Patterns of respiration and heart rate during wakefulness and sleep in elephant seal pups

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Castellini, Michael A., William K. Milsom, Ralph J. Berger, Daniel P. Costa, David R. Jones, J. Margaret Castellini, Lorrie D. Rea, Supriti Bharma, and Michael Harris. Patterns of respiration and heart rate during wakefulness and sleep in elephant seal pups. *Am. J. Physiol.* 266 (*Regulatory Integrative Comp. Physiol.* 35): R863–R869, 1994.—Although breath holding during diving has been studied extensively in seals, the recent observation that these mammals also exhibit long-duration apnea while apparently sleeping has not been systematically examined. This project examined sleep apnea in northern elephant seal pups (*Mirounga angustirostris*). The animals exhibited a sequential sleep pattern of wakefulness-slow-wave sleep (SWS)-rapid eye movement (REM) sleep that resembled the normal pattern of mammalian sleep. The typical respiratory pattern during sleep in 4-mo-old pups consisted of short periods of continuous breathing separated by periods of apnea of up to 12 min. Several cycles of apnea and eupnea could occur during a single sleep episode. Breathing during a sleep cycle occurred only in SWS, never during REM sleep. The eupneic heart rate was characterized by significant sinus arrhythmia, and the apneic heart rate was similar to the minimum value during normal sinus arrhythmia. Patterns of change in breathing and heart rate associated with wakefulness and sleep were similar in seals sleeping underwater and on land. When sleeping underwater, the seals raised their heads to the surface to breathe without awakening. The changes in heart rate associated with normal sinus arrhythmia, sleep apnea, and diving apnea appear to be similar, suggesting regulation by a common homeostatic control mechanism.

marine mammals; apnea; electroencephalogram

FOUR-MONTH-OLD northern elephant seal pups (*Mirounga angustirostris*) have recently been observed to exhibit routine apneas of over 11 min while apparently sleeping (5). Profound changes in cardiovascular variables, such as heart rate and hematocrit, are associated with these periods of apnea and appear very similar to the physiological changes seen during diving (2, 4, 5). There appears to be no attempt to breathe during these periods, suggesting that the apneas are central in origin. Nothing else appears to be known about this phenomenon. It is not known to what extent the apneas are coupled to changes in wakefulness and sleep or to what extent changes in wakefulness and sleep are governed by respiratory drive. It is also not clear to what extent sleep and diving may elicit apnea and associated cardiovascular changes through common mechanisms. Finally, it is not clear to what extent these central sleep apneas in seals may be related to the similar but more pathological events seen in man. Given this, the present study was designed to address three questions in seal pups. *1*) What is the relationship between wakefulness, sleep, and respiratory pattern? *2*) Is this relationship altered when seals sleep submerged in water rather than on land? *3*) How are cardiac patterns altered during apnea-eupnea cycles both under dry and wet conditions?

METHODS

Twelve weaned northern elephant seal pups (~4 mo old) were captured at the elephant seal rookery at Año Nuevo, CA and temporarily held in captivity at the Long Marine Laboratory, University of California, Santa Cruz. Electrocardiographic (ECG), cortical electroencephalographic (EEG), and muscular electromyographic (EMG) activity were recorded using subdermal needle electrodes inserted and anchored beneath the fur. Respiration was recorded with a variable inductance band (Ambulatory Monitoring Systems, Ardsley, NY) placed around the pups' chests, just behind the foreflippers. The pups were allowed to rest and sleep in a large tank in a quiet, dimly lighted room and monitored for at least 12 h. In four cases, the tank was filled with water to a depth of ~0.5 m. Physiological data were displayed on multichannel strip-chart recorders (Grass Instruments, Quincy, MA, and Lafayette Instruments, Lafayette, IN) and stored for later analysis. Wakefulness and sleep states were scored from the EEG and EMG recordings as awake, slow-wave sleep (SWS), or rapid eye movement (REM) sleep according to typical mammalian characteristics of sleep (3) by two independent observers for each 30-s period of recording. The EMG-EEG characteristics associated with each sleep-awake state were easy to identify and consistent from animal to animal. Instantaneous beat-to-beat heart rate was determined from the ECG signal with a cardiotachometer (UFI, Morro Bay, CA) or from digitized ECG traces. Expiratory (T_e) and inspiratory times (T_i) and respiratory frequency (R_f) were computed by digitizing the respiratory traces. Analysis of heart rate and respiratory parameters of awake, eupneic animals are meant to reflect awake, quiet breathing unaffected by apnea. For this reason, analysis of these variables never included data from the 2-min period after an apnea. Recordings were obtained from animals under dry conditions for roughly 10 h each but only 4.5 h under wet conditions. Given the consistency of the results obtained between animals, we feel this was sufficient to allow meaningful calculations of state distribution, but the reduced recording times obtained from animals in the water-filled tank should be kept in mind. After the experiments, the seal pups were returned unharmed to the beach.

