WATER AND ENERGY FLUX IN ELEPHANT SEAL PUPS
FASTING UNDER NATURAL CONDITIONS

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Total water flux, energy utilization, and mass loss were measured in fasting, newly
weaned elephant seal pups, Mirounga angustirostris, in their natural habitat over a
period of 32–52 days. Animals lost mass exponentially averaging 5.3 ± 0.9 g·kg⁻¹·day⁻¹.
At weaning body water comprised 40% of the total mass while the ratio of adipose to
lean body tissue was approximately 1. The mean water turnover rate in all animals
was very low, ~13.0 ± 1.20 ml·liter⁻¹·day⁻¹, and was not affected by entry of the
animal into water, supporting the hypothesis that seawater ingestion is not required
for water balance. Average metabolic rates calculated from water turnover data were
167.6 ± 19.1 kcal·kg⁻³/4·day⁻¹. The biological half-time of water, 53.5 ± 5.2 days, is
about 2.5 times greater than that of starved harbor seals and significantly exceeds
that reported for any other mammal. We conclude that a combination of behavioral and
physiological water conservation mechanisms permit these animals to fast on land
for up to 3 mo, deriving necessary water and energy from the oxidation of fat stores.

INTRODUCTION

Terrestrial breeding among many pin-
nipeds is associated with extended peri-
ods of total abstinence from both food
and water (Harrison and Kooyman
1968; Bartholomew 1970). In some spe-
cies these periods of abstinence may last
for 1 to 3 mo (Le Boeuf and Peterson
1969; Gentry 1970). While the catabolism
of fat stores seems adequate to supply
necessary energy, the problem of water
balance during prolonged fasts remains
unresolved. This problem is especially
acute in those species which breed on
arid or semiarid coastal islands, since
high temperatures and vigorous breeding
activity presumably result in far greater
evaporative water loss than that nor-
mally incurred in the cool marine en-
vironment (Bartholomew 1966). The
major question is: Does the oxidation of
fat alone provide sufficient water to meet
the physiological demands of an active,
fasting marine mammal on land? Some
insight into this problem may be gained
by examining the literature dealing with
water balance and possible seawater
drinking (mariposia) in marine mam-
nals.

With few exceptions, laboratory ex-
periments and observations conducted
over the last 5 decades indicate that
pinnipeds not subject to thermoregula-
tory stress receive sufficient preformed
and oxidative water from their diets
prior to preclude seawater drinking (Irving,
Fisher, and MacIntosch 1935; Smith
1936; Krogh 1939; Bradley, Mudge, and
Blake 1954; Wolf 1958; Pilson 1970;
Bester 1975). Although porpoises and
sea lions appear capable of handling the
added salt load of limited seawater in-
gestion which may occur incidental to feeding at sea, mariposia is apparently not essential for water balance (Pilson 1970; Ridgway 1972). Furthermore, there exists no compelling evidence that pinnipeds possess either exceptional renal concentrating capabilities or extrarenal salt excreting organs found in mariposic species of marine reptiles and birds (Bradley et al. 1954; Tarasoff and Toews 1972; Hill 1976). Whereas these studies have tended to negate the role of seawater ingestion in water balance for feeding individuals, they do not address the critical problem of water balance of fasting pinnipeds on land.

To our knowledge, no measurements of water flux in free living marine mammals are available. Thus, the purpose of this study was to determine water flux and estimate the average metabolic rate in newly weaned northern elephant seals, *Mirounga angustirostris*, in their natural habitat during the 8–10-wk postweaning period. These pups spend approximately the first 2 wk after weaning exclusively on land and then progressively longer periods in the water (Reiter, Stinson, and Le Boeuf 1978). The experiments were designed to answer two basic questions: (1) What are the water turnover and metabolic rates in totally fasting (food and water) animals on land? (2) Do these rates change after animals enter the water? We considered these experiments a relatively direct test of the hypothesis that seawater and food ingestion does not occur during the reproductive cycle of this species.

MATERIAL AND METHODS

ANIMALS AND ENVIRONMENTAL CONDITIONS

All fieldwork was conducted between January 25 and March 30, 1976, on Año Nuevo Island, 30.4 km north of Santa Cruz, California. Approximately 800 female northern elephant seals gave birth here during the 1975–1976 breeding season. The behavior of breeding animals and population dynamics of this colony have been monitored for nearly a decade (Le Boeuf 1974; Le Boeuf and Briggs 1977).

