Development of Cardiorespiratory Patterns Associated with Terrestrial Apneas in Free-Ranging Southern Elephant Seals

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Accepted 7/6/98

ABSTRACT

Elephant seals resting on land show an irregular breathing pattern that combines periods of eupnea and apnea. In this article we describe ontogenetic changes in the breathing pattern and in the associated cardiac response in resting pups and weanlings of the southern elephant seal, *Mirounga leonina*. Apnea duration and the percentage of time spent in apnea were positively correlated with age: mean apnea length was greater in weanlings than in pups, with weanlings holding their breath for up to 8.7 min. Apnea length was not correlated with the duration of preceding or subsequent eupneas. The heart rate of pups and weanlings on land followed the pattern of bradycardia during apnea and tachycardia during eupnea. Young weanlings had a significantly smaller decrease in heart rate during apnea than older weanlings (28% vs. 36%). The instantaneous heart rate response to breathing changed from a variable to a regular pattern. These results suggest that the control processes that modulate the physiological cardiorespiratory changes necessary for diving start to develop on land during the first 11 wk of life.

Introduction

During the terrestrial phase of their annual cycle, elephant seals, *Mirounga* sp., have the most irregular breathing pattern of all phocids (Blackwell and Le Boeuf 1993). While resting on land, they combine periods of breathing (eupnea) with breath holds (apnea) that may last several minutes (Bartholomew 1954; Hubbard 1968; Kenny 1979; Huntley 1984; Castellini et al. 1986, 1994*a*, 1994*b*; Blackwell and Le Boeuf 1993; Castellini 1994).

Blackwell and Le Boeuf (1993) described developmental changes in the breathing pattern of northern elephant seals, *Mirounga angustirostris*, from neonates to adults. They reported that the length of resting apneas and the percentage of time spent in apnea increase steadily from suckling pups to adults. Eupnea duration decreases during the preweaning period, after which it increases in length until adulthood. Quantitative data for comparison with the southern elephant seal, *Mirounga leonina*, are lacking (but see Kenny 1979).

The physiological correlates of the breathing pattern of elephant seals are also poorly known. Castellini et al. (1986) reported that hematocrit values increase in pups as soon as apnea begins and then decrease during ventilation. Blood oxygen declines to low levels and CO_2 increases. However, stable levels of lactate and glucose before, during, and after apnea suggest an aerobic metabolism during breath-holding periods (Castellini et al. 1986; Castellini 1994). The typical cardiac response to terrestrial apnea is a marked bradycardia. A 34% reduction in heart rate during apneas was reported in weanlings of the northern elephant seal in natural conditions (Blackwell 1996), and a 33% decrease was described for restrained pups (Huntley 1984). Juveniles of the northern elephant seal showed a similar cardiac response to both diving and terrestrial apneas (Andrews et al. 1997). However, although the heart rate while the animals were diving was inversely correlated with the duration of the dive, there was no relationship between the heart rate and the duration of the apnea on land. This suggests that the cardiovascular adjustments that occur at sea are an important response to the dive rather than to the apnea (Andrews et al. 1997).

At birth, elephant seal pups do not have a regular cardiac response associated with their breathing pattern (Castellini et al. 1994*b*). Castellini et al. (1994*b*) studied the cardiorespiratory patterns associated with resting apneas in northern elephant seals from birth to weaning. They found that the heart rate of neonates is variable or remains high during apnea and eupnea, suggesting that elephant seals are not born with the cardiac control associated with breath holding. Apnea duration increases with age and is accompanied by a stable heart rate pattern and a well-developed sinus arrhythmia (Castellini et al. 1994*b*).

We studied the ontogenetic changes in the breathing pattern and in the associated cardiac response to breathing in free-

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Physiological and Biochemical Zoology 72(1):64–70. 1999. 1522-2152/99/7201-9761$03.00

ranging southern elephant seal pups and weanlings resting on land. We focused on the cardiac correlates to terrestrial apneas and eupneas, particularly in the degree of cardiorespiratory synchrony. We show that, as the length of apneas increased with age, the heart rate response changed into a regular, rhythmic pattern. This study involved a critical period for the development of elephant seal pups, during which individuals undergo physiological and behavioral changes essential for their pelagic life.