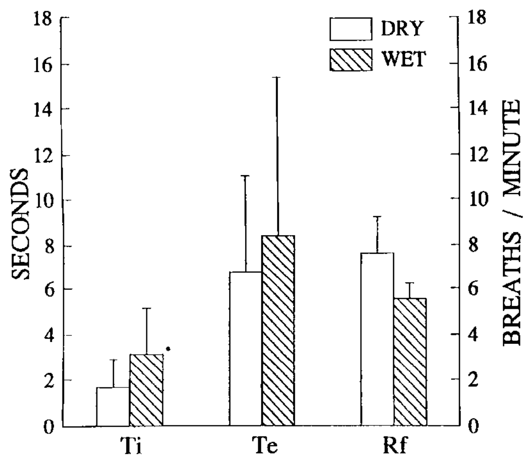

Fig. 1. Average (±SE) durations in s for inspiratory time (T_i), expiratory time (T_e) and respiratory frequency (R_f) for awake seals under dry (open bars; n = 5) and wet (hatched bars; n = 4) test conditions. For each condition mean T_i and T_e represent 6 groups of 10 consecutive breaths for each animal. R_f was calculated from the event time for each group of 10 breaths. ANOVA was used to compare individuals that were tested under both dry and wet conditions to determine significant differences (*$P < 0.05$).

RESULTS

Respiratory patterns associated with wakefulness and sleep under dry conditions. The respiratory pattern of awake seal pups is characterized in Fig. 1. Inspiratory time for an awake, dry pup averaged 1.8 s, expiratory time 6.7 s, and respiratory frequency 7.7 breaths/min (60 breaths/animal for 5 animals). The long expiratory time reflects the fact that many exhalations were followed by short apneas in which no respiratory movements were recorded, and the size of the standard error associated with the expiratory time reflects the variability in the length of the apneas. These apneas could, on rare occasion (mean = 3.9 ± 0.9/150 min) stretch to more than 2 min (mean = 135 ± 23 s). Apneas longer than 3 min were not seen in awake animals. Characteristic mammalian EEG and EMG patterns of wakefulness, SWS, and REM sleep are shown in Fig. 2. Unlike fur seals (15), right-left hemispherical differences were not evident in any of the EEG recordings. Figure 3 depicts how sleep cycles and respiratory patterns were linked in these seals. In Fig. 3, the pup entered SWS while breathing, became apneic, and progressed through two further cycles of eupnea and apnea while remaining in SWS. During the third apnea, the animal entered REM sleep and then awakened and recommenced breathing. This trace shows that seals need not arouse to resume breathing after periods of apnea and, as in this instance, breathing never occurred during REM sleep in any of the pups. Most sleep bouts under dry conditions (> 75%) were associated with only one period of apnea and some (4%) had no apneic periods (Fig. 4). In most animals, the apnea-eupnea cycles were quite regular and the sleep cycles usually followed an awake-SWS-REM sequence (Fig. 5). Transitions between awake-SWS-awake and between eupnea-apnea-eupnea overlapped extensively. Thus 44% of the time pups fell asleep before becoming apneic and 56% of the time the apnea preceded sleep. Sleep episodes usually terminated during apnea, with the pups beginning to breathe after arousal 89% of the time. An average of 83.3% of sleep was spent in apnea (Fig. 6) with an average duration of ~6 min and a mean of slightly less than 3 min of eupnea between apneic episodes (Fig. 6). The seals breathed at an instantaneous rate of ~10 breaths/min for the first five breaths after apnea and produced ~25 breaths during eupnea (Fig. 6).

Respiratory patterns associated with wakefulness and sleep under wet conditions. For four seals, the tank was filled with water to a depth of 0.5 m and the seal pups were allowed to rest to see if they would sleep in water and, if so, to test the hypothesis that the cardiorespiratory patterns associated with diving and sleep apnea were similar.

Figure 1 shows that water exposure increased inspiratory time, thus decreasing respiratory frequency, and had no effect on expiratory time during eupnea in wakefulness (ANOVA; $P < 0.05$, $P = 0.06$, $P = 0.31$, n = 4). Again, the prolonged expiratory time was due to short, highly variable periods of apnea after exhalation. The incidence of awake apneas that stretched to more than 1 min (mean = 109 ± 30 s) was just as rare in wet conditions (mean = 2.8 ± 1.5/100 min). The characteristics of sleep remained similar in water and Fig. 7 shows a sleep cycle for one pup sleeping submerged. Note that the same overall pattern of awake-SWS-REM sleep occurred in seals sleeping underwater as under dry conditions, that seals can rise to the surface to ventilate between periods of apnea without having to awaken from SWS, and that, again, breathing never occurred during REM sleep. Being in water increased the number of multiapnea sleep episodes compared with dry condi-

