4</td>
<td>162.3</td>
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<td>2.0</td>
<td>2.6</td>
<td>0.79</td>
<td>54.3</td>
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<tr>
<td>ALIT</td>
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<td>384</td>
<td>262</td>
<td>122</td>
<td>209.8</td>
<td>150.1</td>
<td>3.2</td>
<td>1.7</td>
<td>3.0</td>
<td>0.58</td>
<td>32.4</td>
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<td>388</td>
<td>308</td>
<td>80</td>
<td>207.9</td>
<td>173.8</td>
<td>3.8</td>
<td>2.5</td>
<td>3.1</td>
<td>0.81</td>
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<td>227.1</td>
<td>136.9</td>
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<td>1.9</td>
<td>3.3</td>
<td>0.58</td>
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<td>310</td>
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<td>222.8</td>
<td>177.6</td>
<td>3.7</td>
<td>2.1</td>
<td>3.2</td>
<td>0.66</td>
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<td>343</td>
<td>78</td>
<td>222.3</td>
<td>188.3</td>
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<td>1.9</td>
<td>2.9</td>
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<td>2.5</td>
<td>3.4</td>
<td>0.75</td>
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Mean 3.0 0.67 46.5 2.0
S.D. 0.3 0.10 16.2 0.6

Mean average daily metabolic rate (ADMR), calculated from water flux data, was 46.5 ± 16.2 MJ d⁻¹ (Table II). This is 2.0±0.6 times that predicted for adult, resting, terrestrial mammals of similar mass (Kleiber, 1975). Water flux data suggest that fat catabolism accounted for 93.6±3.8% of total derived energy and 41.0±14.9% of mass loss. This latter value is not significantly different from the value suggested by body compositional changes (see above) (t-test, d.f. = 11, P > 0.05).

**Discussion**

Moulting seals lost total mass at a rate of 3.0 kg d⁻¹ over the 32-day fast. This suggests that a hypothetical 400 kg seal would lose 96 kg, of which 39.4 kg (41%) would be fat and 56.6 kg (59%) would be FFM. Elephant seal skin and pelage has an average wet mass of 8.7 ± 0.8 kg m⁻², with epidermis and hair accounting for approximately one-third of this and the balance being dermis (n = 3; G. A. J. Worthy, unpubl. data). Estimating the body surface area of a 400 kg elephant seal to be 4.6 m² (Innes et al., 1990), the moulted old pelage and epidermis would amount to a mass loss of 13.5 kg. Due to differences in water content between muscle tissue (73%) and pelage (20%) (Worthy, 1985), the mobilization of adequate dry 'protein' from the FFM to incorporate into new pelage results in a net liberation of 24.0 kg of water. These FFM losses (24.0 kg), plus mass lost from the blubber (39.4 kg) and old pelage (13.5 kg) account for 80% of total mass loss (96 kg). This leaves 19.1 kg of FFM (wet weight), or 5.1 kg of 'protein' (dry mass) potentially available for gluconeogenesis to supply glucose to the brain and central nervous system.

This account of substrate usage requires that all new growth occurs on the beach and comes from on-board reserves. Skin collected from adult female southern elephant seals at their arrival on the beach had active hair follicles, but the hairs were small and undeveloped, suggesting that a great deal of growth must occur on the beach (Ling, 1965). There was no suggestion of a new epidermis on arrival. By the end of the six-day pre-moult period, hairs developed long keratinized shafts extending almost to the skin surface alongside the old club hair which was beginning to be shed (Ling, 1965). Freshly moulted elephant seals are a uniform blackish-grey coloration, and the hairs are initially very short (1–3 mm). Hairs grow quickly and, in the present study, newly
emerged hairs had grown to be 3–4 mm in length by the completion of moult. These data support the hypothesis that most new hair and epidermal growth occurs on the beach.

Worthy & Lavigne (1987) suggested that land-fasting phocid seals utilize their blubber fat stores to a greater degree than phocids that undertake their post-weaning fast in the water, such as harp (*Phoca groenlandica*) or hooded seals (*Cystophora cristata*). The apparently low rate of fat utilization exhibited by adult female northern elephant seals during their moult fast (40% of mass compared to 70% of mass for post-weaning grey seals, *Halichoerus grypus*) appears to be due to the relatively greater use of protein stores for new hair and skin growth. Previous studies of energy utilization during phocid fasting examined energy requirements either during lactation or the post-weaning fast (e.g. Bryden, 1969; Ortiz *et al.*, 1978; Worthy & Lavigne, 1983; Nørdoy & Blix, 1985; Costa *et al.*, 1986; Worthy & Lavigne, 1987). Neither of these periods are associated with large protein requirements nor protein mobilization.