Material and Methods

This study was conducted at Punta Delgada, Península Valdés, Argentina, during three breeding seasons (September–December 1994–1996). Studied animals were known-age individuals marked at birth with a bleaching agent and tagged after weaning with serially numbered plastic tags. Only observations of individuals resting on land that did not show any evidence of disturbance were included in the calculations. Each marked individual was sampled once.

We describe the breathing pattern and parameters (apnea and eupnea length, ventilatory rate, and percentage of time spent in apnea), and the cardiac response to ventilation in free-ranging, resting elephant seals from birth to the end of the postweaning fast (approximately 80 d after birth).

Breathing Parameters and Pattern

Breathing was studied in 142 animals (41 preweaning pups and 101 weanlings). Pups were categorized as neonates (1–4 d old; $n = 22$) and suckling individuals (5–23 d old; $n = 19$; Blackwell and Le Boeuf 1993). Weanlings from Patagonia spend a maximum of 80 d at the beach before their first pelagic trip (V. Falabella, unpublished data). On the basis of the length of the weaning period, weanlings were categorized as younger (24–40 d old; $n = 39$) and older (50–80 d; $n = 46$). For a better differentiation between weanling categories, individuals 41–49 d old ($n = 16$) were not included in the calculations except for correlation analyses.

"Apnea" was defined as a period of time during which the animal remained with its nostrils closed for more than 30 s. We recorded breathing activity of only those animals that were resting on land and apparently sleeping. As we do not have any hard evidence that these animals were asleep, we will refer to breath holds as resting apneas. "Eupnea" was the part of the breathing phase when the animal opened and closed its nostrils regularly. Breathing parameters were calculated on the basis of two consecutive apneic-eupneic cycles for each individual (see Blackwell and Le Boeuf 1993). The ventilatory rate was defined as number of exhalations per minute during eupnea. The breathing pattern was described from a sequence of apneas and eupneas lasting on average 29 min (SD = 7 min). The length of the eupnea preceding and following long apneas was compared to the mean eupnea duration for each age category. Long apneas were defined as those that were at least 1 SD longer than the mean for that age category. The proportion of preceding and subsequent eupneas that were longer than the mean for each age category were tested with chi-square comparisons (χ^2).

Cardiac Response to the Breathing Pattern

We studied apneic and eupneic heart rate, heart rate stability during apnea (measured as the variance of the instantaneous heart rates recorded during an apnea), and the transition periods from apnea to eupnea and vice versa. We monitored the heart rate during at least one complete apneic and eupneic cycle for six resting neonates, nine suckling pups, and 46 weanlings (16 young, 21 older, and nine of intermediate age, with the latter only included in correlation analyses).

A custom-made heart rate monitor was deployed to record heartbeats by means of a differential amplifier and an R-wave peak detector. The detector identified the R-wave of the QRS complex and generated a 0.1-s audio tone. Each tone was recorded with a tape recorder. The tape registered the heartbeats and the voice of the observer describing the breathing pattern in separate channels. The accuracy of the heart rate monitor was tested with a simultaneous register of EKG (electrocardiogram) in humans.

The leads of the monitor were placed and held gently by hand on the surface of the fur on both sides of the thorax (beside the flippers) of animals that were resting on the shore. The lead area in contact with the animal's fur was wetted with electrode gel. Records were analyzed using a computer interface to calculate instantaneous heart rates (beats per minute as estimated from the time between two heartbeats). A specially designed software program allowed storage of instantaneous heart rate associated with the breathing phase (apnea or eupnea). We tested the accuracy of the software that measure instantaneous heart rate using a tape with standardized rates of 30, 60, and 120 beats min^{-1}. The accuracy was close to 100% for the three rates.

The instantaneous heart rates recorded during one complete cycle of apnea and eupnea were used to calculate mean apneic and eupneic heart rates and the decreasing heart rate percentages between eupnea and apnea for each individual (measured as the percent difference between the mean instantaneous heart rate during eupnea and apnea).

