

THE CONTRIBUTION OF NASAL
COUNTERCURRENT HEAT EXCHANGE TO WATER
BALANCE IN THE NORTHERN ELEPHANT SEAL,
MIROUNGA ANGUSTIROSTRIS

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SUMMARY

1. Elephant seals fast completely from food and water for 1–3 months during terrestrial breeding. Temporal countercurrent heat exchange in the nasal passage reduces expired air temperature (T_e) below body temperature (T_b).
2. At a mean ambient temperature of 13.7°C, T_e is 20.9°C. This results in the recovery of 71.5% of the water added to inspired air.
3. The amount of cooling of the expired air ($T_b - T_e$) and the percentage of water recovery varies inversely with ambient temperature.
4. Total nasal surface area available for heat and water exchange, located in the highly convoluted nasal turbinates, is estimated to be 720 cm² in weaned pups and 3140 cm² in an adult male.
5. Nasal temporal countercurrent heat exchange reduces total water loss sufficiently to allow maintenance of water balance using metabolic water production alone.

INTRODUCTION

Northern elephant seals, *Mirounga angustirostris* (Gill), are exceptional among pinnipeds in the duration of their terrestrial breeding fast. During this time, they voluntarily forgo both food and water while remaining active on the rookery. The length of these fasts varies with age, sex and social status. Bulls may fast 3 months while vigorously defending a harem (Le Boeuf & Peterson, 1969), while females fast for 5 weeks prior to and during nursing (Le Boeuf, Whiting & Gantt, 1972). Following weaning, pups fast 8 to 12 weeks before departing from the rookery (Reiter, Stinson & Le Boeuf, 1981). During this time, total water loss does not exceed metabolic water production (MWP) (Ortiz, Costa & Le Boeuf, 1978). Ortiz *et al.* (1978) suggested that respiratory evaporation represents the predominant avenue of water loss and that 'the

complex turbinate processes in the nasal passages of pinnipeds may function as countercurrent heat exchanger, thereby reducing respiratory water loss'.

Cooling of expired air results in a significant reduction in respiratory evaporative water loss in several terrestrial vertebrates (Jackson & Schmidt-Nielsen, 1964; Collins, Pilkington & Schmidt-Nielsen, 1971; Schmid, 1976; Langman, Maloiy, Schmidt-Nielsen & Schroter, 1979; Schmidt-Nielsen, 1981). In temporal countercurrent heat exchange, the nasal lining is cooled by convection and evaporation upon inhalation, which results in heating and saturation of incoming air. During exhalation, air saturated with water at body temperature (T_b) passes over this cooled lining, losing heat and water. The relative decline in expired air temperature (T_e), and hence the quantity of water recovered, is a function of the geometry and temperature of the surfaces available for heat exchange. In animals where water recovery *via* temporal nasal countercurrent exchange is high, this area is large (Collins *et al.* 1971).

Few studies of nasal heat exchange in marine birds and mammals have been undertaken. In penguins, 82% of the water and 83% of the heat added to ambient air are recovered upon exhalation (Murrish, 1973); in two species of porpoise T_e falls below T_b (Coulombe, Ridgway & Evans, 1965).

In the present study we investigated temporal nasal countercurrent heat exchange in the northern elephant seal by analysis of nasal morphology, measurement of nasal mucosal temperature gradients and expired air temperatures. These data yield an estimate of the contribution of countercurrent exchange to overall water economy in this species.

MATERIALS AND METHODS

Nasal morphology

Measurements of heat exchange surface area and the smallest and largest widths were made on 20 separate, sectioned turbinate structures taken from 10 skulls of weanlings and of an adult male skull. The total surface area of a single turbinate was estimated by photographing each end of 1-cm serial cross sections. Each photograph was then enlarged 10 \times . The length of the total exposed cross-sectional surfaces was estimated by tracing their outlines with a rolling map measure (Keuffel & Esser Co). Each sectional area was calculated by multiplying the mean of the total cross-sectional lengths of a section by the section length (1 cm). The total area of the turbinate was estimated as the sum of the section areas.

Nasal temperature gradient

Eight weanling elephant seal pups were collected at Ano Nuevo State Reserve and transported to the Long Marine Laboratory at the University of California, Santa Cruz, where all laboratory measurements were made on resting, restrained animals.

The temperature gradient within the nasal capsule was measured on two animals at $T_a = 15^\circ\text{C}$ and at $T_a = 5^\circ\text{C}$, near the low temperature normally encountered in the natural habitat. A 30-gauge copper-constantan thermocouple, attached to a 26-gauge stainless steel stiffening wire, was threaded into the nasal cavity and temperatures were recorded at 1-cm intervals for approximately 10 cm using a Bailey Model 3 telethermometer.