The island is devoid of fresh water except during rainstorms. It is noteworthy that this study was conducted during one of the driest periods ever recorded in this area; measurable rainfall during the study period was only 12.7 cm.

The mean air temperature and relative humidity during this study were 10 ± 5 °C and 80% ± 19%, respectively.

Five weaned pups of known age (±5 days) and sex (♀, ♂) served as experimental subjects. Except during *H*₂O administration, blood sampling and weighing, all animals were completely unrestrained and associated freely with their peers. Individual animals were marked with paint or bleach and hind flipper tags as previously described by Le Boeuf and Peterson (1969). The behavior and specific location of each animal was noted four to six times per week in order to determine time of molting and initial entry into the water.

**ADMINISTRATION OF TRITIATED WATER, BLOOD SAMPLING AND WEIGHING**

Under fasting conditions the turnover of *H*₂O in the body pool provides an accurate and inexpensive method of estimating both water flux and metabolic rate since essentially all water entering the body pool is derived from catabolism of body stores (Nagy 1975). Both the theoretical and practical aspects of this method as well as potential sources of error have been discussed in detail elsewhere (Pinson and Langham 1957; Lifson and McClintock 1966; Mullen 1973; Nagy 1975; Nagy and Costa, in preparation).

For *H*₂O injection, blood sampling, and weighing, animals L1, L2, and L3 were restrained initially by intramuscular administration of 3.0 mg/kg Ketav-
mine hydrochloride (Briggs, Hendrickson and Le Boeuf 1975). This procedure usually produced immobilization within 10 min, but the degree of immobilization and duration of action were variable. Therefore, all subsequent manipulations were accomplished by simply rolling animals into a large cargo net rigged in the manner of a hammock and securing it with nylon ties. While pups were not particularly enamored of their predicament, we considered it the most expeditious and humane method of restraint. Weighing, injection, or blood withdrawal could be accomplished within 10 min with no obvious physical ill effects to the pups. All experimental animals appeared to develop normally and, except for their markings, could not be distinguished from nonexperimental individuals. Weighing was accomplished with a tripod and a precalibrated Dillon scale with ±0.5-kg accuracy.

Initial injection of $^3$H$_2$O and blood sampling of L1 and L2 were performed by the method of Harrison and Tomlinson (1956) utilizing the extradural vein. This procedure, however, proved unsatisfactory in animals not immobilized with Ketamine. We subsequently adopted a modified form of the technique suggested by Geraci (1970) using the pelvic flipper.

Whole blood samples were immediately transferred to 10-ml glass centrifuge tubes and spun for 10 min at $\sim$4,000 rpm in an International Equipment Company (IEC) clinical centrifuge. Plasma was decanted into polyethylene vials, labeled, and stored at 4°C until returned to the laboratory. All samples were then frozen at $-20$° C until analysis.

**Analytical Procedures**

Specific radioactivity of $^3$H$_2$O in plasma water was determined by evaporated-freeze capture as depicted in fig. 1. Approximately 50 µl of plasma was weighed

![Diagram](attachment:evaporation_freeze_capture.png)

**Fig. 1.—Diagram of evaporation-freeze capture procedure for recovering tissue water for specific activity determinations. Water recovery was $\geq 97\%$. See text for details.**

to the nearest 0.01 mg on a Mettler H-20 analytical balance and evaporated to dryness as shown. The dry pellet was reweighed and the water evolved computed by difference. Recovery of radioactivity using this method was >97%. Plasma water specific activity, \( S_A_p \), was taken as the ratio of the radioactivity in the scintillation vial (cpm) to the weight of water evolved (g); \( S_A_p = \text{cpm} \cdot \text{g}^{-1} \).

In all experiments plasma samples and controls were run in triplicate and varied ≤1%.

Preformed water in adipose tissue was equated with the mass loss incurred upon heating a small sample (~100 mg) of subcutaneous blubber to constant mass at 105°C. Two samples were obtained from weaned pups and one from a known female who was apparently killed by sharks. Adipose tissue water content in pups was indistinguishable from that of the female.