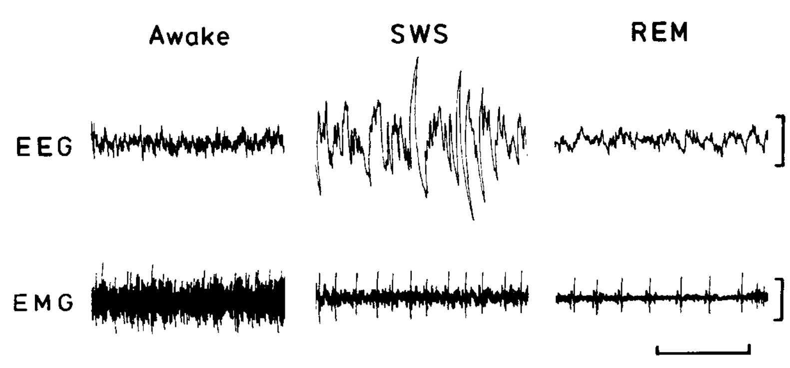

Fig. 2. Electroencephalogram (EEG) and electromyogram (EMG) traces during awake, slow-wave sleep (SWS), and rapid eye movement (REM) sleep in elephant seal pups.

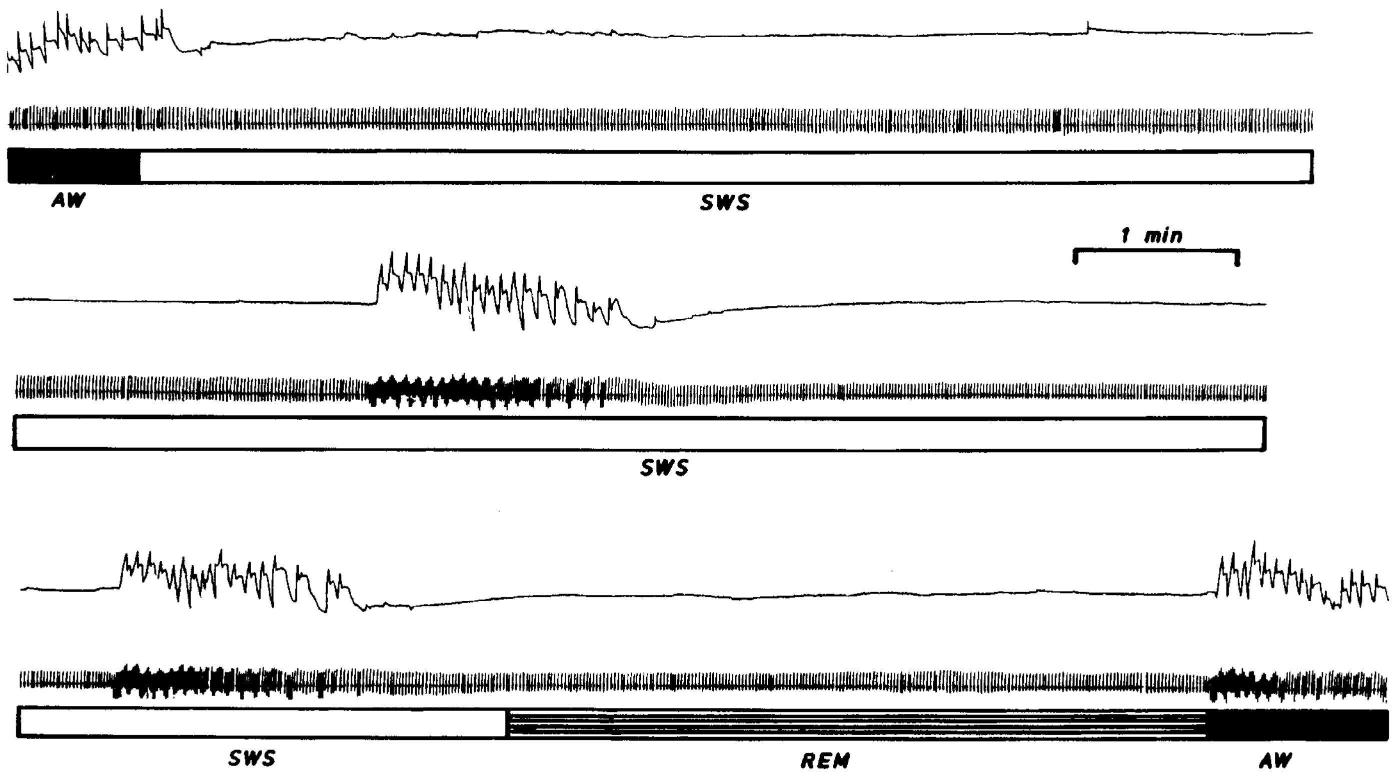

Fig. 3. Respiratory impedance and electrocardiogram (ECG) traces during a single sleep period in a seal pup sleeping under dry conditions. The horizontal histograms under each pair of traces depict the awake-sleep state as scored from simultaneously recorded EMG and EEG traces. The 3 sets of traces are continuous. Aw, awake.