The stability of the heart rate during apneas was described using the variance (mean sum of squares [MSS]) in instantaneous heart rates. We defined a cardiac rhythm during apnea as stable when the variance in instantaneous heart rates was less than 50. Variances larger than 50 were associated with unstable rhythms. The transitions of apnea-eupnea and eupnea-apnea were categorized as either abrupt or gradual. In abrupt transitions the mean instantaneous heart rates during the last and first 10 beats of each event differed by more than 20 beats min^{-1}. Differences of 20 beats min^{-1} or less were considered gradual transitions. Anticipatory tachycardia was described as an abrupt increase in heart rate immediately preceding the first breath (Thompson and Fedak 1993).

Results

Breathing Parameters and Pattern

The length of resting apneas on land was (*a*) negatively and significantly correlated with age during the entire suckling period (i.e., from birth to weaning; Spearman $r = -0.52$, $n = 39$, $P < 0.01$) and (*b*) positively and significantly correlated during the entire weaning period (Spearman $r = 0.52$, $n = 103$, $P < 0.01$; Fig. 1*a*). During the first weeks of life, neonates showed apnea 1.7 times longer than suckling pups (Mann-Whitney $U = 60$, $P < 0.01$). After this initial drop, apneas increased steadily during the rest of lactation and the postweaning fast. Weanlings had apneas 2.7 times longer than those of pups (Table 1; Mann-Whitney $U = 173$, $P < 0.01$). Older weanlings held their breath for periods of up to 8.7 min and had the longest mean apneas of all age categories (Table 1). Apnea length increased by 4.3 times between the ages of suckling pups and old weanlings.

Eupnea length did not correlate significantly with age (Spearman $r = -0.14$, $P > 0.05$). Median eupnea length for suckling pups was 2.1 min, compared with 2.6 min for older weanlings (Table 1; Kruskal-Wallis test $H(3,\ n = 126) = 6.68$, $P > 0.05$).

Ventilatory rate was negatively correlated with age (Fig. 1*b*). Neonates had a mean ventilatory rate of 20 breaths min^{-1}, compared with 14 breaths min^{-1} in older weanlings (Table 1; for pups vs. weanlings, Mann-Whitney $U = 324$, $P < 0.01$).

The length of apneas was not associated with the preceding or subsequent eupneas in any of the age categories (chi-square tests for preceding and subsequent eupneas, respectively: neonates, $\chi^2 = 0.33$ and 3.0; suckling pups, $\chi^2 = 3.57$ and 0.14; young weanling, $\chi^2 = 3.00$ and 0.22; older weanlings, $\chi^2 = 0.53$ and 0.53; $P > 0.05$).

Intraindividual variability in the duration of eupneas decreased as the animal matured (Fig. 2). Consequently, as eupnea length became more constant, the breathing pattern was more regular (Fig. 2, *inset*). Intraindividual variance in apnea duration was constant for all age categories (Fig. 2).

There was no sex difference in any of the breathing variables reported above (Mann-Whitney *U*, $P > 0.05$).

Cardiac Correlates to the Breathing Pattern

The heart rate followed the pattern of bradycardia during apnea and tachycardia during eupnea in all age classes (Table 1; *t*-test for mean apneic heart rate vs. mean eupneic heart rate: neonates, $t = -3.26$, df = 10; suckling pups, $t = -6.44$, df = 16; young weanlings, $t = -6.82$, df = 30; older weanlings, $t = -11.81$, df = 40; $P < 0.01$; Fig. 3). The heart rate during apnea was significantly higher in pups than in weanlings (Table 1; $t = 9.17$, $P < 0.001$, df = 59) and in young weanlings than in older ones ($t = -2.05$, $P < 0.05$, df = 35). The lowest instantaneous heart rate recorded (15 beats min^{-1}) occurred in a 76-d-old weanling during an 8-min-long apnea. The percentage decrease in heart rate from eupnea to apnea was negatively correlated with age (Spearman $r = 0.61$, $P < 0.01$; Table 1). The heart rate in pups dropped 18% between eupnea and apnea compared with a drop of 32% in weanlings (Table 1; *t*-test of percentage decrease in heart rate from eupnea to apnea in pups vs. weanlings, $t = -5.50$, $P < 0.01$, df = 59). Weanlings showed a significant decrease in heart rate between eupnea and apnea, which was significantly larger in older than in young weanlings (36% vs. 28%; $t = -2.72$, $P < 0.01$, df = 35; Table 1).

