Developmental aspects of sleep apnoea in northern elephant seals, 
*Mirounga angustirostris*

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(With 3 figures in the text)

Northern elephant seals, *Mirounga angustirostris*, breathe irregularly while sleeping on land, alternating bouts of breath-holding (apnoea) that can last up to 25 min with periods of breathing (eupnoea). Our aims were to quantify changes in this behaviour during development and to determine the correspondence between these ontogenetic changes and those independently recorded in the dive durations of free-ranging seals. We observed 163 seals during periods of apparent sleep, ranging in age from new-born to adult, at Año Nuevo, California. Mean length of apnoea and percentage time spent in apnoea were 3.1 min and 59% in neonates (0-4 days old). These values decreased to 1.8 min and 37% in suckling pups (5-28 days old), then increased with age thereafter, reaching about 8.0 min and 60% in adults of both sexes. Sleep apnoea duration and percentage time spent in sleep apnoea increased most markedly after weaning, when the animals were learning to swim and dive. Mean sleep apnoea duration and mean dive duration increased in a similar way during the first year of life; thereafter, mean sleep apnoea duration reached an asymptote while mean dive duration continued to increase. We conclude that the elephant seal’s ability to sustain long apnoeas is not only an adaptation for foraging underwater but also a means for conserving water and energy while fasting on land.

Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>437</td>
</tr>
<tr>
<td>Background information</td>
<td>438</td>
</tr>
<tr>
<td>Methods</td>
<td>438</td>
</tr>
<tr>
<td>Results</td>
<td>439</td>
</tr>
<tr>
<td>Discussion</td>
<td>442</td>
</tr>
<tr>
<td>Characteristics of the breathing pattern</td>
<td>442</td>
</tr>
<tr>
<td>Comparison of terrestrial sleep apnoea duration and free-ranging dive duration</td>
<td>443</td>
</tr>
<tr>
<td>Function of sleep apnoea</td>
<td>444</td>
</tr>
<tr>
<td>References</td>
<td>445</td>
</tr>
</tbody>
</table>

Introduction

Spontaneous variation in breathing rhythm is characteristic of most aquatic mammals (Parker, 1922; Swindle, 1926; Scholander & Irving, 1941; Gunther, 1949; Harrison & Kooyman, 1968; Kenny, 1979). Among pinnipeds, the most irregular respiratory pattern is found in elephant seals. Bartholomew (1954) described the breathing pattern in northern elephant seals, *Mirounga angustirostris*, sleeping on land. He reported prolonged breath holds (apnoeas) of 2–8 minutes in duration in juveniles and adults of both sexes, alternating with equally long periods of breathing.
In suckling neonates, the periods of suspended respiration were less than two minutes long.

Kenny (1979) found a similar variable rhythm of breathing in resting southern elephant seals, *M. leonina*. He noted an increase in apnoea duration with age and a concomitant decrease in the duration of eupnoeas. The longest apnoea observed was over 10 minutes in an adult male. Unlike adults, the breathing of pups was shallow, rapid and comparatively regular, with only a few individuals showing the aperiodic breathing pattern of adults. Harnisch (1937) reported spontaneous apnoeas in a captive elephant seal lasting up to 6-8 min.

Bartholomew (1954) concluded that the prolonged apnoeas of the two species of elephant seals are the longest spontaneous suspensions of respiration reported for any pinniped. This behaviour led Kenny (1979) to suggest that adult elephant seals on land experience apnoeic periods of similar duration as typical dives. Recent studies of the free-ranging dive pattern of both species (Le Boeuf *et al.*, 1986, 1988, 1989; DeLong & Stewart, 1991; Hindell *et al.*, 1991, 1992) provide data for a test of this hypothesis. If there is a tight link between the ontogeny of terrestrial sleep apnoea and apnoea during diving, then similar underlying mechanisms may be involved, such as changes in heart rate, in metabolism and in circulatory patterns. This would offer the possibility of using terrestrial sleep apnoea as a model for studying certain aspects of diving physiology which are difficult to investigate at sea.