tions (Fig. 4; ANOVA; $P < 0.05$) but did not affect the percentage of total time spent in apnea (Fig. 6; ANOVA; $P = 0.77$), the duration of the apneas (ANOVA; $P = 0.13$), or the mean eupnea duration (ANOVA; $P = 0.17$; Fig. 6). The total number of breaths per period of eupnea and the instantaneous respiratory frequency also did not differ between the two conditions (Fig. 6; ANOVA; $P = 0.28$; $P = 0.58$).

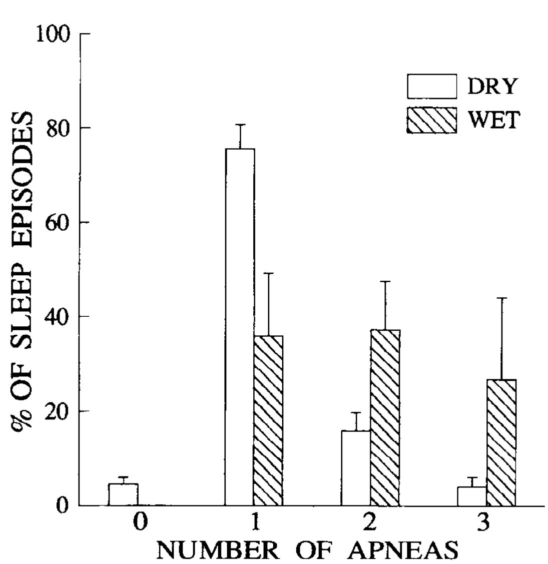

Fig. 4. The sleep episodes containing different numbers of apneas expressed as a percentage of the total number of sleep episodes recorded in each animal under wet and dry conditions. ($n = 4$ dry and wet; $n = 47$ episodes dry, 19 episodes wet).

Again, as under dry conditions, the apnea-eupnea cycles were quite regular, the sleep cycles usually followed an awake-SWS-REM sleep sequence, and transitions between awake-SWS-awake and between eupnea-apnea-eupnea overlapped extensively. Pups in water fell asleep before becoming apneic 50% of the time and sleep episodes terminated during apnea (with pups beginning to breathe after arousal) 68% of the time.

Sleep patterns. Of the total recorded time under dry conditions, ~55% was spent awake, 40% in SWS, and 5% in REM sleep (Fig. 8). Of the total number of sleep periods, 52.7% contained REM (Table 1), which constituted 12.5% of the total sleep time (Fig. 8). Exposure to water did not affect sleep patterns. Thus neither the percentage of time spent awake, in SWS, or in REM sleep differed (Fig. 8; paired t tests; $P > 0.05$), nor did the periodicity of the sleep cycle or the REM sleep cycle differ (ANOVA; $P = 0.16$; $P = 0.63$). Although there was no significant difference in the percentage of sleep periods that contained REM sleep (Table 1) under wet or dry conditions (ANOVA; $P = 0.41$), the length of sleep episodes increased in water (ANOVA; $P = 0.035$) while the length of the REM periods decreased (ANOVA; $P = 0.025$). As a consequence, the latency to REM also increased (ANOVA; $P = 0.036$).

Heart rate. The mean eupneic heart rate was 54–60 beats/min and apneic heart rate was 41–44 beats/min regardless of wakefulness or sleep state (Table 2), although during REM occasional transient instances of very low instantaneous heart rate occurred (25–35 beats/min). There were no significant differences in

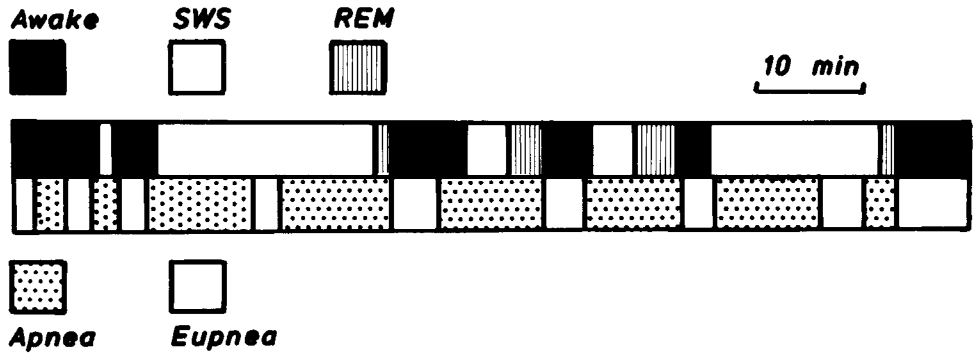

Fig. 5. Graphical representation of awake-sleep state and apnea-eupnea patterns recorded during ~1 h of recording from a dry seal pup.