The heart rhythm during eupnea followed one of two patterns: decreasing or constant instantaneous heart rate (Fig. 4). Pups showed both patterns, but the decreasing pattern was most common in weanlings (Fig. 4). The heart rate during eupnea was higher in pups than in weanlings (Table 1; $t = -6.41$,

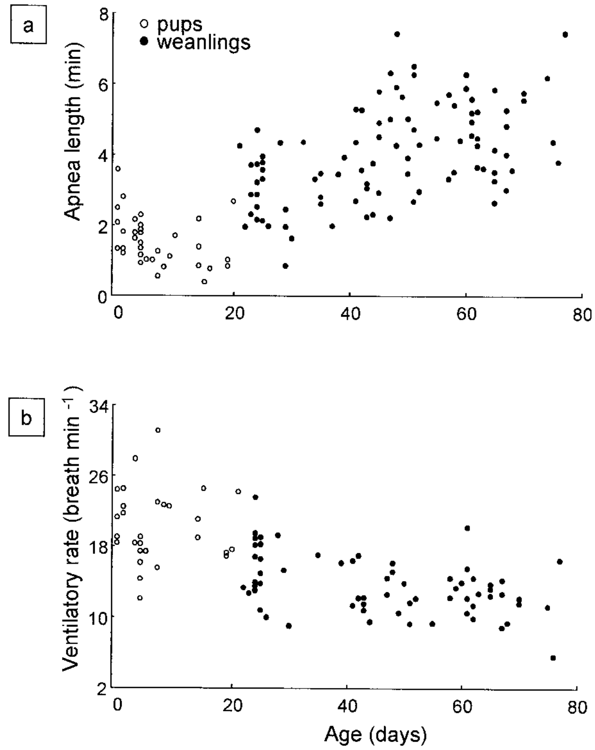

Figure 1. Development of breathing parameters as a function of age for 142 individuals (0–80 d postpartum). *a*, Length of apnea (pups: Spearman $r = -0.52$, $n = 39$, $P < 0.01$; weanlings: Spearman $r = 0.52$; $n = 103$; $P < 0.01$). *b*, Breathing rate during eupnea (Spearman $r = -0.67$; $P < 0.01$).

Table 1: Breathing and cardiac parameters as a function of age categories

	All Pups (0–23 d)	Neonates (0–4 d)	Suckling (5–23 d)	All Weanlings (24–80 d)	Young (24–40 d)	Old (50–80 d)
Breathing parameters:						
Sample size	41	22	19	101	39	46
Apnea length (min)	1.48 ± .69	1.84 ± .59	1.07 ± .57	3.98 ± 1.34	3.06 ± .91	4.64 ± 1.12
Time spent in apnea (%)	33 ± 14.40	36.38 ± 14.90	29.49 ± 14.97	58 ± 13.75	49.44 ± 13.80	64.19 ± 10.36
Eupnea length (min)	2.78	3.29	2.07	2.65	2.87	2.60
Ventilatory rate (breaths min^{-1})	19.83 ± 4.32	18.99 ± 4.27	20.85 ± 4.32	13.95 ± 3.58	16.35 ± 3.70	12.23 ± 2.64
Cardiac response:						
Sample size	15	6	9	46	16	21
Heart rate:						
Apnea	89.07 ± 7.89	85.08 ± 8.94	91.74 ± 6.24	61.17 ± 9.62	64.29 ± 10.54	57.92 ± 7.82
Eupnea	109.54 ± 9.78	104.57 ± 11.05	112.85 ± 7.79	90.30 ± 9.52	89.67 ± 10.32	89.80 ± 9.67
Decrease in heart rate from eupnea to apnea (%)	18.38 ± 6.81	18.40 ± 6.03	18.37 ± 7.64	31.93 ± 8.69	28.48 ± 7.67	36.16 ± 7.18

Note. Mean ± 1 SD, except for eupnea length (median). Mann-Whitney tests for pups versus weanlings for breathing parameters showed significant differences ($P < 0.01$), except for eupnea length ($P > 0.05$). t-tests for cardiac parameters showed significant differences between pups and weanlings ($P < 0.01$).

