Respiratory Water Exchange in Two Species of Porpoise

Abstract. *Measurements of the respiratory water exchanges of* Tursiops truncatus *and* Lagenorhynchus obliquidens *indicate that these species lose, respectively, only 30 and 77 percent as much water through evaporation as would terrestrial mammals of the same body weight. Control of temperature and pressure within the respiratory system and a lower ventilation rate account for this relatively small loss of water.*

We have sought to determine the amounts of water lost through respiration in two species of small cetaceans. Six adult Atlantic bottlenose porpoises, *Tursiops truncatus* (mean weight, 142 kg), and two adult Pacific white-sided porpoises, *Lagenorhynchus obliquidens* (63 and 80 kg), were studied at the cetacean research colony maintained at Point Mugu, California.

During the experiments the porpoises were placed on a hospital stretcher and kept moist with sea water. Rectal temperatures (25 cm depth) were continually monitored with a thermistor probe. Wet- and dry-bulb air temperatures were recorded with a portable thermistor psychrometer (*1*). Measurements inside the respiratory passages were made with a modified otoscope probe placed over the end of the psychrometer barrel (see Fig. 1), and readings were taken during several respiratory cycles. The animals were able to seal their blow holes effectively with the probe in position. A tight-fitting mask with a breathing bag from an anesthesia apparatus was placed over the blow hole to collect expired air, which was immediately measured with the psychrometer. Similar measurements were made of the expired air of three humans.

The relative humidities of the samples were determined from standard psychrometric tables (*2*). Absolute humidities were calculated with the formula

$$H_A = 0.986 \times 10^{-2} (H_R) (P_{ta}) \qquad (1)$$

where the absolute humidity, H_A, is grams of water per cubic meter, H_R is the percentage relative humidity, and P_{ta} is the vapor pressure of water in millimeters of mercury at the dry-bulb temperature.

The temperatures recorded in the upper respiratory tracts of both species of porpoises were about 9°C lower than the mean deep body temperature (mean $T_b = 36.5°C$). Exhaled air was 3.5°C to 4.3°C warmer than inhaled air, but it was about 4.5°C cooler than air in the upper respiratory tract. The relative humidity of residual air in the upper respiratory tract was 95 to 100 percent. We assume that air in the lungs is saturated at deep-body temperature. Inspired air had a mean relative humidity of 75 percent for both species, while expired air had a mean relative humidity of 75 percent in *Tursiops* and 85 percent in *Lagenorhynchus*. The absolute humidities with corresponding temperatures of the air before, during, and after passage through the respiratory tracts of the porpoises are given in Table 1.

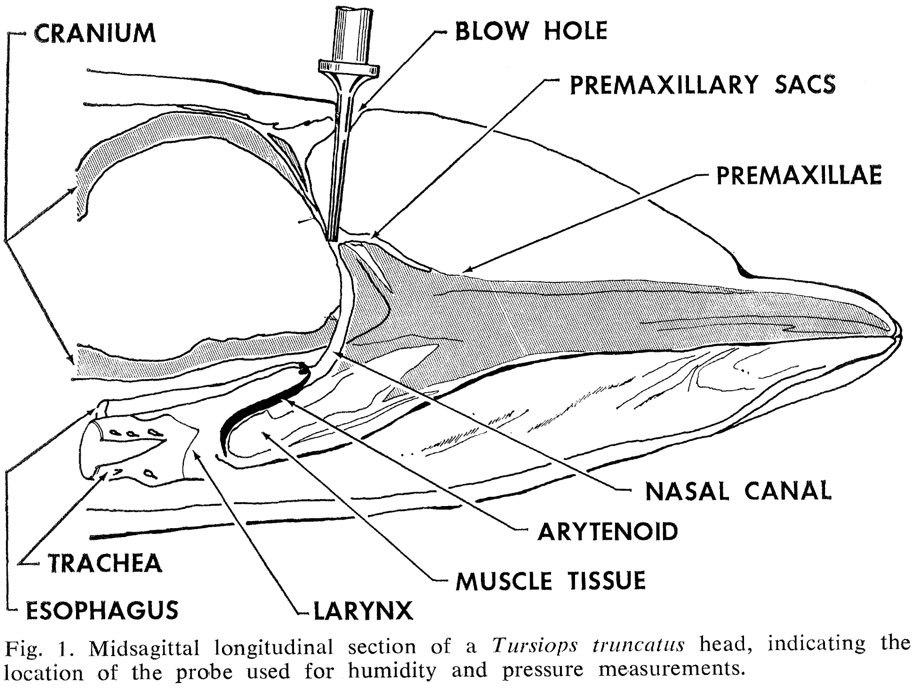

Fig. 1. Midsagittal longitudinal section of a *Tursiops truncatus* head, indicating the location of the probe used for humidity and pressure measurements.