eupneic or apneic heart rate between the wet or dry conditions (ANOVA; $P = 0.51$; $P = 0.92$ for awake and SWS eupnea; $P = 0.40$; $P = 0.78$ for SWS and REM apnea). Analysis of instantaneous heart rate, however, showed that this was not a simple bradycardia associated with the onset of apnea. Figure 9 shows how heart rate and respiration were related during a period of SWS. In this example, the apneic heart rate was ~50 beats/min during an 8.3-min apnea. At the onset of the subsequent 2 min of eupnea, there was a clear tachycardia up to ~100 beats/min that slowly diminished. A sinus arrhythmia was present throughout but became more pronounced as the tachycardia decreased during recovery. By the end of the period of eupnea, heart rate cycled between 50 and 80 beats/min during expiration and inspiration respectively. During the last expiration before the subsequent apnea, the heart rate fell to ~50 beats/min and remained there throughout the apnea. Similar patterns of tachycardia and sinus arrhythmia were observed during postapneic respiration regardless of whether this was during a eupneic episode in sleep or during the recommencement of breathing after sleep. Marked sinus arrhythmia existed under both dry and wet conditions (Table 2).

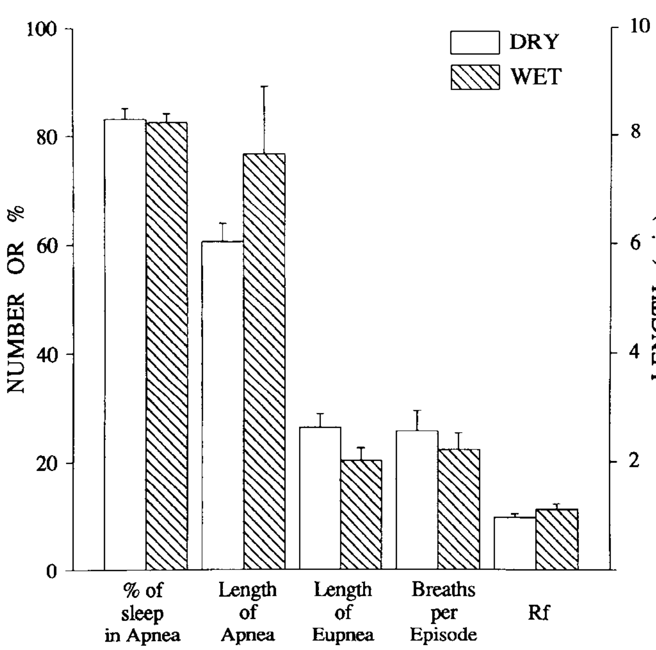

Fig. 6. The percentage of time asleep spent in apnea, the average durations of apnea and eupnea, the number of breaths/episode of eupnea, and the instantaneous respiratory frequency at the beginning of the episodes of eupnea (calculated from the first 5 breaths) (±SD) under dry and wet conditions during bouts of apnea ($n = 4$ dry and wet; $n = 47$ episodes dry, 19 episodes wet).

DISCUSSION

The foregoing results indicate that the long duration apneas observed in northern elephant seal pups while apparently sleeping are indeed dependent upon wakefulness and sleep state. We only observed prolonged apneas (>3 min) during sleep, never during wakefulness. The apneas, however, may begin either before or after the transition from wakefulness to sleep and breathing may recommence either before or after the transition from sleep to wakefulness. Furthermore, breathing episodes do not necessarily reflect brief periods of wakefulness, as several cycles of apnea-eupnea can occur in a single sleep episode. Ventilation during sleep occurred only during SWS, never during REM sleep. The complete absence of breathing during REM sleep has not been reported in other species, although respiration can become erratic during REM sleep (7, 21). REM sleep in these seals was characterized by muscle atonia accompanied by increased facial twitching, as in other mammals. Whether the complete cessation of breathing during REM in these animals represents a greater extension of this muscle atonia to the diaphragm and respiratory muscles compared with other mammals remains an intriguing question. REM constituted only 13% of total sleep time compared with ~40% in human infants of 3–5 mo of age (20). It is generally assumed that the proportion of REM sleep and SWS reflect the degree of maturity of the nervous system. Rat pups and kittens that are relatively immature at birth initially exhibit sleep consisting almost exclusively of REM, whereas guinea pigs, which are relatively mature, show proportionately more SWS at birth (10). Studies of young sleeping harp seals show a distribution of wakefulness, SWS, and REM sleep similar to that of northern elephant seal pups but the harp