Expired air temperature

Field measurements of expired air temperatures were made on 27 animals at Ano Nuevo State Reserve, California, from February through May: four adult males, five subadult males, three adult females and 15 juvenile or weaned pups.

Exhaled air and body temperatures were measured with copper-constantan thermocouples calibrated against a mercury thermometer to $\pm 0.1^\circ\text{C}$. Ambient temperatures and relative humidity (RH), measured with a sling psychrometer or dial reading hygrometer, were recorded at the beginning and end of each observation period.

Weanlings and juveniles were restrained manually during measurements (Pernia, Hill & Ortiz, 1980). The nasal probe was inserted 1 cm into the nasal cavity, in the air stream, where the temperatures of ten or more expirations were recorded. Measurements obtained from restrained and unrestrained animals were not significantly different. Body temperature was measured by inserting the rectal probe approximately 20 cm into the anus.

Temperature of expired air in unrestrained adults was recorded using a thermocouple threaded into a 0.6 m length of rigid polyethylene tube (1 mm diameter) with the distal 1 cm exposed. The temperature of 10 or more expirations was measured in each animal.

In the laboratory, a series of similar recordings was made on each of eight weanlings at ambient temperatures between 1.2 and 17°C.

Respiratory flow

Mean respiratory flow was measured in three animals (average weight: 97.8 kg). Each animal was restrained with its head in a plastic hood. Flexible neoprene provided an airtight seal around the neck. One-way valves were used on the incurrent and excurrent port. To test for consistency, gas volumes were measured in one of two ways, using a Singer volume meter. In the first experiments, 5-min samples from the excurrent port were trapped in an 80-l Douglas bag equipped with a tight-fitting gas valve. This volume was subsequently drawn through the meter at approximately 30 l min^{-1} using a vacuum system. In the second method, the entire excurrent flow was routed directly through the Singer meter. Experiments were conducted on all three animals at ambient laboratory temperatures (15–17°C) and on two animals at 5°C. In each case a minimum sample of 1 h was obtained from each animal. For subsequent calculations, volumes were adjusted to expired air temperature, barometric pressure (P_b) of 760 mmHg, and assumed to be saturated. The volume at the point of actual respiratory water loss is most accurately reflected at the expired air temperature, ambient barometric pressure and fully saturated with water (ETPS).

Calculations

The percentage of water recovered by the nasal heat exchange process was calculated using the method of Collins *et al.* (1971):

$$\% \text{ recovery} = (w_b - w_e / w_b - w_a) \times 100,$$

where w_b is the water content of the air in the lung, w_e is the water content of the expired air sample, and w_a is the water content of the ambient inspired air. We

assumed air in the lung was saturated at body temperature and expired air was saturated at T_e . Absolute water content of ambient air was calculated from relative humidity using the equation of state for water vapour:

$$w_a = (2.90)(P_w)(RH)/(273 + T_a),$$

where w_a is the water in the ambient air (absolute humidity) in $\text{g H}_2\text{O m}^{-3}$, RH is the relative humidity and P_w is the vapour pressure of water at T_a . Where body temperatures of individual animals were unavailable, a mean value, 35.8°C , was used (Bartholomew, 1954; McGinnis & Southworth, 1971).

RESULTS

The configuration of the elephant seal nasal passage is complex (Fig. 1). The nasal turbinates provide a very large surface area for exchange of heat and water. The total surface area of both turbinate structures in weanlings is approximately $720 \pm 23 \text{ cm}^2$ (\pm s.d., $N = 20$) and in an adult male this area was estimated to be 3140 cm^2 .

The temperature gradients within the nasal passage of a weanling at 15°C and 5°C are shown in Fig. 2. The distal nasal mucosa is well below core temperature. The temperature rises continuously through the turbinates until T_b is reached.

The expired air temperatures of 35 elephant seals of various ages at T_a values from 1.2°C to 21°C are summarized in Table 1. Expired air temperature increases linearly with T_a (Fig. 3). The cooling of the exhalant stream ($T_b - T_e$) and the percentage water recovery vary inversely with T_a . The efficiency of the system is increased at lower ambient temperatures. At a mean T_a of $13.72 \pm 5.4^\circ\text{C}$ ($N = 35$) the mean water recovery is $71.5 \pm 5.5\%$. At $T_a = 21^\circ\text{C}$, T_e is 7.2°C below T_b and water recovery is 50.7% , while at $T_a = 1.2^\circ\text{C}$, T_e is 21.9°C below T_b and water recovery is 79.1% . Percentage water recovered does not vary significantly with sex, age or restraint.

Mean respiratory flow for all animals under all conditions was $12.2 \pm 4.3 \text{ l ETPS min}^{-1}$. There was no significant difference between respiratory flows at different temperatures.