$P < 0.001$, $df = 59$), but no significant difference was found between neonates and suckling pups ($t = -1.69$, $P > 0.05$, $df = 13$) or between young and older weanlings ($t = 0.07$, $P > 0.05$, $df = 35$). When the heart rate during eupnea was estimated according to the pattern of the heart rhythm we found: (*a*) for a constant heart rhythm, mean eupneic heart rate was 107.10 ± 10.81 beats min^{-1} for pups ($n = 8$) and 92.70 ± 11.85 beats min^{-1} for weanlings ($n = 8$); and (*b*) for a decreasing heart rhythm, the mean heart rate during the first 30 s of the recorded eupnea was 113.18 ± 7.23 beats min^{-1} for pups ($n = 7$) and 99.17 ± 8.99 beats min^{-1} for weanlings ($n = 29$). For the last 30 s of the eupnea, mean heart rate was 105.59 ± 11.37 beats min^{-1} for pups ($n = 7$) and 78.05 ± 9.61 beats min^{-1} for weanlings ($n = 29$). There was no difference in the heart rate registered during the first and last 30 s of decreasing eupneas between neonates and suckling pups, or between young and older weanlings. There was no sex difference in the cardiac parameters associated with the breathing pattern (t-tests, $P > 0.05$).

The variance of all instantaneous heart rates during an apneic event decreased as a function of age. Consequently, older weanlings had a more stable cardiac response to apnea than young weanlings and pups (Figs. 3, 4). During the apnea-eupnea transition, the heart rate increased gradually in pups and abruptly

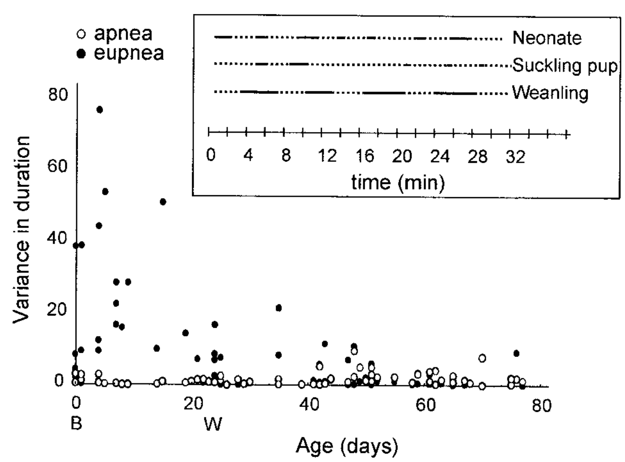

Figure 2. Variance in apnea and eupnea duration and changes in the breathing pattern as a function of age (*B*, birth; *W*, weaning). Each data point represents the variance of all recorded apneas and eupneas for one individual. The breathing pattern (*inset*) is illustrated by one representative sample per age category (*filled lines*, apneas; *dotted lines*, eupneas).