Table 1. *Arousal patterns of seals on land and in water*

	Dry	Wet
Length of sleep episodes, s	504.8 ± 46.6	1,094.0 ± 354.1*
% Of sleep periods containing REM	52.7 ± 6.9	59.1 ± 5.8
Length of REM, s	222.0 ± 14.3	150 ± 25.8*
Total recording time, h	9.99 ± 0.37	4.43 ± 0.87

Values are means ± SE. REM, rapid eye movement. *Significantly different from dry values (ANOVA, $P < 0.05$).

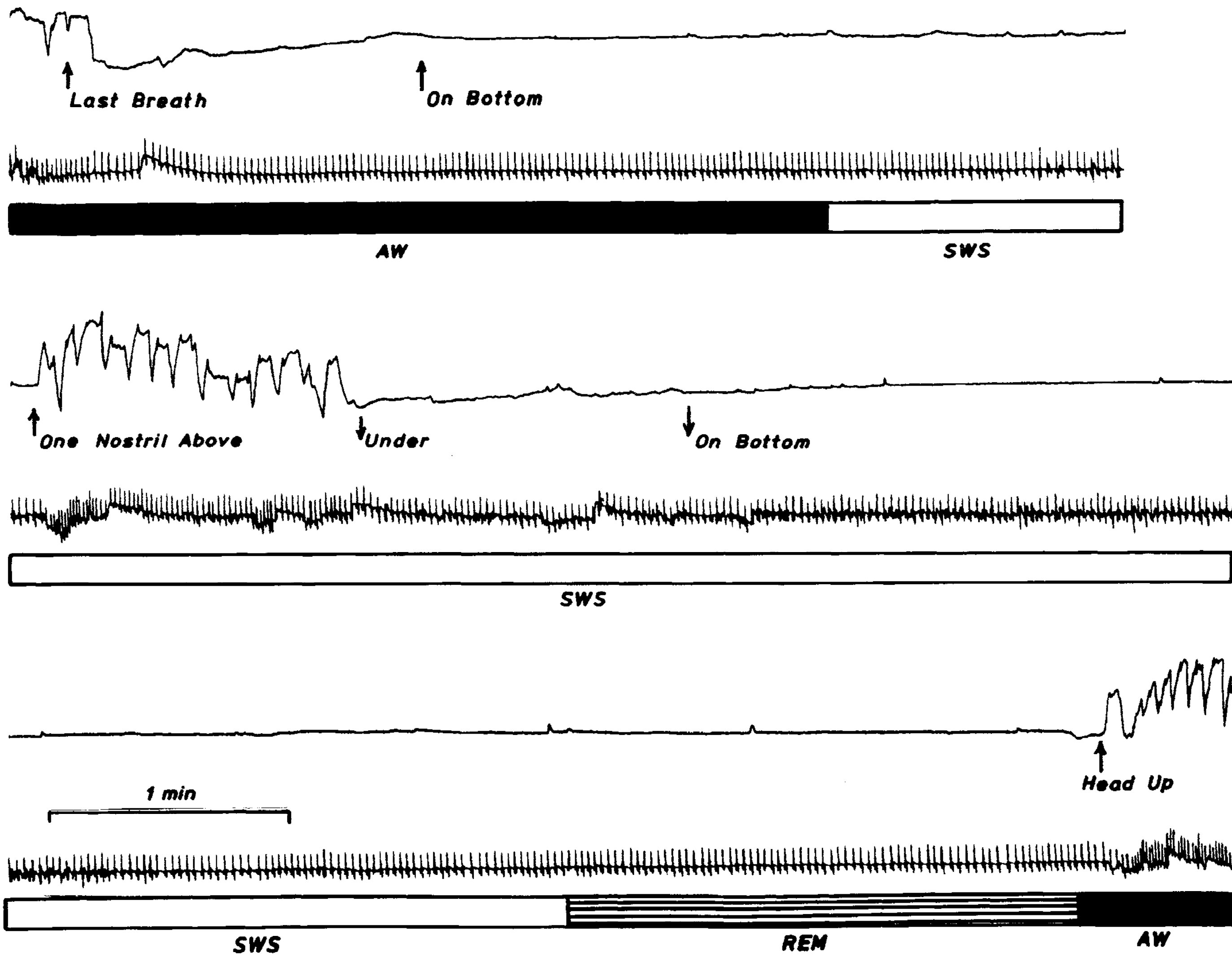

Fig. 7. Respiratory impedance and ECG traces during a single sleep period in a seal pup sleeping in water. The horizontal histograms under each pair of traces depict the awake-sleep state as scored from simultaneously recorded EMG and EEG traces. The 3 sets of traces are continuous. Arrows, when seal sank to the bottom of the tank, came to the surface to breathe, and submerged again.