The purpose of this study was to add to our knowledge of the terrestrial breathing pattern of free-ranging northern elephant seals during sleep by describing the breathing pattern of individuals of both sexes in age categories ranging from neonate to adult. Specifically, we aimed to describe age-specific changes in the breathing pattern during terrestrial sleep, and to compare developmental changes in the terrestrial apnoeic pattern with dive duration data obtained from free-ranging seals (Le Boeuf *et al.*, 1988, 1989). Thus, we have extended the initial observations of Bartholomew (1954) by enlarging the sample size, examining developmental changes, and by comparing breath-holding ability on land to that at sea.

**Background information**

From early December to mid-March, northern elephant seals haul out on the beaches of Año Nuevo State Reserve to breed (Le Boeuf, Whiting & Gantt, 1972). Adult males arrive before females and establish dominance hierarchies in areas where females congregate. Each female gives birth to a single pup that is nursed for about 28 days, while the female fasts. Pups are weaned when their mother departs for the sea. Weanlings remain near the Año Nuevo rookery for an additional 8–12 weeks (Reiter, Stinson & Le Boeuf, 1978) without feeding. Within about two weeks of weaning, the weanlings begin entering the water daily and, in a short time, become proficient swimmers and long breath-hold divers.

Adults dive continuously, spending 85–90% of their time underwater, and range over a vast area of the Pacific Ocean (DeLong, Stewart & Hill, 1992; Le Boeuf *et al.*, 1993; Le Boeuf, 1994). Their dives have a mean duration of about 20 minutes, a maximum of 90 min and a mean depth of 300–500 m (Le Boeuf *et al.*, 1989, 1993).

**Methods**

Observations of northern elephant seals were conducted during daylight hours at Año Nuevo, California, during the years 1977, 1979–1983 and 1990–1992. Adults, subadults and suckling pups were observed during...
the breeding season (January to March), and weanlings during the post-weaning fast (February to May). Juveniles were observed during the breeding season and into the spring moult (January to May).

Observations were conducted on seals apparently sleeping on land, apparent sleep being defined as lying supine with eyes closed for more than 2 min. Huntley (1984) showed that weanlings recorded in the laboratory are generally, but not always, asleep during apnoeas lasting over a minute. Castellini (1994) reports that awake apnoeas in weanlings have a limit of about 5 min. The animals may or may not be sleeping during eupnoea (M. Castellini, pers. comm.), but unless disturbed, they keep their eyes closed. The observer approached downwind to within 5 m and took up a station where opening and closing of the nares could be seen and exhalations and inhalations could be heard.

Recording with a digital time piece began when the respiratory phase in progress (apnoea or eupnoea) ended. During eupnoea, ventilatory rate was recorded. An apnoea was defined as a period of no breathing, starting with an exhalation (if several exhalations followed the last inhalation, then timing started at the first one) and ending with an inhalation that lasted 60 sec or more. If the animal awoke and opened its eyes because it was disturbed by another animal or by an environmental event such as noise, or if it simply took notice of the observer, the observation was terminated and the last apnoea or eupnoea was discarded. Two consecutive apnoea–eupnoea cycles during apparent sleep were used for each animal; additional uninterrupted cycles were increasingly difficult to collect. In 8 adult animals for which 4 or more uninterrupted cycles were obtained, no tendency for an increase or decrease in apnoea or eupnoea duration was observed as more cycles were obtained. To achieve statistical independence of data points, a mean length of apnoea and eupnoea was calculated for each animal, and used to compute a class average.

Subjects fell into one of 8 categories: neonates (1–4 days old), suckling pups (5–28 days old), young weanlings (25–60 days old), old weanlings (61–100 days old), juveniles (1.2 years old), subadult males (5–7 years old), lactating adult females (3–10 years old), and adult males (8–14 years old). Sixty percent of the subjects had been tagged at weaning and were of known age. The remainder were easily placed into one of the 8 categories on the basis of size and general appearance. Individuals were sampled only once to satisfy the statistical assumption of independence. Sample sizes ranged from 11 to 34 individuals per category.

Mean differences across groups were tested with analysis of variance. Two-tailed Student t-tests were used for between-group comparisons. When applicable, the t-test P-values were corrected for 28 possible pairwise comparisons using the Bonferroni procedure (Rice, 1989). Descriptive statistics are presented as mean ± one standard deviation.