Gales & Burton (1987) employed blubber depth measurements, obtained using ultrasound from 18 body sites, together with circumference and length measurements to estimate total subcutaneous blubber volume and hence blubber mass in southern elephant seals. Ultrasound is a safe, non-invasive and logistically practical technique, which has been used on a wide variety of pinniped species to measure blubber depth (i.e. Worthy & Lavigne, 1983, 1987; Gales & Burton, 1987). The utilization of blubber depth to estimate blubber mass is easy to perform and the accuracy of the technique appears to be good (Gales & Burton, 1987; Ryg *et al.*, 1990), but it only gives information on the hypodermis and not on total body stores of fat. In some species, such as the harp seal, this would significantly underestimate total body fat (e.g. Worthy & Lavigne, 1983, 1987), while in other species, such as the grey seal, it would give a reasonable estimate of total fat stores (e.g. Worthy & Lavigne, 1987).

The use of tritiated water to measure body composition allows for the estimation of total body fat. The potential errors associated with this technique have been discussed previously and relate primarily to errors associated with the assumption of hydration state and routes of water loss (see Costa, 1987 for a review). The benefit of using tritiated water is that the measurement of its turnover rate can be converted to a metabolic expenditure. Comparison of fat estimates derived using tritiated water and ultrasound suggests that virtually all of the body fat stores in the northern elephant seal are in the hypodermis.

Both ultrasound and tritiated water techniques have errors associated with them. The advantage of using the two together is the capability of separating the total body fat stores into those in the hypodermis (insulation) and those which are stored elsewhere in the body (energy stores).

Present data suggest that fasting, moulting female northern elephant seals meet their energetic needs, and lose body energy stores, in a different manner than fasting, lactating elephant seals. Female elephant seals are approximately 35% fat at the start of lactation and 24% fat at the end of the 28-day nursing period (Costa *et al.*, 1986). A large proportion of these fat stores are transferred to the pup in the form of fat-rich milk and are therefore not part of the female’s maintenance costs (Costa *et al.*, 1986). Standard metabolic rate (SMR) of a fasting, lactating female elephant seal is approximately 2-4 times that predicted for an adult, terrestrial mammal (Kleiber, 1975; Costa *et al.*, 1986). When the cost of lactation is included, this figure increases to six times the predicted value (Costa *et al.*, 1986).

All seals sampled in this study had pupped successfully that year. One female, PAU, gave birth to a pup but soon deserted it and therefore did not experience the high energetic cost of lactation. PAU’s body composition, at the beginning of moult, was similar to other sampled females...
(Table 1). This suggests that: 1) PAU may have abandoned her pup because she had insufficient energy stores at the commencement of nursing; or 2) she left her pup for some other reason but subsequently lost her lactational fat stores. This latter scenario suggests that there may be a 'set-point' value for body fat during the non-breeding season.

Lactation is normally followed by an intensive feeding period at sea (Le Boeuf et al., 1988), during which body reserves depleted during the expensive nursing period are replenished (Costa et al., 1986). Female elephant seals gain an average of 74.3 ± 20.0 kg while feeding at sea for 73.8 ± 6.7 days or approximately 1 kg per day (Le Boeuf et al., 1988, 1989). Since composition at departure (24% fat) is similar to that after more than two months of feeding at sea, mass increases must occur approximately equally in both the fat and FFM components (Costa et al., 1986). The present data also suggest that virtually all fat reserves are stored in the subcutaneous blubber layer. The enlargement of fat stores is significant for the energy it supplies during the moult-fast, and the increased FFM is important for the protein it supplies for the growth of new skin and hair.

ADMR, as measured on moulting females in the present study, includes SMR plus the costs of activity and growth. The similarity between the SMR of a lactating female and the ADMR of a moulting female suggests that there is minimal energy expenditure incurred by moulting females to grow a new pelage and epidermis. Even though elephant seals undergo a moult in which all of the epidermis and hair is shed (Ling, 1970), the direct energetic cost of rearranging stored proteins to form these new tissues apparently is low.

Harbour seals exhibit a reduction of 17–18.6% in SMR during their annual moult (Ashwell-Erickson & Elsner, 1981; Ashwell-Erickson et al., 1986). It was proposed that this reduction enabled these animals to meet their daily energy requirements without excessive depletion of energy reserves (Ashwell-Erickson et al., 1986) at a time when they must stay on land to attain the circulatory and thermal states conducive to hair growth (Feltz & Fay, 1966; Fay & Ray, 1968; Ling, 1974). The data suggest that the same depression of SMR occurs in elephant seals.

Summary

We have documented that female northern elephant seals utilize fat as the primary energy substrate during the moult fast (94% of energy and 41% of mass lost). We also reason that a realistic accounting of new pelage growth and gluconeogenic precursors can be derived from body composition analysis. The ADMR of fasting female northern elephant seals, like that of harbour seals, appears to be relatively low and may aid in reducing metabolic overheads during the fasting period. The end result is that the unusual moult of the northern elephant seal is no more ‘expensive’ than the less dramatic moult experienced by other phocids.

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