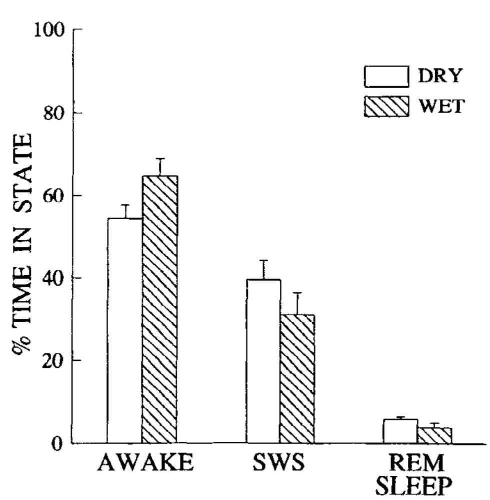

Fig. 8. The percent time spent awake or in SWS or REM sleep in seals under dry and wet conditions.

seals do exhibit occasional periods of irregular breathing during REM sleep (14). The sequential sleep patterns of these northern elephant seal pups of wakefulness-SWS-REM sleep resemble the normal pattern of mammalian sleep. This pattern was unaltered in animals sleeping in water, which together with the complete absence of ventilation during REM sleep contrasts with an earlier report on gray seals that described ventilation during REM sleep at the surface and no presence of REM sleep during underwater sleep (19). These contradictory findings between northern elephant seal pups and gray seals deserve comparative studies under similar conditions.

Interesting similarities and differences in sleep and respiratory patterns were observed when the seals were placed in water. They could sleep in water and could still breath episodically, even when the water level was such that they would submerge completely during apneic periods. Under these conditions, they would raise their heads to the surface to breathe during SWS without awakening and, as when sleeping in air, they never

Table 2. *Heart rate during the different arousal states under dry/wet conditions*

	Dry			Wet		
	Mean*	Inspiration	Expiration	Mean*	Inspiration	Expiration
Awake (Eupnea)	60 ± 12	86 ± 5	51 ± 3	54 ± 5	80 ± 3	44 ± 2
SWS (Eupnea)	60 ± 11	84 ± 6	51 ± 5	54 ± 3	75 ± 5	48 ± 1
SWS (Apnea)	44 ± 5			42 ± 4		
REM (Apnea)	42 ± 5			41 ± 5		

Values are means ± SE; n = 6 animals for dry, 3 for wet. SWS, slow-wave sleep. *ANOVA of mean heart rate, comparing only individuals tested under both dry and wet conditions, did not reveal any significant differences ($P < 0.05$) between dry and wet states for any awake-sleep state.

breathed during REM. The length of sleep bouts doubled when the animals were wet, while the length of the REM episodes decreased and the period of time spent in sleep did not change significantly. The number of sleep periods with multiple apneas increased when the animals were in water, presumably due to the increased length of the sleep episodes, since neither the length of an average apnea nor period of eupnea differed under dry or wet conditions. Northern elephant seals, while at sea, dive continuously 24 h a day for several months, pausing for only a few minutes at the surface between dives (13). This has raised the question of when do they sleep, if at all?. The data from this study indicate that they could sleep underwater, but whether they do sleep while diving remains to be seen.

The reduction in heart rate during sleep apnea was not a sudden event associated with the onset of apnea nor a progressive event developing throughout the apnea. The apneic heart rate was simply the minimal heart rate observed during the expiratory phase of the normal respiratory driven cardiac sinus arrhythmia. The heart rate during sleep apnea underwater did not differ from the rate during sleep apnea in air, indicating that head immersion did not elicit a further dive response. Similar findings have been reported for hooded seals (*Cystophora cristata*) considered to be sleeping in air or water (18) and in freely diving elephant seals (1), although periods of more extreme bradycardia have been observed under the latter conditions. This, combined with the similarities between apnea duration and hematocrit change during sleep and diving apnea in the northern elephant seal pups (5), suggests that both forms of apnea possibly may be governed by the same homeostatic control mechanisms.