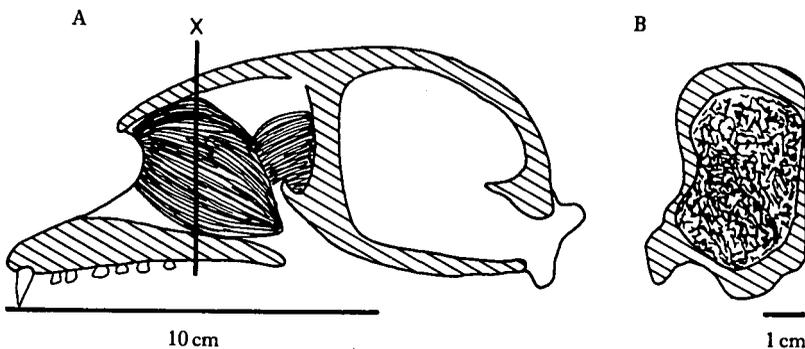


Fig. 1. (A) Sagittal skull section of an elephant seal weanling. (B) Cross section through one half of the skull at the level indicated by line 'X' in drawing A. Black areas indicate turbinate bone.

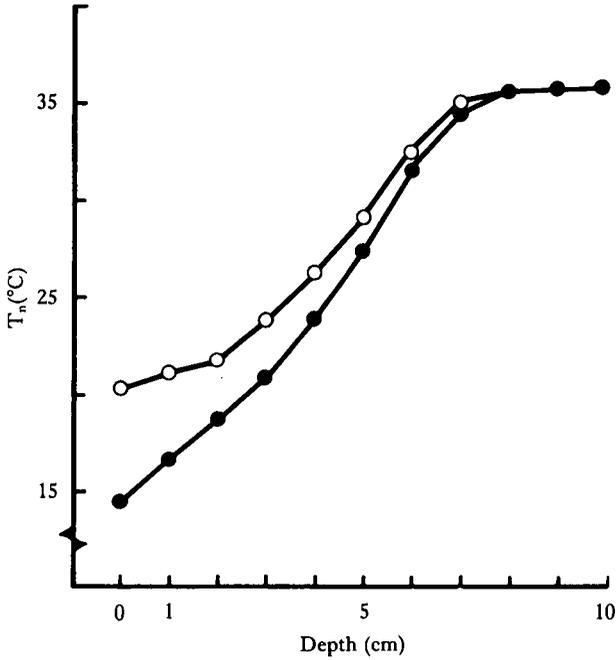


Fig. 2. Temperature (T_n) at 1-cm intervals within the nasal passage of an elephant seal weanling at ambient temperatures of 15°C (open circles) and 5°C (solid circles).

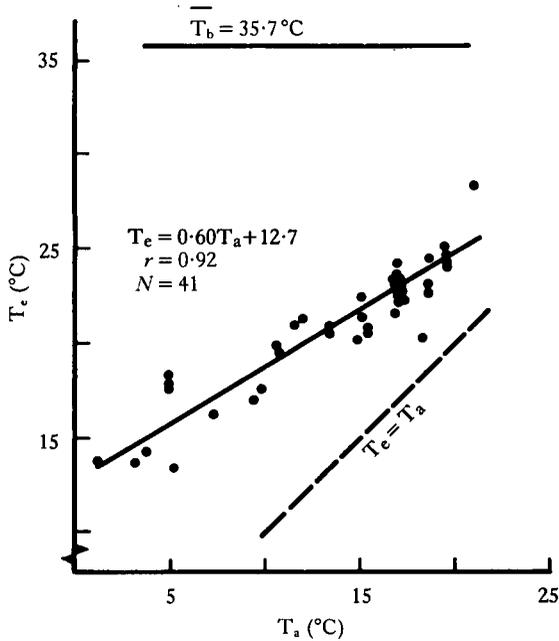


Fig. 3. Temperature of the exhalant air stream (T_e) of the northern elephant seal at different ambient temperatures (T_a). Regression line by least squares method. Dashed line indicates hypothetical case where T_e is cooled to T_a . Solid upper line indicates mean body temperature (T_b) over the indicated T_a range. $T_b = 35.7 \pm 4.5$ ($N = 15$).

Table 1. *Mean parameters for northern elephant seal*

Age class	N	T _a	T _b	T _e	T _b -T _e	w _b	w _e	w _a	% Recovery
Weanlings	22	12.2	35.7	18.7	17.1	41.1	16.0	8.2	71.9 + 4.9
Females and subadult males	9	17.2	35.8*	23.1	12.7	41.2	20.9	11.8	69.1 + 3.6
Adult males	4	16.5	35.8*	21.3	14.5	41.2	18.6	10.8	74.5 + 1.6

T_a=ambient temperature (°C), T_b=body temperature (°C), T_e=expired air temperature (°C), w_b=water content of air in lungs (mg l⁻¹), w_e=water content of expired air (mg l⁻¹), w_a=water content of ambient air (mg l⁻¹).
 All values are means, ± standard deviations where indicated.
 * Body temperatures from Bartholomew (1954), McGinnis & Southworth (1971) and A. C. Huntley & D. P. Costa, unpublished results.