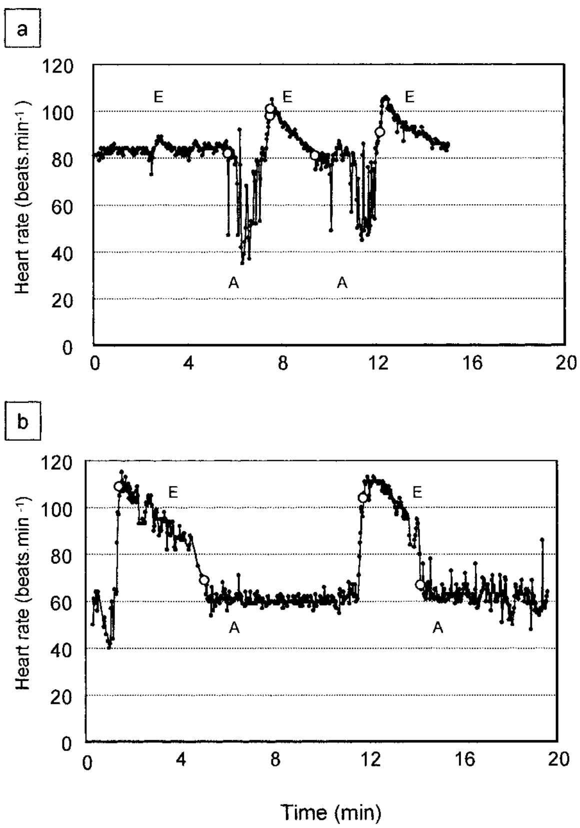

Figure 3. Instantaneous heart rate plotted against time in a 14-d-old suckling pup (*a*) and a 60-d-old weanling (*b*). Open circles point out the change of breathing event (*A*, apneas; *E*, eupneas).

in weanlings (Fig. 4). The inverse transition (eupnea-apnea) was also gradual for pups, but no trend was apparent in weanlings (Fig. 4).

Heart rate during apnea was not correlated with the length of the apnea in any age category.

Sinus arrhythmia, in which the heart rate increased during inhalation and decreased as the animal exhaled, was found in four of 46 weanlings. The heart rate in these animals varied from a high of about 100 beats min^{-1} to a low of about 40 beats min^{-1}, with a mean heart rate of 75 beats min^{-1} during eupnea.

We observed a steep increase in heart rate before the eupnea in 33% of the animals. The heart rate increased from a mean of 56 beats min^{-1} to 86 beats min^{-1} up to 55 s before the initiation of eupnea (23.27 ± 11.16 s).

Discussion

The breathing parameters and the ontogenetic changes of southern elephant seals while on land and during early stages of development were similar to those reported for their northern counterpart. Apnea length increased and eupnea length and breathing rate decreased with age in both species (Bartholomew 1954; Kenny 1979; Blackwell and Le Boeuf 1993; Castellini et al. 1994*b*; V. Falabella, unpublished data).

In neonates and suckling pups, the breathing pattern was an irregular combination of apneas and eupneas of variable length. Weanlings had a regular and stable periodic pattern with extended apneas and short eupneas.

No correlation was found between the length of apneas and the duration of the preceding or subsequent eupnea for pups and weanlings. Similar findings were previously reported in the northern elephant seal for different age categories (Hubbard 1968; Castellini 1994; Andrews et al. 1997; but see Huntley 1984). The previous mentioned findings are in agreement with the lack of correlation between dive duration and time spent at the surface breathing before or after a dive (Le Boeuf et al. 1996). On the basis of correlates of blood and cardiovascular parameters of breath holding on the surface and during diving, Blackwell and Le Boeuf (1993) and Castellini (1994) conclude that breath holding during resting and diving apneas may have a common physiological basis.

The heart rate of free-ranging pups and weanlings on land followed the pattern of bradycardia during apnea and tachycardia during eupnea typical of diving phocids (Kooyman 1985). Bartholomew (1954) first noted a decrease in heart rate in sleeping adult elephant seals. His observations were later confirmed in natural conditions and in captivity (Hubbard 1968; Kenny 1979; Huntley 1984; Blackwell and Le Boeuf 1993; Castellini 1994; Castellini et al. 1994*b*).

We confirmed the results of Castellini et al. (1994*b*) in that the level of bradycardia in resting pups is age related, and that older weanlings have a steadier heart rate during apnea than younger animals. We differ from Castellini et al. (1994*b*) in that we found a mild bradycardic response in newborn pups. Neonates showed a lower heart rate associated with apnea, and this pattern was accentuated in weanlings.