**Results**

All subjects exhibited a similar respiratory pattern: periods of arrested breathing (apnoea) alternated with periods of eupnoea. Mean apnoea duration ranged from 1.8 ± 0.5 to 9.7 ± 3.5 min and mean eupnoea duration ranged from 2.2 ± 0.8 to 5.1 ± 1.1 min across age/sex classes (Table I). Mean apnoea duration, illustrated graphically in Fig. 1, varied significantly across animal classes (F = 29.89, d.f. = 7,155, P = 0.0001). After an initial significant decrease between neonates and suckling pups (t = 4.79, d.f. = 27, P < 0.028), mean apnoea duration increased during the first 3.5 months of life, from 1.8 ± 0.5 min in suckling pups older than 4 days to 8.0 ± 1.6 min in old weanlings. The differences are significant between suckling pups and young weanlings (t = −7.04, d.f. = 50, P < 0.028), and between the two weanling classes (t = −10.12, d.f. = 53, P < 0.028). There was no significant variation in mean apnoea duration across old weanlings, juveniles, subadults and adults of either sex (F = 2.13, d.f. = 4,95, P = 0.083).

There was significant variation in mean eupnoea duration across age/sex classes (F = 4.95, d.f. = 7,155, P = 0.0001, see Table I).

The mean absolute difference in duration between the first and the second apnoea, respectively eupnoea, was calculated for each class to illustrate intra-individual variation in the length of
Mean and standard deviation of apnoea and eupnoea, mean absolute difference in length of apnoea and eupnoea, mean percentage time spent in apnoea, longest apnoea, ventilatory rate during eupnoea and overall ventilatory rate (apnoea and eupnoea combined), in northern elephant seals. The data are based on two consecutive apnoea-eupnoea cycles per individual, during apparent sleep. Sample size is in parentheses.

<table>
<thead>
<tr>
<th>Class</th>
<th>Mean apnoea (min)</th>
<th>Mean absolute difference in apnoea duration (min)</th>
<th>Mean eupnoea (min)</th>
<th>Mean absolute difference in eupnoea duration (min)</th>
<th>Apnoea (%)</th>
<th>Longest apnoea (min)</th>
<th>Breaths per min (apnoea)</th>
<th>Breaths per min (eupnoea)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neonates (11)</td>
<td>3.1 ± 0.9</td>
<td>0.9 ± 0.8</td>
<td>2.2 ± 0.8</td>
<td>1.0 ± 0.5</td>
<td>8.7 ± 7.9</td>
<td>5.5</td>
<td>19.9 ± 5.4</td>
<td>8.2 ± 2.5</td>
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<tr>
<td>Suckling pups (18)</td>
<td>1.8 ± 0.5</td>
<td>0.5 ± 0.5</td>
<td>3.9 ± 3.6</td>
<td>2.4 ± 4.3</td>
<td>3.7 ± 12.6</td>
<td>3.2</td>
<td>20.5 ± 4.2</td>
<td>12.7 ± 3.2</td>
</tr>
<tr>
<td>Young weanlings (34)</td>
<td>4.0 ± 1.3</td>
<td>1.1 ± 1.0</td>
<td>3.6 ± 1.7</td>
<td>2.0 ± 2.0</td>
<td>5.7 ± 12.6</td>
<td>8.2</td>
<td>14.5 ± 3.4</td>
<td>6.6 ± 2.1</td>
</tr>
<tr>
<td>Old weanlings (21)</td>
<td>8.0 ± 1.6</td>
<td>2.0 ± 1.9</td>
<td>3.0 ± 1.0</td>
<td>0.8 ± 0.6</td>
<td>7.0 ± 5.1</td>
<td>12.4</td>
<td>11.3 ± 2.1</td>
<td>3.0 ± 0.7</td>
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<tr>
<td>Juveniles (20)</td>
<td>9.7 ± 1.3</td>
<td>2.3 ± 1.4</td>
<td>4.9 ± 1.9</td>
<td>1.4 ± 1.3</td>
<td>6.5 ± 9.0</td>
<td>16.4</td>
<td>8.4 ± 1.6</td>
<td>2.8 ± 0.9</td>
</tr>
<tr>
<td>Subadult males (20)</td>
<td>9.7 ± 1.5</td>
<td>2.8 ± 2.1</td>
<td>3.8 ± 1.1</td>
<td>1.4 ± 1.1</td>
<td>7.1 ± 6.6</td>
<td>23.1</td>
<td>5.5 ± 1.0</td>
<td>1.6 ± 0.4</td>
</tr>
<tr>
<td>Adult females (20)</td>
<td>8.7 ± 3.9</td>
<td>2.5 ± 2.0</td>
<td>5.1 ± 1.1</td>
<td>1.6 ± 1.4</td>
<td>6.0 ± 10.4</td>
<td>21.2</td>
<td>5.0 ± 1.1</td>
<td>1.9 ± 0.6</td>
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<tr>
<td>Adult males (19)</td>
<td>7.4 ± 2.7</td>
<td>2.4 ± 2.4</td>
<td>4.8 ± 1.8</td>
<td>1.7 ± 1.4</td>
<td>6.0 ± 8.8</td>
<td>14.3</td>
<td>4.5 ± 1.0</td>
<td>1.7 ± 0.4</td>
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</tbody>
</table>