Rates of respiratory water loss (W_L) in grams per day were estimated from the difference in water present in inhaled and exhaled air (Table 1) by using the formula

$$W_L = (\Delta H_A) (V) C \qquad (2)$$

where ΔH_A is the net difference in grams of water per cubic meter between inhaled and exhaled air, V is ventilation rate in liters per minute, and C is m^3 $liter^{-1} \times minute$ day^{-1}. Ventilation rates were determined from tidal volumes taken from Irving et al. (*3*), and breathing rates were determined during our experiments.

At a ventilation rate of 16.4 liters per minute, a 140-kg *Tursiops* would lose about 290 g of water per day if the water content of the exhaled air were the same as that in its air sacs (Table 1). However, under the experimental conditions, only about 60 g of water per day would be lost. Thus it appears that about 80 percent of the water present in the air of the upper respiratory tract was reclaimed prior to exhalation.

The rate of water loss in relation to oxygen consumed can be compared with values for other mammals reported by Schmidt-Nielsen (*4*) by calculating the water loss of *Tursiops* when inhaling dry air. With an oxygen consumption of 0.9 liter per minute (*3*) and a loss of 381 g of water per day in dry air at 19°C, *Tursiops* would lose 0.294 mg of water per milliliter of oxygen consumed. The respiratory water loss of *Tursiops* is considerably lower than evaporative water losses reported in the literature for terrestrial mammals, even those which live in deserts (*2*).

We estimated the respiratory water loss for *Lagenorhynchus*, making the same assumptions as were made for *Tursiops*. With a ventilation rate of 12.6 liters per minute, a 71.5-kg *Lagenorhynchus* would lose about 91.7 g of water per day under our experimental conditions. If it were breathing dry air at 17°C the animal would lose about 246 g of water per day. With an oxygen consumption of 0.25 liter of oxygen per minute (*5*), *La-*

genorhynchus would lose water at the rate of 0.684 mg of water per milliliter of oxygen consumed. This figure is within the range of values reported by Schmidt-Nielsen for nondesert mammals (*4*).

For a man weighing 94 kg the expected ventilation rate would be 8.9 liters per minute, and at 27°C the rate of oxygen consumption would be 0.30 liter per minute (*6*). Our data (Table 1) indicate that water would be evaporated from the respiratory tract of a man in dry air at 26.8°C at a rate of 0.845 mg of water per milliliter of oxygen consumed. This value is not significantly different from the evaporation rate for a man breathing dry air at 25°C reported by Schmidt-Nielsen (*4*): 0.84 mg of water per milliliter of oxygen consumed.

The respiratory water loss of porpoises can be compared with those calculated for "theoretical terrestrial mammals" from equations given by Adolph (*6*). From his data and Eq. 2, a terrestrial mammal weighing 140 kg would be expected to lose 1261 g of water per day in dry air, if the water content of the exhaled air were assumed to be the same as that of man (Table 1). If this mammal consumed 0.92 liter of oxygen per minute (*6*), the respiratory water loss would be 0.979 mg of water per milliliter of oxygen consumed (compared to 0.294 mg for *Tursiops*). Calculations for a 71.5-kg mammal are 3.9 g of water per day, or 0.911 mg of water per milliliter of oxygen consumed (compared to 0.684 for *Lagenorhynchus*) at a metabolic rate of 0.25 liter of oxygen per minute.

In *Tursiops*, the respiratory water loss is only 30 percent of that predicted for a mammal of the same body weight, while the water loss of *Lagenorhynchus* is 77 percent of the predicted value.

There are several ways in which porpoises could control their respiratory water loss: (i) by reducing the ventilation rate, (ii) by cooling the air in the upper respiratory passages, and (iii) by controlling the pressure in the upper respiratory tract.

The relatively large amounts of oxygen extracted from inspired air by porpoises (*3*) and their low ventilation rate favor a low rate of respiratory water loss, as Krough has stated (*7*). For example, the ventilation rate of a 140-kg *Tursiops* is 15.2 liters of air per minute less than that predicted for a terrestrial mammal of the same weight (*6*). Calculations with Eq. 2 show that this difference in ventilation rate could account for the conservation of 131 g of water per day by *Tursiops*, if the water content of its inspired and expired air were the same as we observed (Table 1).