Two additional changes in heart rate associated with apneustic breathing are worth noting: sinus arrhythmia and anticipatory tachycardia. Sinus arrhythmia was absent in northern elephant seal neonates but developed quickly in pups even before weaning (Castellini 1994; Castellini et al. 1994*b*). Weanlings had a well-developed pattern of sinus arrhythmia (Castellini 1994; Castellini et al. 1994*b*). On the basis of this fact, it was suggested that the bradycardia associated with resting apnea is actually the low heart rate of a normal respiratory cycle and that the apnea is just a long breath pause, at least in terms of cardiac control (Castellini 1994). We were unable to identify sinus arrhythmia in most of our animals. Only a few weanlings showed an increase in heart rate during eupnea followed by sinus arrhythmia by the end of the eupnea. This result may be because of variations in methodology. We analyzed two consecutive apnea-eupnea cycles for each individual. In these cycles, eupneas were always short, and the heart rate during this

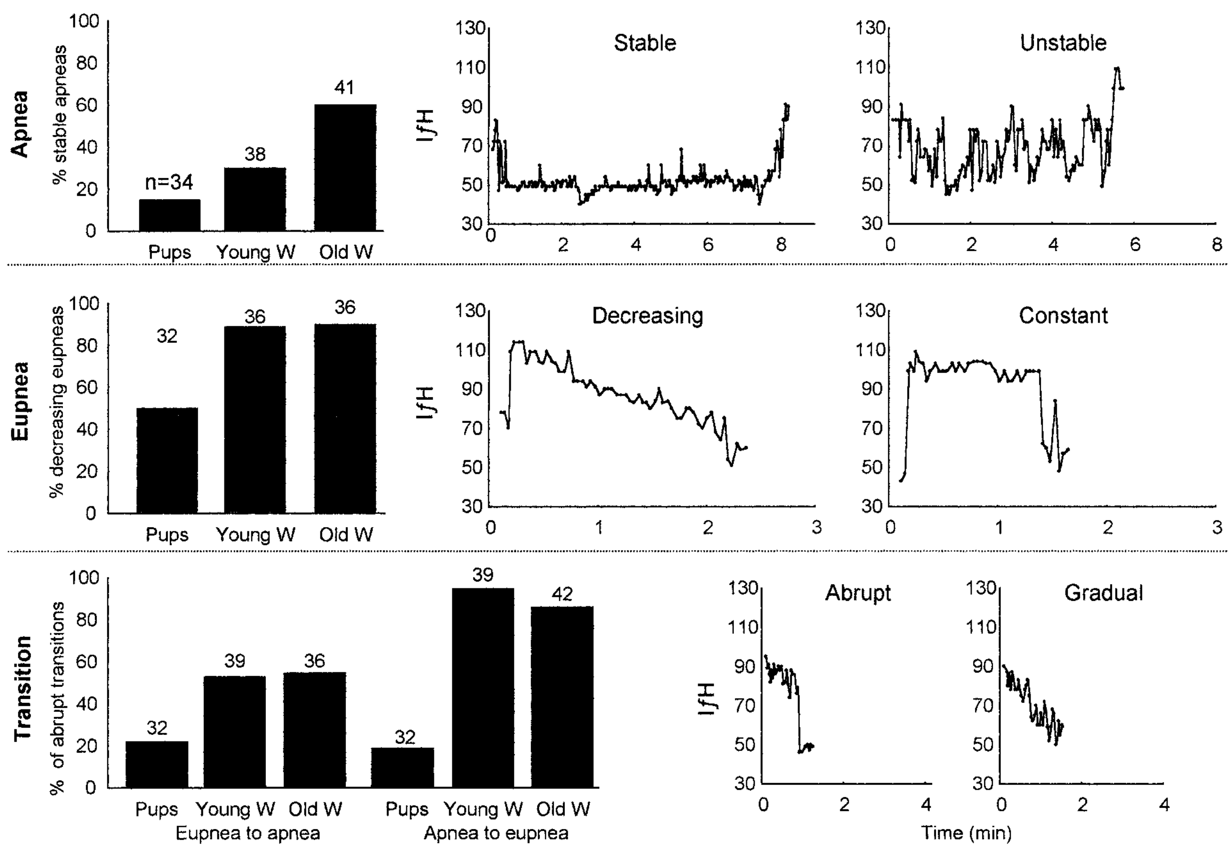

Figure 4. Frequency distribution of cardiac patterns for three age categories (n = 14 pups, 16 young weanlings [W], and 20 old weanlings), and illustrations of different heart rhythms during apnea, eupnea, and transition periods of the ventilatory cycle. The number above each bar indicates sample sizes of all events registered.