The percentage of time during apparent sleep that was spent in apnoea dropped significantly between neonates and suckling pups (t = 5.10, df = 27, P < 0.028), then increased rapidly during the post-weaning fast and reached adult levels in older weanlings on the verge of going to sea for the first time (Table I, Fig. 2). Differences were significant both between suckling pups and young weanlings (t = -4.52, df = 50, P < 0.028) and between the two weanling classes (t = -6.68, df = 53, P < 0.028).

A similar ontogenetic pattern is also evident in the longest apnoea duration shown by each class (Table I). Maximum apnoea duration initially dropped from 5.5 min in neonates to 3.2 min in suckling pups. Thereafter, it nearly quadrupled during the first 3.5 months of life, reaching 12.4

![Fig. 1](image-url) Mean length of apnoea, ± one standard deviation, for various age and sex classes of northern elephant seals. N = neonate, SP = suckling pup, Yg W = young weanling, Old W = old weanling, J = juvenile, SA = subadult, Ad = adult, M = male, F = female. Sample size is indicated above standard deviation.
**APNOEA IN NORTHERN ELEPHANT SEALS**

**Figure 2.** Mean percentage time spent in apnoea during apparent sleep for 29 neonates and suckling pups and 27 weaned pups as a function of age.

**Figure 3.** Mean length of terrestrial apnoeas and free-ranging dives, ± one standard deviation, for various classes of northern elephant seals (see Fig. 1 legend for abbreviations). The juveniles 1 are 4 months old, and the juveniles 2 are 1.2 years old for the terrestrial apnoea data, and 1.4 years old for the free-ranging dive data. The adult females are post reproductive and not pregnant. The weanling dive data come from Thorson & Le Boeuf, 1994; n = 121 dives from seven individuals. The dive data for the other sex/age classes come from Le Boeuf et al., 1988, 1989, and P. Morris & B. Le Boeuf, unpubl. data. Mean dive durations were calculated with an average of 3585 ± 2243 dives per individual. Sample size is indicated above standard deviation.
min in old weanlings, and nearly increased by a factor of five within the first year of life, reaching 16-4 min in juveniles.

There was significant variation in overall ventilatory rate, apnoea and eupnoea combined, across sex/age classes ($F=110.02$, $d.f.=7,155$, $P=0.0001$), as well as in ventilatory rate during eupnoea alone ($F=97.27$, $d.f.=7,155$, $P=0.0001$, see Table I). Overall ventilatory rate increased significantly between neonates and suckling pups ($t=-4.07$, $d.f.=27$, $P<0.028$), then dropped rapidly until the end of the post-weaning fast (Table I), the differences being significant between suckling pups and young weanlings ($t=8.26$, $d.f.=50$, $P<0.028$), and between the two weaning classes ($t=7.54$, $d.f.=53$, $P<0.028$), but not between old weanlings and juveniles ($t=0.94$, $d.f.=39$, $P>0.5$).