Table 1. Absolute humidities (H_A) and temperatures (T) during respiration by two species of porpoise and man. Absolute humidities are given in grams of water per cubic meter of air and temperatures are in degrees Celsius. Each entry represents the mean ± the standard error. The number of samples taken (n) is given; at least two measurements were taken from each subject for each phase of respiration.

Inhaled air			Upper-respiratory-tract air			Exhaled air		
n	H_A (g H_2O/m^3)	T(°C)	n	H_A (g H_2O/m^3)	T(°C)	n	H_A (g H_2O/m^3)	T(°C)
Six Tursiops truncatus								
15	14.0 ± .34	19.4 ± .47	16	26.2 ± 1.2	27.4 ± 1.2	15	16.7 ± .54	22.9 ± .74
Two Lagenorhynchus obliquidens								
5	13.2 ± .45	17.3 ± .59	4	26.5 ± .75	26.4 ± .74	8	18.4 ± .71	21.6 ± .83
Three Homo sapiens								
4	11.5 ± .01	26.8 ± .01		(*8*)	(*8*)	18	28.7 ± .77	30.2 ± .81

Water loss in porpoises could be reduced by lowering the temperature of air in the nasal passages so that warm, saturated air from the lungs would condense on the cooler tissues, as postulated for kangaroo rats (*Dipodomys*) (*4*). The temperature in the air sacs of the porpoises we examined averaged 27.1°C (both species), which is about 9.8°C cooler than simultaneously measured rectal temperatures. If we assume that lung temperature is the same as rectal temperature, cooling of the entire tidal volume of air during exhalation could yield a net condensation of 514 g of water per day in *Tursiops*.

In the porpoises we studied the exhaled air was not saturated with water vapor. Although condensation due to cooling could account for the retention of 230 g of water per day, this process by itself cannot account for the observed saturation deficit of the expired air. This deficit can, however, be accounted for by pressure changes in the respiration system. Pressure measurements were made in the sac system of an 80-kg *Lagenorhynchus* by placing a slender stainless steel tube through the blow hole into the nares (see Fig. 1). The probe was connected by a piece of surgical rubber tubing to a sensitive air-pressure gauge. Between expirations, pressure in the air sac was the same as atmospheric pressure and the glottis was tightly closed. However, prior to exhalation, when the animal compressed the air sacs, pressures of 0.170 atm to 0.238 atm above atmospheric pressure were recorded.

While we were obtaining a number of measurements from the air-sac systems, air temperatures rose as much as 5°C in a few seconds, particularly in *Tursiops*. At this time wet-bulb temperatures rose briefly to as much as 40 percent above the dry-bulb readings. This anomalous condition can be related to the pressure changes.

As the pressure in the air sacs increases, the amount of water vapor in the contained air must decrease in direct proportion; moisture from this compressed air will condense in the upper respiratory tract. If compression of the air sacs is performed quickly (and therefore adiabatically), most of the external work done on the system will be converted to internal energy (heat) in the compressed air. This could cause a sudden rise of air temperature in the air sacs. The latent heat of vaporization released during the condensation process should be more effectively transferred to the wet-bulb thermistor than to the dry-bulb thermistor because of the conductive properties of water. Therefore, the condensation of water on the wet-bulb thermistor during air-sac compression could cause a temporary rise in wet-bulb temperatures above those of the dry-bulb thermistor.

If, during the process of compression, a portion of the resultant heat were lost to the surrounding tissues, the release of pressure during the blow would result in the expired air being at a lower temperature than before the pressure changes occurred, as we found. The mixing of relatively dry air from the sac system with the rest of the tidal volume during a blow could account for the observed saturation deficit of the expired air.

Thus reduced ventilation, cooling

of the respiratory tract, and control of pressure within the sac system could account for the retention of 875 g of water per day of the 935 g of water that could be lost by respiration in a 140-kg *Tursiops* under the conditions we assumed for our calculations.

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References and Notes

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5. This value was extrapolated from the reported values for the smaller species *Phocena communis* and for *Tursiops* (*2*).
6. E. F. Adolph, *Science* **109**, 579 (1949).
7. A. Krogh, *Osmotic Regulation in Aquatic Animals* (Cambridge Univ. Press, London, 1939), pp. 162–5.
8. If it is assumed that air in the human respiratory tract is at 36.4° to 37.2°C and saturated (95 to 100 percent relative humidity), the water content would be 42.7 to 46.9 g of water per cubic meter.
9. We thank G. A. Bartholomew, Michael Smyth, and F. G. Wood, Jr., for reading this manuscript. This work was supported by the U.S. Naval Missile Center, Point Mugu, California.