Cardiorespiratory control in mammals is known to evolve after birth (11, 12) and it would be useful to know if the pups monitored in this study are representative of the adults in the population. We are currently investigating the development of apnea duration and cardiac control in northern elephant seals from birth until departure to sea and in adults. Empirically, the pups in this study (10 wk postweaning) are similar to adults in terms of cardiac and ventilatory control (unpublished observations). Whether respiratory pattern during wake-

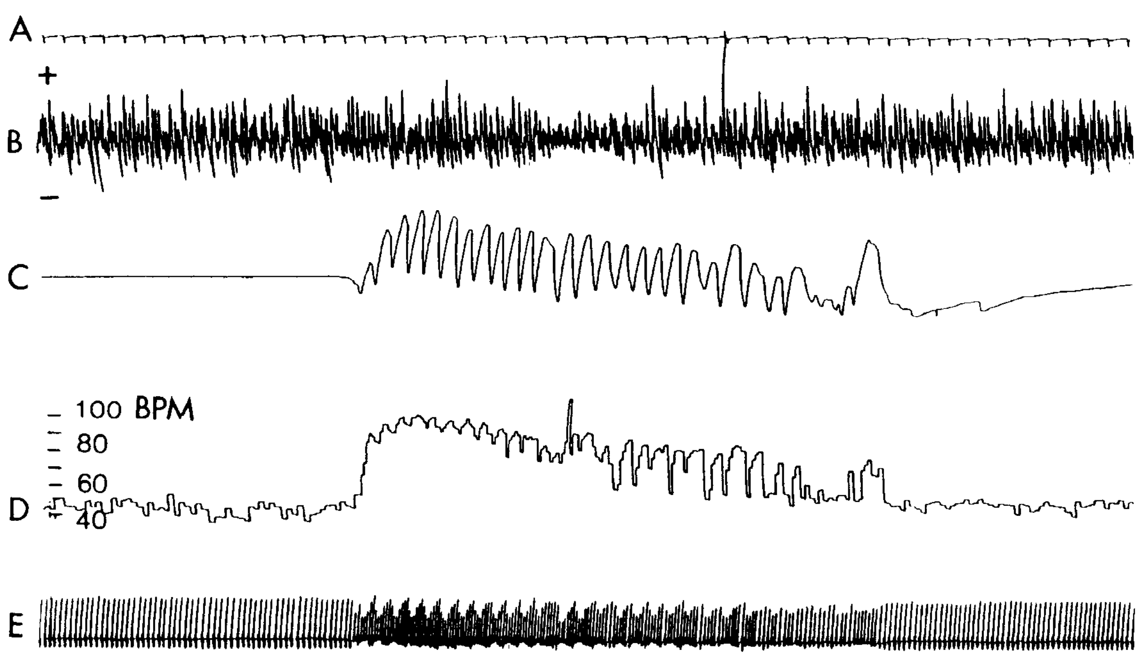

Fig. 9. Electrophysiological recordings associated with an episode of eupnea during SWS under dry conditions. The 5 traces, from *top* to *bottom*, show *A*: 5-s time marks; *B*: the EEG depicting continuous SWS (signal range from +100 μv); *C*: the respiratory trace showing the end of an 8-min apnea followed by 2.5 min of eupnea and the beginning of another apnea; *D*: the cardiotachograph depicting a low heart rate during the apnea, a ventilatory driven tachycardia, the appearance of the normal sinus arrhythmia, which becomes more prominent late in the eupnea, and finally the low heart rate during the ensuing apnea; and *E*: the ECG.

fulness and sleep varies with age in northern elephant seals is unknown at this time.

During REM sleep in northern elephant seal pups, the heart rate usually became irregular, which is normal in sleeping mammals (17). The variable heart rate in REM in most mammals, however, is thought to be due in part to associated changes in respiration (9). Clearly, this is not the case for northern elephant seals, since respiration ceases completely before entry into REM.

In contrast to humans, prolonged and repetitive sleep apnea is a normal event in these seals, not a potentially pathological syndrome. In seals, sleep may lower metabolic rate to the point at which continuous ventilation is no longer required to meet their metabolic needs, in which case, these apneas would be adaptive. A somewhat similar situation may arise in obese humans who display hypometabolic states. Although most sleep apneas in these individuals are obstructive, many of these are secondary to an initial central apnea (i.e., a mixed apnea) (6, 8, 16). The prolonged central apneas in the elephant seals may simply be an analogous extension of these normal events.

In conclusion, the northern elephant seal pup spends most of its sleep time apneic and thus may represent an extremely useful model for the study of central sleep apnea and its underlying mechanisms. We have found that the seals need not awaken to breathe, ventilation never occurs during REM sleep, and the apneic heart rate is similar to the minimal heart rate of the normal eupneic sinus arrhythmia. While changes in sleep duration and pattern occur in animals sleeping in water, there were no significant differences in the major cardiorespiratory variables regardless of whether seals sleep underwater or on land.

This work was supported by grants from the National Institutes of Health (M. Castellini), the National Sciences and Engineering Research Council of Canada (W. Milsom and D. R. Jones), and the British Columbia and Yukon Heart and Stroke Foundation (D. R. Jones).

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Received 12 April 1993; accepted in final form 27 July 1993.

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