Radioactivity was assayed in 10 ml of scintillation cocktail containing 8.4 g Butyl PBD [2-(4’-butylphenyl)-5-4(4’-biphensl)-1,3,4-oxadiazole] and 75 ml Biosolve (Beckman Inst.) per 1,000 ml analytical grade toluene using a Beckman LS230 liquid scintillation system at full \( ^3\text{H} \) window setting (efficiency, 46%). Decreased counting efficiency due to water quenching was negligible for sample volumes ≤400 \( \mu \)l; \( ^3\text{H}_2\text{O} \) (1 mCi/ml, New England Nuclear [NEN]) was diluted 1:3 with sterile saline for field injection and an aliquot assayed subsequently for specific activity. Usually 3 ml (~1.0 mCi \( ^3\text{H}_2\text{O} \)) was injected.

Plasma \([\text{Na}^+]\) and \([\text{K}^+]\) were measured in duplicate by flame photometry (Instrumentation Labs) using standard techniques.

**Calculations**

Total body water at equilibration, \( N_0 \) is given by \( N_0 = \text{cpm}_{(\text{inj})}/S_A_p(t = 0) \) where \( \text{cpm}_{(\text{inj})} = \text{total} \ ^3\text{H}_2\text{O} \text{ injected and} \ S_A_p(t = 0) = \text{specific activity of equilibrated body H}_2\text{O}. \) The value \( S_A_p(t = 0) \) may be obtained empirically by analysis of plasma water specific activity at equilibration (approximately 3 h after injection) or by extrapolation of the \( \ln S_A_p \) versus time curve to \( t = 0 \) (fig. 2). Both methods yield nearly identical values for \( S_A_p(t = 0) \). The daily fractional turnover of \( ^3\text{H}_2\text{O} \) in the body water pool, \( K_{\text{eff}} \) is given by \( -\Delta \ln S_A_p \cdot \Delta t^{-1} \), i.e., minus the slope of \( \ln S_A_p \) versus time curve (fig. 2). The straight line was fit to the data points by the method of least squares.

When total body water is not constant but changes exponentially in time, the efflux rate equation takes the form, \( \dot{r}_{\text{H}_2\text{O}} = [N_0K_N(K_{\text{eff}} - K_N)\Delta t]/[1 - \exp(-K_N\Delta t)] \) (Lifson and McClintock 1966) where \( K_N = \Delta \ln N \cdot \Delta t, N_0 = \text{body water at equilibration} (t = 0), \dot{r}_{\text{H}_2\text{O}} = \text{average water efflux (ml/day).} \)

The average daily water input rate, \( \dot{r}_w \) was calculated as \( \dot{r}_w = \dot{r}_{\text{H}_2\text{O}} - \Delta N/\Delta t \) where \( \Delta N \) is the change in body water volume over the measurement interval, \( \Delta t. \) Both \( \dot{r}_{\text{H}_2\text{O}} \) and \( \dot{r}_w \) are given as average values since neither was measured directly and probably varied over the measurement interval, \( \Delta t \) (Lifson and McClintock 1966).

In two cases \( K_N \) was determined directly by measuring the body water volume by \( ^3\text{H}_2\text{O} \) reinjection 8–10 wk after the initial injection. These data consistently showed that the loss of body water was equal to 10 ± 1% of the total body mass loss experienced during that period. This result was confirmed in three more animals during the 1976–1977 season. Since body mass data were collected for all animals, the following empirical equation was used to estimate \( N_{\text{t}}; \)

\[ N_{\text{t}} = N_0 - 0.1 \ (m_0 - m_t) \] where \( N_{\text{t}} = \text{body H}_2\text{O volume at t, N}_0 = \text{initial volume, and m}_0 \text{ and m}_t \text{ are the body mass at t = 0 and t}. \) The slope of the \( \ln N_{\text{t}} \)
Fig. 2.—Natural logarithm of plasma water specific activity, cpm·g⁻¹, as a function of time after systemic injection of ³H₂O. Straight lines are least-squares fit to the data points. Data points are mean values ± 1 SD. The inset gives: m(slope) = −K₂H, y-intercept = SAₚ(t = 0), and r, correlation coefficient for each animal. Arrows signify first entry of animal into water. All data points run in triplicate.
VERSUS TIME PLOT EQUALS \( K_N \). THE ISOTOPIC HALF TIME OF \(^3\text{H}_2\text{O}\) IN THE BODY POOL, \( t_{1/2} = 0.693K_{2H}^{-1} \).