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Stimulus Variables Determining Space Perception in Infants

Abstract. *It was shown previously that infants who have neither reached nor crawled discriminate changes in spatial position on the basis of cues other than the projective size of objects displaced in space. It is now shown that binocular vision is not necessary for discrimination and that pictorial cues are not sufficient for discrimination. Parallax variables provide the information used by such infants for the discrimination of size and distance.*

In a previous study (*1*) evidence was presented that 10- to 12-week-old infants can discriminate changes in spatial position on the basis of cues other than changes in the size of the retinal image. The nature of the variables used by infants is of some theoretical importance, since it bears on the question of the "primary cues" to spatial order. The data in this report indicate that motion parallax is the necessary variable, a result in accord with other studies (*2*).

Twenty-seven infants aged 40 to 60 days at testing served as subjects. They were divided into three groups of nine. All three groups were trained and tested in a room bare of furniture save that described below. The walls of the room were of coarsely textured brick and overhead strip lights ran along its length directly above the experimental set-up, shadows thus being minimized. Each infant was placed in a crib on a brown wooden table (5 m long), the crib being inclined at 45 degrees to the table. The head of the infant was clasped between two yielding pads; the left-hand pad contained a microswitch whose closing operated an event-recorder placed below the table. Immediately in front of the crib was a gap beneath which an experimenter was stationed. When the event-recorder operated, the experimenter emerged and peek-a-booed at the infant for 15 seconds and then disappeared from sight. This event served to reinforce the conditioned leftward head movement. The experimenter was able to introduce a translucent screen between himself and the infant for rest-periods and changes of stimulus.

The conditioned stimulus for group 1 was a white paper cube (30 by 30 by 30 cm) placed on the table 1 m from the infant's eyes; the stimulus was viewed binocularly. The conditioned stimulus for group 2 was the same, save that these infants wore a patch over one eye and thus viewed the stimulus monocularly. Both groups could see only one side of the cube, that in their fronto-parallel plane; neither the top nor the sides were visible. The conditioned stimulus for group 3 was a projection, on a translucent screen 1.25 m from the infants' eyes, of the cube to a size such that the visual angles, luminances, fronto-parallel aspects, and vertical and horizontal deviation from a constant line of regard of the projected objects were the same as for the other two groups.

The infants were trained in daily 30-minute sessions. Initially, reinforcement was continuous and the conditioned stimulus continually present. During this period a great deal of response differentiation seemed to occur. General motility decreased greatly and the head movement became more economical. When the response rate reached a criterion of one conditioned head-turn every 2 seconds (excluding intervals during which reinforcement was given) and remained at this rate for 15 minutes, stimulus differentiation was begun. The infants were trained to respond only in the presence of the conditioned stimulus. For group 3, a projection of the table without the cube served as a negative stimulus. The two types of presentation were alternated randomly for 30-second periods, with responses to the conditioned stimulus being continuously reinforced and responses to the negative stimulus never being reinforced. This was carried on until the negative stimulus had been presented 4 times without eliciting a response. After this criterion was reached, the negative stimulus was discontinued and a variable-ratio (VR) reinforcement schedule introduced. Behavior was shaped in four sessions from a VR 2 to a VR 5 schedule (that is, one reinforcement per five responses on average, the exact number of responses varying randomly). This schedule was maintained for 1 hour, after which discrimination testing was begun.

Table 1. Mean numbers of responses elicited by the four presentations.

Group and conditions of viewing	Presentation and visual angle (degrees)			
	(i) 16	(ii) 5	(iii) 54	(iv) 16
1, binocular	98.70	58.10	54.20	22.10
2, monocular	101.00	60.90	53.60	22.91
3, projection	94.78	52.00	44.11	96.00

The three groups were compared with respect to the rate of formation of the discrimination response and the rate of discrimination response at the end of the training period. The mean numbers of responses elicited by the negative stimulus in the three groups were, respectively, 81.84, 82.18, and 80.17 (chi square 1.014; df, 16, not significant). The mean terminal response rates were respectively 1.240 per second, 1.246 per second, and 1.241 per second (chi square 4.06; df, 16, not significant). Since neither of these measures differentiated the groups, it was assumed that any differences in performance in the subsequent tests would not reflect differences in training.

Discrimination tests were conducted as follows. Four presentations were used: (i) the 30-cm cube placed 1 m away from the eyes, (ii) the same cube