The correspondence between mean sleep apnoea duration and mean dive duration for elephant seals ranging in age from weanlings to adults is shown in Fig. 3. The dive data for weanlings come from Thorson & Le Boeuf (1994); the five weanling age classes were matched with sleep apnoea data from 21 young and old weanlings whose exact age was known. Comparisons showed significant differences between dive durations and sleep apnoea durations for all age/sex classes. For weanlings, sleep apnoea durations were significantly longer than dive durations ($t=-4.97$, $d.f.=13$, $P<0.001$ for the 5-6.9 week class; $t=-5.56$, $d.f.=8$, $P=0.001$ for the 7-8.9 week class; $t=-7.15$, $d.f.=9$, $P<0.001$ for the 9-10.9 week class; $t=-3.10$, $d.f.=7$, $P=0.017$ for the 11-12.9 week class and $t=-6.30$, $d.f.=3$, $P=0.008$ for the 13-14.9 week class), while in the other sex/age classes the opposite was found ($t=3.10$, $d.f.=26$, $P=0.005$ for juveniles; $t=5.80$, $d.f.=21$, $P<0.001$ for subadult males; $t=12.97$, $d.f.=43$, $P<0.001$ for adult females and $t=11.58$, $d.f.=23$, $P<0.001$ for adult males).

Discussion

Characteristics of the breathing pattern

Our results confirm and extend Bartholomew's observations (Bartholomew, 1954) that northern elephant seals of both sexes and all age classes show an irregular apnoeic breathing pattern on land, consisting of alternating periods of breath-holding and breathing. Two features of this breathing pattern, the duration of the apnoeas and the slow ventilatory rate, are strikingly different from that of other mammals.

The periods of terrestrial apnoea in northern elephant seals, which can last for over 20 minutes in adults, are longer than those observed in other mammals. Other phocids characteristically exhibit apnoeas while sleeping, but none reaches the durations observed in northern elephant seals, with the possible exception of the southern congener, *M. leonina* (Kenny, 1979). The maximum terrestrial apnoea duration recorded in Weddell seals, *Leptonychotes weddellii*, is 13-5 min (Castellini, Kooyman & Ponganis, 1992), and 7-6 min in Hawaiian monk seals, *Monachus schauinslandi* (Whittow, 1978). Apnoeas of comparable or longer durations are found in certain small mammals, showing Cheyne-Stokes breathing during hibernation (e.g. Kristoffersson & Soivio, 1964; Pajunen, 1970), a state considered by some as homologous to sleep (Walker & Berger, 1980; Berger, 1984) but of diminished metabolism.

The mean overall ventilatory rate of adult northern elephant seals was $1.7 \pm 0.4$ breaths per minute (B/M) in males and $1.9 \pm 0.6$ B/M in females. During eupnoea alone, it was $4.5 \pm 1.0$ B/M in males and $5.0 \pm 1.1$ B/M in females (Table I). This is noticeably lower than the predicted values of 7-6 and 11-7 B/M calculated for a 1800 kg male and a 350 kg female, respectively, based on an
allometric equation for mammals (Stahl, 1967). Kooyman (1968) gives a mean ventilatory rate during eupnoea of 8.0 B/M in resting Weddell seals. Among phocids, only Hawaiian monk seals show ventilatory rates comparable to those of elephant seals: 2.1 B/M overall and 5.2 B/M during eupnoea (Whittow, 1978).

It is noteworthy that sleep is associated with the long terrestrial apnoeas observed in quiescent elephant seals. This was confirmed by Huntley (1984) who recorded the electroencephalogram (EEG) of animals sleeping in the laboratory. More recent research confirmed this observation and showed that sleep may also, but not inevitably, occur during eupnoeas between long apnoeas (M. Castellini, pers. comm.). Moreover, terrestrial sleep differs from that of most mammals in its daily rhythm; it does not follow the common die1 pattern (Campbell & Tobler, 1984), but rather, like 'cat-napping', occurs opportunistically at any time of day or night and appears to be related to lack of social activity and disturbance.

**Comparison of terrestrial sleep apnoea duration and free-ranging dive duration**

Terrestrial apnoeas and breath-hold dives share fundamental similarities as well as striking differences. During cessation of breathing, the former serves sleep, an inactive state, while the latter serves mainly foraging and transit and involves exercise. To what extent do the same respiratory states in the two different environments, and involving different levels of activity, have a common physiological basis? Information bearing on this question comes from comparison of the onset and duration of apnoea during terrestrial sleep with the beginning of diving and changes in mean dive duration during development.