**SUMMARY OF PROCEDURES, EQUATIONS AND SYMBOLS**

1. Total body water, \( N_0 \):
   a) determined by \(^3\text{H}_2\text{O}\) dilution;
   b) \( N_0 = \text{^{3}H}_2\text{O} \) radioactivity injected (cpm) \( \cdot \) plasma \( \text{H}_2\text{O} \) specific activity (cpm \( \cdot \) ml\(^{-1}\)), i.e., \( N_0 = \text{cpm(inj)} \cdot SA_p^{-1} \).

2. Average daily water efflux, \( \bar{\dot{r}}_{\text{H}_2\text{O}} \):
   a) \( \bar{\dot{r}}_{\text{H}_2\text{O}} = \frac{N_a K_N (K_N - K_N \Delta t)}{1 - \exp (-K_N \Delta t)} \);
   b) \( K_N \) = fractional daily change in body water volume, i.e., \( \ln \left( \frac{N_0}{N_0 - N_0 \Delta t} \right) \cdot \Delta t^{-1} \);
   c) total body water at time \( t \), \( N_t \), determined by \(^3\text{H}_2\text{O} \) reinjection in two cases;
   d) body water loss = 10 ± 1\% body mass loss.

3. Average daily water input, \( \bar{\dot{r}}_{w} \):
   a) \( \bar{\dot{r}}_{w} = \bar{\dot{r}}_{\text{H}_2\text{O}} - \frac{\Delta N}{\Delta t} \);
   b) \( \bar{\dot{r}}_{w} \) assumed to be derived solely from lipid oxidation.

4. Average daily metabolic rate, \( \overline{MR} \):
   a) calculated from energy and oxidative water yield of fat only; \( \overline{MR} = \bar{\dot{r}}_{w} \cdot 8.43 \text{ kcal/g} \text{ H}_2\text{O} \).

5. Mean body mass, \( \bar{m} \):
   a) \( \bar{m} = \frac{m_0}{k} \cdot \Delta t (1 - e^{-k \Delta t}) \), obtained by integration of exponential mass loss function and division by \( \Delta t \);
   b) used to compute:
      i) mean daily mass loss, \( \bar{r}_m(\text{H}_2\text{O}) = \frac{\bar{m}}{\Delta t} \);
      ii) mass specific metabolic rate = \( \frac{\overline{MR} \cdot m^{-3/4}}{m_3/4} \);
      iii) mean basal metabolic rate, \( \overline{MR}_b = 70 \bar{m}^{3/4} \).

**RESULTS**

The decline in body mass (as percentage of initial mass) with time for all experimental animals is depicted in fig. 3. These data were best fit by a simple exponential form \( m(t) = m_0 e^{-k \Delta t} \) where \( m(t) = \text{mass at time} \ t \); \( m_0 = \text{initial mass} \), and \( k = \text{rate constant} \) (kilograms lost \( \cdot \) kg\(^{-1}\) body mass \( \cdot \) day\(^{-1}\)). The calculated rate constants were relatively similar, the mean for all animals was \( 5.32 ± 0.96 \) g lost \( \cdot \) kg\(^{-1}\) \cdot \) day\(^{-1}\). The correlation coefficient, \( r \), for the linear regression fit of \( \ln m \), versus \( t \), was \( >.97 \) in all cases. Mean body mass \( \bar{m} \), is given by

\[ \bar{m} = \frac{m_0}{\Delta t} \int_0^t e^{-k \Delta t} dt = \frac{m_0}{k \Delta t} (1 - e^{-k \Delta t}) \]

where \( \Delta t \) is the interval over which water flux measurements were taken. These values are 141.9, 117.5, 113.5, 126.3, and 102.6 kg for L1-L5, respectively, and were used to calculate average mass specific metabolic rate and mean daily mass loss to be discussed later. As a correlate, pectoral girth declined steadily during the study period in all animals with no concomitant change in overall body length. For example, pectoral girth in subject L1 declined 29 cm (153-124 cm) over 65 days.