DISCUSSION

Nasal countercurrent heat exchange results in a significant reduction of respiratory evaporative water loss (EWL) in the northern elephant seal. Reduction in T_e and calculated water savings are comparable to those reported for several large and small animals adapted to arid habitats (Jackson & Schmidt-Nielsen, 1964; Collins *et al.* 1971; Langman *et al.* 1978, 1979). When compared to that of other large animals, the relative length of nasal passage in elephant seals is short; however the total turbinate surface area is very large. In weanlings, which have an average weight of 136 kg (Reiter *et al.* 1981), this surface area is 720 cm², which approaches the 1000 cm² area reported for camels (Schmidt-Nielsen, 1981); this same area is approximately 3000 cm² in adult male elephant seals, which weigh in excess of 2000 kg (Sheffer, 1958). On a weight-specific basis, the surface area of the turbinates falls from 5.29 cm² kg⁻¹ in weanlings to 1.57 cm² kg⁻¹ in adult males; however, there are no significant differences in the calculated water recovery. The approximate surface area of the turbinates is related to weight by the following equation:

$$A = (30.2)W^{0.63},$$

where A is the surface area in cm² and W is weight in kg.

The adaptive value of the proposed mechanism is associated with the terrestrial breeding behaviour of elephant seals. Since Ortiz *et al.* (1978) have clearly demonstrated long-term positive water balance in these animals, all avenues of water loss must be reduced to levels below or equal to metabolic water production (MWP). Costa & Ortiz (1980) have shown that respiratory EWL accounts for 65 % of the metabolic water production. The remaining 35 % is lost as urine, faeces and cutaneous evaporation. This low EWL/MWP ratio is comparable to that found among several small, desert endotherms (Bartholomew, 1972; MacMillen, 1972; MacMillen & Grubbs, 1976).

What is the contribution of the described mechanism to overall water balance in a typical weanling? Daily EWL for a 100-kg weanling at 19°C and 68 % RH may be estimated from the calculated water content of the expired air minus the water content of the ambient air and the measured respiratory flow at 730 l_{ETPS} h⁻¹. This calculation yields a loss of approximately 140 ml day⁻¹ as compared to a direct measurement of 209 ml day⁻¹ at similar T_a and RH (Costa & Ortiz, 1980). In the absence of nasa

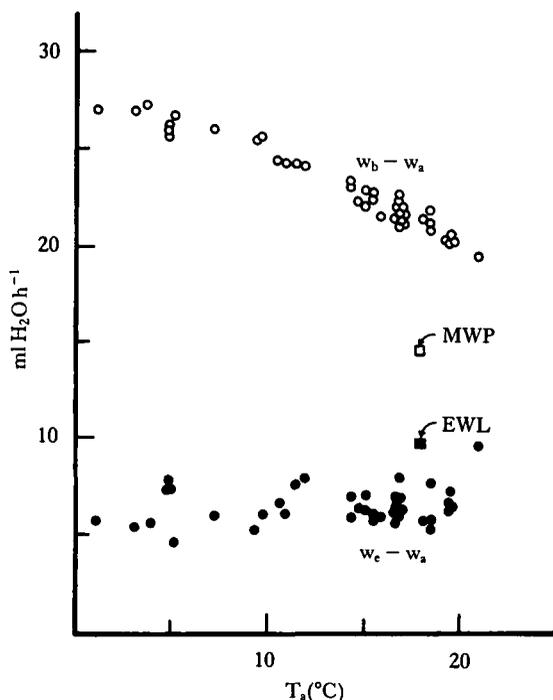


Fig. 4. Comparison of net calculated respiratory water loss ($w_c - w_a$) and net expected water loss ($w_b - w_a$) in the absence of nasal countercurrent mechanism. MWP is the average metabolic water production, EWL is the average evaporative water loss at 19°C (from Costa & Ortiz, 1980).

countercurrent exchange, air exhaled at T_b would contain 534 ml day⁻¹, and thus exceed the available MWP of 326 ml day⁻¹ (Costa & Ortiz, 1980). Under these conditions, maintenance of positive water balance during the prolonged terrestrial fast would be impossible (Fig. 4).

Nasal countercurrent heat exchange is a major factor in the reduction of EWL and maintenance of positive water economy in the northern elephant seal. This mechanism may contribute to water balance in other pinnipeds and perhaps marine mammals in general.

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