Parallel aspects of development of sleep apnoea and dive duration suggest a similar physiological basis. Indeed, changes in sleep apnoea coincide with changes in diving capacity. Newly weaned northern elephant seals begin entering the water at five to eight weeks of age (Reiter et al., 1978). Diving time is brief at first but increases quickly to a mean of about 6 min at 14 weeks of age (Thorson & Le Boeuf, 1994, and Fig. 3), the same time period in which the mean duration of terrestrial apnoeas increases markedly from 4.0 ± 1.3 min to 8.0 ± 1.6 min (Fig. 1). Furthermore, haematocrit and mass-specific blood volume increase during this period, as body mass falls due to fasting (Thorson & Le Boeuf, 1994). Shortly after weaning, sleep apnoeas on land and dive durations in shallow water near the rookery show similar developmental increases (Fig. 3). The shorter dive durations are probably due to different sampling methods and different activities performed during dives, e.g. play, exploration or rest. All dives of weanlings were recorded in Thorson & Le Boeuf's study, even those lasting well under a minute. When the seals left the rookery on their first pelagic trip, dive durations increased markedly (Fig. 3).

The lack of a close fit between sleep apnoea duration and dive duration in adulthood may be due to several variables. Our behavioural observations suggest that sleep apnoea is curtailed in breeding adults, more so than in younger animals, because the former are more vigilant and wary. This accounts, in part, for the decreasing correlation between sleep apnoea duration and dive duration with increasing age. For example, high-ranking adult males reside in or near harems where they must be ready to fight to keep other male intruders from mating. The social context does not allow males to sleep long and deeply unless everyone else is doing so. Subadult males, in contrast, often choose to sleep away from breeding activities where they are unthreatened and undisturbed. The longest sleep apnoea ever recorded was 25 min for a subadult male sleeping away from a harem (B. Le Boeuf, unpubl. obs.). Deutsch (1990) showed that alpha males defending harems have significantly shorter apnoeas than subordinate males competing at the periphery of
harems, who in turn have significantly shorter apnoeas than subordinate males away from harems. On the other hand, several factors may contribute to lengthening dive times in free-ranging animals, such as cold water temperatures that may be associated with lower metabolic rates than when resting on the beach. Furthermore, finding a rich prey patch several hundred metres below the ocean’s surface would be a strong incentive for a foraging seal to prolong its dive.

There is further evidence for a common physiological basis between terrestrial sleep apnoea and breath-hold diving. Physiological changes observed in diving mammals during submersion include bradycardia, peripheral vasoconstriction and a reduction of the metabolic rate. Bradycardia during free dives has been observed in several species of pinnipeds (Scholander, 1940; Elsner, Franklin & van Citters, 1964; Jones et al., 1973) as well as in other mammals (e.g. Scholander & Irving, 1941; Johansen, Lenfant & Grigg, 1966; Calder, 1969). Andrews et al. (1991) recorded heart rates in submerged, free-ranging juvenile elephant seals that decreased more than 50%, on average, from rates at the surface. In Weddell seals, the heart rate at the beginning of a dive is as low as 25% of the value during eupnoea (Kooyman & Campbell, 1972). Bartholomew (1954) observed heart rates during terrestrial apnoeas of adult northern elephant seals that were 15% lower than during eupnoeas. Päsche & Krog (1980) found similar levels of bradycardia during diving and during terrestrial apnoeas in harbour seals, *Phoca vitulina*, and a hooded seal, *Cystophora cristata*. In both species, the heart rate decreased to 30% of the rate during breathing.

Depression of the metabolic rate during diving, first observed by Scholander (1940), has since been confirmed in several studies on restrained seals and ducks (Scholander, Irving & Grinnell, 1942; Andersen, 1959; Pickwell, 1968). Castellini et al. (1992) show that metabolism in freely diving Weddell seals was no different than resting values. They hypothesize that the increase in metabolic rate due to physical exercise cancels out the decrease in metabolic rate due to submergence. Huntley (1984) estimated a 23.1% net energy saving, over the basal metabolic rate, accrued as a result of reduced metabolism during sleep apnoea in 3-month-old northern elephant seal weanlings. T. Tuáño (unpubl. data, cited in Rea, 1990: 32) replicated this observation.