The dilution of \(^3\text{H}_2\text{O}\) in the total body water pool after the initial equilibration period (3 h) is shown in fig. 2. Note that the data are plotted as \( \ln SA \), versus time. Two important values are obtained from this graph: (1) \( K_{2H} \); defined as
$-\Delta \ln S_{A_p} \cdot \Delta t^{-1}$, and (2) $S_{A_p} (t = 0)$, body water specific activity at $t = 0$, the $y$-intercept. The arrows designate the first observed entry of each animal into the water. After this time pups spend progressively longer periods in the water learning to swim and dive (Reiter et al. 1977). It is interesting to note that the $^3$H$_2$O dilution rate is not significantly increased after this occurrence, a result that corroborates behavioral observations that seawater and food are not ingested (Le Boeuf et al. 1972; Reiter et al. 1978) and which suggests strongly that skin absorption-exchange of H$_2$O or increased oxidation of food stores are minimal. Moreover, for all animals regardless of initial body mass or body volume, the values of $K_{2H}$ are remarkably similar (range 11.4–14.4 ml H$_2$O lost·liter$^{-1}$ body water·day$^{-1}$). Table 1 summarizes the relevant information derived from the experimental water turnover data.

In the completely fasting state (food and H$_2$O), both energy and water requirements must be met by oxidation of body stores. If weaned elephant seals are considered in physiological water balance, i.e., all tissues remain in normal hydration states, it becomes possible to estimate the daily energy expenditure from water flux data. Thus, if average water input, $\bar{r}_w$ is assumed to derive solely from the oxidation of fat, it then follows that the average metabolic rate, $\bar{MR} \approx \bar{r}_w \cdot 8.43$ kcal/g H$_2$O. The constant is taken from the values provided by Schmidt-Nielsen and Schmidt-Nielsen (1952) and

![Graph](image)

Fig. 3.—Total body mass (as percentage of initial mass) as a function of time for experimental animals L1–L5. Data were best fit to exponential, $m_t = m_0 e^{-k \Delta t}$. Inset gives the computed rate constant, $k$, for each animal.
Wolf (1958) for the oxidation of fat. Average metabolic rate calculated in this manner is contrasted with that derived from the general equation for basal metabolic rate, $\bar{MR}_b$, for fasting adult animals at rest formulated by Kleiber (1975); $\bar{MR}_b = 70m^{3/4}$, where $m$ is the mean body mass (table 1). The mean $\bar{MR}_b$ for all animals was $2.54 \pm 0.23 \times 10^3$ kcal·day$^{-1}$.

If it is assumed that the free water in adipose and lean body tissues constitutes 10% and 73% of their mass, respectively (Pace and Rathbun 1945), it is possible to estimate the relative contribution of these tissues to the total body mass knowing only body mass, $m_t$ and H$_2$O volume, $N_t$ at time $t$. Water content in three samples of fresh elephant seal adipose (adi) tissue was $10 \pm 1\%$ by weight. To illustrate, since total body water $N_t$ is given by $N_t = 0.1 m_{ad1} + 0.73 m_{lean}$ (1) and total body mass $m_t$ is simply $m_t = m_{adi} + m_{lean}$ (2), then by substitution and rearrangement it follows that $m_{adi} = 1.16m_t - 1.59N_t$. The ratio $m_{adi}:m_t$ for animals L1-L5 at $t = 0$ are 0.55, 0.53, 0.47, 0.52, and 0.41, respectively. That is, at weaning the mass of an elephant seal pup is approximately 50% adipose tissue. Comparable values have been reported for newly weaned pups of both southern elephant seals (43.5%, Bryden and Stokes 1969) and ringed seals (45.5%, Stirling and McEwan 1975).

### DISCUSSION

Clearly, the exceptionally low rate of water turnover measured in weaned elephant seal pups is the most significant finding of this study. Our data are not only concordant with the behavioral observation that these animals may fast entirely for up to 10 wk after weaning (Reiter et al. 1978), but also partially elucidate the mechanisms by which homeostasis is maintained during these extraordinary fasts.