period reflected a recovery phase from the previous apnea. We rarely saw long eupneas in which the heart rate became stable. It is possible that after an extended apneic period the recovery tachycardia would conceal the normal sinus arrhythmia (M. A. Castellini, personal communication). The clearest phenomenon of sinus arrhythmia observed in this study occurred in a resting weanling that showed a eupnea of 11 min. Even though neonates and suckling pups showed extensive eupneas (up to 13 min), sinus arrhythmia was not observed.

Anticipatory tachycardia was described in diving harbor seals (*Phoca vitulina*), grey seals (*Halichoerus grypus*), and Weddell seals (*Leptonychotes weddelli*) by Fedak et al. (1988), Thompson and Fedak (1993), and Hill et al. (1987). Hill et al. (1987), in their study of Weddell seals, observed a steep increase in heart rate up to 1 min before surfacing and even before the animal started swimming to the surface. This cardiac response may be related to a removal of residual oxygen from the blood prior to breathing, increasing oxygen uptake and decreasing time spent at the surface (Thompson and Fedak 1993). We observed a steep increase in heart rate before the eupnea in 33% of resting pups and weanlings. Such an increase is reminiscent of the anticipatory tachycardia described for seals during diving (Fedak et al. 1988; Thompson and Fedak 1993), despite the fact that our animals were not constrained to decrease the length of eupneas to minimize time at the surface.

Heart rate rhythm during eupnea was mostly decreasing in weanlings. Ventilatory tachycardia at the beginning of eupnea would allow a fast gas exchange. Thus, the decrease in heart rate may be a consequence of a return to the normal blood oxygen levels.

Our results suggest that the control processes that modulate the physiological cardiorespiratory changes that occur during diving developed on land during the first 11 wk of life, before the first foraging trip. The breath-holding capabilities increased 2.7 times, while eupnea length remained similar to birth levels. Consequently, the absolute time in apnea increased significantly. The breathing pattern also showed ontogenetic changes. As the animals matured, consecutive eupneas became progressively regular, while consecutive apneas remained similar in length, turning breathing into a stable sequence of long breath holds followed by short ventilatory events. The heart responded with the pattern of apnea bradycardia and eupnea tachycardia typical of all phocids during diving, and the heart rate remained stable throughout the apnea. These physiological adaptations set the functional basis for a successful foraging behavior.

This work with animals in natural conditions confirms the results of Castellini et al. (1994*b*), who found that pups must make certain physiological adaptations in order to sustain deep and long dives. Long apneic duration is correlated with heart rate control so that young elephant seal pups have neither the tolerance for voluntary long apnea nor the cardiac control that would be necessary to sustain a long dive (Castellini et al. 1994*b*). By the time animals were ready for their first pelagic excursion, they were capable of long apneas associated with a stable bradycardic response. In a period of about 2.5 mo of life, young elephant seals modified their breathing and cardiac parameters to a point that, on the basis of data from the northern species (Blackwell and Le Boeuf 1993; Thorson and Le Boeuf 1994; Andrews et al. 1997), brought them close to the capabilities of juveniles that had already survived their first trip to sea.

Acknowledgments

This project was supported by the Consejo Provincial de Ciencia y Técnica de la Provincia del Chubut. We thank Ing. J. Digniani for building the heart rate monitor and the software used during the fieldwork; Dr. Susanna Blackwell, Dr. Michael Castellini, and an anonymous reviewer for comments on the manuscript; C. Ramirez and C. Villegas for field assistance; Dirección de Fauna and Organismo Provincial de Turismo de Chubut for permits to work at Península Valdés; and E. Prado, E. Olazabal, Universidad Nacional de la Patagonia, and Centro Nacional Patagónico for logistical support.

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