Finally, Kooyman et al. (1980) and Qvist et al. (1986) observed elevated haemoglobin (Hb) and haematocrit (Hct) values just after diving in free-ranging Weddell seals. These values subsequently decreased to pre-dive levels. Castellini, Costa & Huntley (1986) found an increase in haematocrit levels throughout long-duration sleep apnoea in northern elephant seal weanlings. The peak values were reached at the end or just after the end of a bout of apnoea, just as during a dive. The authors concluded that sleep apnoea in the elephant seal has physiological aspects that are similar to those in freely diving seals.

**Function of sleep apnoea**

What is the function of sleep apnoea? Ortiz, Costa & Le Boeuf (1978) hypothesized that the irregular breathing pattern of northern elephant seals, acting in concert with other elements of the dive response (Irving, 1939; Scholander, 1940) and morphology (such as nasal countercurrent heat exchange, see Huntley, Costa & Rubin, 1984), facilitates water and energy conservation. This is important because elephant seals rely on their fat reserves during lengthy fasts: 34 days in lactating females (Le Boeuf et al., 1972; Reiter, Panken & Le Boeuf, 1981), up to 75 days in newly weaned pups (Reiter et al., 1978), and over 100 days in mating adult males (Deutsch, 1990). During these fasts, water balance is maintained and energy is provided by metabolizing fat (Ortiz et al., 1978). Irregular breathing with long apnoeas means fewer breaths taken than would be the case if the animal breathed regularly. Costa & Ortiz (1980) showed that 64% of the metabolic water production in fasting weanlings is accounted for by respiratory evaporative water loss. Reducing
this avenue of water loss conserves energy. How much energy is saved depends on the amount of time per day spent in apnoea, as well as physiological variables such as lung volume and moisture in the expired air, and environmental variables such as ambient temperature and humidity. Since newly weaned elephant seals fast for 2-5 months before going to sea, we would expect the development of energy-saving mechanisms to appear at this time. This is precisely when our results show the greatest increases in mean length of apnoea (Fig. 1) and in percentage time spent in apnoea (Fig. 2). During the period of development between the stage of suckling pup (up to 3-4 weeks of age) and the end of the post-weaning fast (3-3.5 months of age), the overall ventilatory rate decreases by 73% (Table I). These factors all contribute to a reduction of evaporative water loss and energy expenditure.

The adaptive function of apnoea may have originated in the birth process of mammals, during which the transition from placental to lung respiration threatens the infant with asphyxia (Elsner & Gooden, 1983). Terrestrial neonates are, indeed, more resistant to asphyxia than adults (Dawes, 1968), but the reverse seems to be true in pinnipeds, maybe because the trait is so well developed in adults (see Elsner & Gooden, 1983). In most mammals, this tolerance to asphyxia disappears early in development. In our own data (Table I, Fig. 2), neonates spent 56% of their sleeping time in apnoea and had a maximum apnoea duration of 5.5 min. This high percentage of time spent in apnoea declined over the lactation period and increased again after weaning. This developmental pattern is consistent with the hypothesis that the evolution of apnoea as a natural phenomenon is related to survival during the transition from placental to lung respiration.

If the above reasoning is correct, elephant seals and, to a lesser extent, other phocids, have taken a trait, originally selected as an adaptation to surviving parturition, retained and expanded it in adulthood as a fundamental adaptation for procuring prey while diving, and for conserving water and energy during prolonged fasts on land. This reasoning predicts that terrestrial apnoea duration in other species of the phocid family should be related both to diving capacity and to the need for water and energy conservation. Thus, an irregular breathing pattern with long apnoeas should be found in: (1) pinnipeds capable of making dives of long duration, i.e. generally large species with great blood volumes and high haematocrits; and (2) in species that fast for lengthy periods and have no source of water except by metabolizing fat. Besides northern elephant seals, these two categories include southern elephant seals (Hindell, 1990), Weddell seals (Kooyman, 1968), Hawaiian monk seals (Kenyon & Rice, 1959) and grey seals Halichoerus grypus (Fedak & Anderson, 1982). Ice-eating in some pagophilic pinnipeds is expected to modify apneustic behaviour, since these animals do not then solely rely on their fat stores as a source of water. The scant data that exist on terrestrial apneustic behaviour in the above-mentioned species tend to support our hypothesis, but further systematic observations are needed to confirm it.

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