To our knowledge no measurements of water flux in free living pinnipeds have been conducted; therefore, no direct comparisons are possible. Nevertheless, the data reported by Depocas, Hart, and Fisher (1971) for two yearling harbor seals force-fasted in the laboratory is relevant. Over 14 days of starvation average efflux rates, $\dot{r}_{H_2O}$, in these animals was somewhat lower than that of elephant seal pups, $509 \pm 7$ versus $790 \pm 60$ ml·day$^{-1}$, but when computed on a metabolic mass specific basis, i.e., $\dot{r}_{H_2O} \cdot \bar{m}^{-3/4}$, they are considerably higher, $19.9 \pm 2.4$ (elephant seal) versus $44.1 \pm 3.7$ ml·kg$^{-1}$ day$^{-1}$ for the harbor seal. This difference cannot be explained by

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**TABLE 1**

<table>
<thead>
<tr>
<th>Animal</th>
<th>$m_{ini}$ (kg)</th>
<th>$N_t$ (liters)</th>
<th>$N_{ini}$ (liters)</th>
<th>$K_v$ ($\times 10^2$)</th>
<th>$\dot{r}_w$ (ml·day$^{-1}$)</th>
<th>$\dot{r}_{H_2O}$ (ml·day$^{-1}$)</th>
<th>$t_{1/2}$ (Days)</th>
<th>$\bar{MR}$ (kcal·day$^{-1}$)</th>
<th>$\bar{MR}_b$ (Kleiber 1975)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1 p...154</td>
<td>58.6</td>
<td>.38</td>
<td>-1.08</td>
<td>670</td>
<td>732</td>
<td>60.78</td>
<td>5.65</td>
<td>1.96</td>
<td></td>
</tr>
<tr>
<td>L2 p...134</td>
<td>52.1</td>
<td>.39</td>
<td>-1.18</td>
<td>719</td>
<td>779</td>
<td>50.17</td>
<td>6.06</td>
<td>2.43</td>
<td></td>
</tr>
<tr>
<td>L3 p...126</td>
<td>54.5</td>
<td>.43</td>
<td>-1.70</td>
<td>666</td>
<td>756</td>
<td>56.80</td>
<td>5.61</td>
<td>2.30</td>
<td></td>
</tr>
<tr>
<td>L4 p...139</td>
<td>56.1</td>
<td>.40</td>
<td>-1.49</td>
<td>808</td>
<td>890</td>
<td>48.12</td>
<td>6.81</td>
<td>2.58</td>
<td></td>
</tr>
<tr>
<td>L5 p...115</td>
<td>54.2</td>
<td>.47</td>
<td>-1.30</td>
<td>723</td>
<td>796</td>
<td>51.71</td>
<td>6.09</td>
<td>2.70</td>
<td></td>
</tr>
</tbody>
</table>

Note.—$m_{ini}$ = initial body mass; $N_t$ = initial body water volume; $K_v = \Delta \ln N_t/\Delta t$; $\dot{r}_{H_2O}$ = average daily water efflux; $\dot{r}_w$ = average daily water influx; $\bar{MR}$ = average metabolic rate; basal $\bar{MR}_b = 70m^{3/4}$.
disparate amounts of adipose stores since the adipose content of the harbor seals based on water pool and total mass (see above) is nearly the same as that obtained in weaned elephant seal pups. This suggests that water conservation under natural conditions of food and water deprivation may be significantly more efficient than that observed in the laboratory, or that the elephant seal is significantly better adapted in this respect than the harbor seal.

Survival under the physiologically austere conditions of total starvation depends critically on the difference between the rate of metabolically generated water and obligatory water loss due to evaporation and urine formation. Hill (1976) provides an excellent discussion of the factors governing water balance during starvation. He points out that if protein catabolism and the associated obligatory use of water in nitrogen excretion is minimal and only lipid and carbohydrate catabolism are considered, the problem of water balance may be simplified to the amount of metabolic water produced versus the obligatory evaporative water loss per unit volume oxygen consumed. Carbohydrate stores in most mammals are small and rapidly consumed, thus the problem reduces further to considering lipid catabolism as the sole source of water and cutaneous and respiratory evaporation the predominant avenues of loss. Since lipid catabolism yields \( \sim 0.54 \text{ g H}_2\text{O} \cdot \text{liter}^{-1} \text{O}_2 \) consumed; evaporative loss cannot exceed this value if water balance is to be maintained. The upper limit of respiratory water loss may be obtained by assuming that elephant seals: (a) inhaled air which contained 5.88 mg H\(_2\)O·liter\(^{-1}\) (10°C at 80% RH), (b) exhaled air saturated at a body temperature of 35°C (39.6 mg H\(_2\)O·liter\(^{-1}\)), (c) extracted 8% of the O\(_2\) in inhaled air and catabolized only stored lipids. The value obtained is 0.42 gm H\(_2\)O lost·liter\(^{-1}\) O\(_2\) consumed, i.e., 78% of the total evaporative loss limit. It seems reasonable that the apneustic breathing habits of these animals (Bartholomew 1954; Costa and Ortiz, unpublished data) may increase O\(_2\) extraction efficiency and thus further improve water economy. Oxygen extraction values far in excess of 8% have been reported for a diving elephant seal (Ridgway 1972) and other diving and surface breath-holding marine mammals (Irving, Scholander, and Grinnell 1941; Ridgway 1972).

Of course, other physiological or behavioral mechanisms which reduce respiratory water loss would certainly be advantageous. Several reports indicate that in porpoises and sea lions water loss via respiration is considerably lower than the theoretical minimum (Coulombe, Ridgway, and Evans 1965; Matsuura and Whittow 1974). The complex turbinate processes in the nasal passages of pinnipeds may function as a countercurrent heat exchanger, thereby reducing respiratory water loss by condensation (Schmidt-Nielsen, Hainsworth, and Murrish 1970). In addition, the large blood volume, high hemoglobin O\(_2\) binding capacity, and deep-diving cardiovascular adaptations of Phocidae (Andersen 1966) favor breath holding and minimize respiratory water loss on land. We have no data on the magnitude of cutaneous water loss in elephant seals, but it seems reasonable to assume that its relative contribution to total evaporative loss is no greater than that measured in sea lions (70%; Matsuura and Whittow 1974). In any event, water loss from both the skin and respiratory tract cannot greatly exceed total water production.
since total body water declines only slightly.

If the decline in body water volume were much greater than our estimate based on body mass, i.e., if the animals were in severe negative water balance, our calculations would underestimate \( \tilde{r}_{H_2O} \) and overestimate \( t_{1/2} \). However, the following observations argue against severe dehydration: (1) Measurements of \( N_t \) by reinjection of \( ^3H_2O \) in two animals were within 5% of that predicted by the change in body mass. Similarly small changes in total body water were measured in starved harbor seals by Depocas et al. (1971). (2) Plasma concentrations of \( Na^+ \) and \( K^+ \) in all animals remained very constant throughout the study period, fluctuations being random in time (table 2). (3) The plasma protein:plasma \( H_2O \) ratio remained extremely constant in all animals throughout the study (Ortiz and Costa, unpublished data). (4) Gross physiological or behavioral signs of dehydration such as dry or encrusted mucous membranes, loss of skin turgor, severe lethargy, etc., were never observed. Thus, we conclude that errors in \( \tilde{r}_{H_2O} \) resulting from underestimates of \( K_N \) are trivial.

The computed metabolic rates (\( MR \), table 1) include both resting and active metabolism over the entire study period. For comparative purposes, the average metabolic rate for all animals computed on a metabolic mass specific basis was 167.6 ± 19.1 kcal·kg\(^{-3/4}\)·day\(^{-1}\). In other words, the average metabolic rate of fasting elephant seal pups is slightly more than twice the expected basal level of 70 kcal·kg\(^{-1}\)·day\(^{-1}\). These results are concordant with short-term oxygen consumption measurements in active and inactive elephant seal pups recently reported by Heath, McGinnis, and Alcorn (1977).

Although our water flux analysis minimizes the importance of protein catabolism in fasting elephant seal pups, it is clear that neither protein synthesis nor degradation has ceased entirely. For example, pups molt their natal pelage 1–3 wk after weaning, and this process necessitates synthesis of new integument (Le Boeuf, Whiting, and Gantt 1972); the blood hematocrit of fasting pups rises steadily during fasting (Costa and Ortiz, unpublished data), again requiring protein synthesis for turnover and increase of red cells. (We consider this rise in hematocrit to represent synthesis and not dehydration for reasons stated above.) Since there is no exogenous source of amino acids, especially the essential amino acids, it is clear that certain proteins must be degraded to provide these compounds. This inevitably results in some amino acid oxidation and urea load.

In totally fasting animals metabolizing stored fat, mass is lost primarily as water. We envisage this water to be derived from adipose tissue, that is, from the oxidation of fat and the "sparing" of interstitial fluid as the tissue is utilized. Subcutaneous adipose tissue contains 10 ± 1% free \( H_2O \) and ~90% esterified fat composed of long-chain fatty acids,

| TABLE 2 | Plasma [Na\(^+\)] and [K\(^+\)] in Fasting Northern Elephant Seal Pups |
|---|---|---|---|
| \textbf{Animal} | \textbf{[Na\(^+\)]} meq·liter\(^{-1}\) | \textbf{[K\(^+\)]} meq·liter\(^{-1}\) | \textbf{[K\(^+\)]:[Na\(^+\)]} |
| L1 (7) | 142.4±11.8 | 4.5±.27 | .032 |
| L2 (7) | 141.1±10.4 | 5.1±.94 | .036 |
| L3 (6) | 151.7±10.9 | 4.9±.54 | .032 |
| L4 (4) | 141.0±9.3 | 5.0±.77 | .035 |
| L5 (5) | 142.1±10.3 | 4.8±.87 | .034 |

\textbf{Note.}—Values are mean ± 1 SD. Number in parentheses equals number of sampling days corresponding to data points in fig. 3.
C_{14}-C_{22} (Bryden and Stokes 1969). These fats yield \( \sim 1.1 \) g H_{2}O g\(^{-1}\) fat oxidized (Schmidt-Nielsen and Schmidt-Nielsen 1952). If it is assumed that 1 g adipose tissue is completely catabolized, the water yield would be \( \sim 1.09 \) g (metabolic and “spared”) interstitial H_{2}O to be used in urine formation and lost via evaporation. However, elimination of this water reduces total body mass by only 0.92 g g\(^{-1}\) H_{2}O lost. Therefore, it is possible to predict the average daily mass loss, \( \dot{r}_m(H_{2}O) \), based on water turnover data alone, i.e., \( \dot{r}_m(H_{2}O) = 0.92 \dot{r}_H_{2}O \). Table 3 compares the average daily mass loss calculated in this manner with that observed experimentally, \( \dot{r}_m = k \dot{m} \), where \( k \) = mass loss rate constant (fig. 2) and \( \dot{m} \) = mean body mass (\( \dot{r}_H_{2}O \) is not strictly independent of mass [see Methods] but does not introduce errors exceeding 10\%).

Considering the approximations inherent in this computation, the agreement between these values is remarkably good. It is tempting to attribute the discrepancy to overestimates of \( \dot{r}_H_{2}O \) resulting from small amounts of seawater in-gestion or exchange-dilution of H_{2}O in inspired air (Lifson and McClintock 1966). Since, in our experiments, other potential sources of error in the \(^6\)H_{2}O dilution technique have been taken into account (Lifson and McClintock 1966; Nagy and Costa, in preparation), we consider exchange-dilution effects to be the most probable candidate.

The internal consistency of the water flux and mass data adds support to our contention that water derived from the oxidation of adipose tissue satisfies most physiological requirements of fasting elephant seal pups. If this hypothesis is correct, the elephant seal pup may serve as a model for the fasting adult who is subject not only to the same environmental and nutritional stress but also the additional stress of nursing in the female and a prolonged period of fighting and mating in males.

How does the biological half-time of water, \( t_{1/2} \), measured in fasting elephant seal pups, compare with other mammals under similar conditions? With complete water deprivation, \( t_{1/2} \) was approximately 18.5 days in harbor seals (Depocas et al. 1971), 15.6 days in Perognathus formosus (Mullen 1970), and about 13 days in the kangaroo rat (Richmond, Trujillo, and Martin 1960). A preliminary report by Ohata (1975) suggests that in the northern fur seal \( t_{1/2} \) is about 13 days when the animals were provided food but no water. In contrast, the biological half-time of water in fasting elephant seal pups, 53.5 \( \pm \) 5.2 days, surpasses these examples by at least a factor of 2.5 and is, to our knowledge, exceeded in no other mammalian species.

<table>
<thead>
<tr>
<th>Animal</th>
<th>( \dot{r}<em>m(H</em>{2}O) ) (g(\cdot)day(^{-1}))</th>
<th>( \dot{r}_m ) (g(\cdot)day(^{-1}))</th>
<th>( \dot{m} ) (g(\cdot)day(^{-1}))</th>
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<tr>
<td>L1</td>
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<tr>
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<td>726</td>
<td>.99</td>
</tr>
</tbody>
</table>

\( \dot{m} = .92 \pm .05 \)

**LITERATURE CITED**


---. 1966. Interactions of physiology and behavior under natural conditions. Pages 39–45 in


