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Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*

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The relative importance of a water-repellent fur was assessed by changes in oxygen consumption ($\dot{V}O_2$) and in body and subcutaneous temperatures before and after oiling and washing in 15°C water. In addition, changes in posture and $\dot{V}O_2$ in five sea otters were measured while immersed in water from 5 to 30°C. Measurements were made in an enclosed water bath with $\dot{V}O_2$ determined by open-flow respirometry. Core body and subcutaneous temperatures were telemetered. Resting $\dot{V}O_2$ was 11.7 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ and did not significantly increase with decreasing temperature. Average and active $\dot{V}O_2$ increased with decreasing temperature. Average $\dot{V}O_2$ (16.0 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) increased 41% (22.0 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) after oiling 20% of the total fur surface and more than doubled (32.6 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) after washing. Oiling and washing reduced the fur's insulating quality. The result was an energetic liability, since the average maintenance $\dot{V}O_2$ doubled in 15°C water; this temperature is above typical water temperatures for this species, which range from 0°C (Alaska) to 12°C (California). Average $\dot{V}O_2$ returned to control levels after a minimum of 8 days.

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L'importance relative d'une fourrure imperméable a été estimée avant et après le huilage et le lavage dans de l'eau à 15°C, par mesure de la consommation d'oxygène ($\dot{V}O_2$) et des températures interne et sous-cutanée. De plus, les changements dans la posture et dans la consommation d'oxygène ont été évalués chez cinq loutres de mer immergées dans de l'eau de 5 à 30°C. Les mesures ont été prises dans un bain d'eau fermé et la consommation d'oxygène a été déterminée au moyen d'un respiromètre à débit continu. Les températures interne et sous-cutanée étaient mesurées par télémétrie. La consommation d'oxygène au repos est de 11,7 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ et ne change pas significativement lorsque la température baisse. La consommation moyenne d'oxygène et la consommation au cours d'une activité augmentent lorsque la température baisse. La consommation moyenne (16,0 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) augmente de 41% (22,0 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) après huilage de 20% de la surface totale et fait plus que doubler (32,6 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) après le lavage. Le huilage et le lavage réduisent donc les propriétés isolantes de la fourrure. Il s'agit là d'une perte énergétique puisque la consommation moyenne de maintien double dans l'eau à 15°C; cette température est plus élevée que les températures auxquelles l'espèce est habituée, soient de 0°C (Alaska) à 12°C (Californie). La consommation moyenne d'oxygène ne revient à la normale qu'après au moins 8 jours.

[Traduit par le journal]

Introduction

Sea otters, *Enhydra lutris*, are dependent upon their fur for inuslation against the cold marine environment. They possess the densest fur of any mammal (131 000 hairs$\cdot$cm^{-2}), twice the density found in river otters, *Lutra canadensis*, or in fur seals, *Callorhinus ursinus* (Tarasoff 1974; Kenyon 1969). Sea otter fur provides insulation by retaining air within it and by preventing water penetration to the skin. Otters are known for their susceptibility to fur soiling and contamination (Stulken and Kirkpatrick 1955; Kenyon 1969) and spend as much as 3 h each day grooming and maintaining their fur (Loughlin 1977). Removal of this trapped air in other aquatic endotherms reduces their insulation, resulting in severe thermal stress (McEwan and Koelink 1973; McEwan *et al.* 1974; Kooyman, Gentry, and McAlister 1976; Kooyman, Gentry, Bergman *et al.* 1976). The importance of this trapped air and the hydrophobic quality of the fur for thermoregulation have been suggested but not directly measured in sea otters (Kenyon 1969; Tarasoff 1974; Morrision *et al.* 1974). In view of current offshore oil development within the range of the sea otter and the susceptibility of captive sea otters to fur contamination and subsequent cold stress, more information on the insulative properties of the fur is important.

In this study, we measured the metabolism and calculated the changes in insulative properties of the fur. This was accomplished by measuring oxygen consumption ($\dot{V}O_2$) and subcutaneous (T_{sq}) and core (T_b) temperatures in water before and after oiling and washing of the fur. We observed that oiling and washing significantly reduced the fur's insulating quality. The result was an energetic liability, since the average maintenance $\dot{V}O_2$

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increased twofold in 15°C water; such a temperature is above typical water temperatures for this species, which range from 0°C (Alaska) to 12°C (California).

Materials and methods

Animals and facilities

Five female sea otters with a mean mass of 17.3 kg (range 15.3–19 kg) were captured near Pacific Grove, CA, by the California Department of Fish and Game and were flown to the Physiological Research Laboratory, Scripps Institution of Oceanography, San Diego, CA. The time from capture to release in the holding pools was 5 h. Animals were maintained 2 months to 2 years in a holding pool 6.1 m wide, 12.2 m long, and 3 m deep filled with seawater to a depth of 1.2 m. A flow of 110 L·min^{-1} of new seawater was continuously added to the pool. Holding tank water temperature varied with ambient ocean water (mean temperatures: 20°C, summer; 16°C, winter). Five times a day otters were fed an assortment of commercially obtained frozen clam, *Spissula solidissima*, squid, *Loligo opalescens*, rock crab, *Cancer* spp., abalone trimmings, *Haliotus* spp., and locally collected sea urchins, *Srongylocentrotus franciscanus*.

Metabolic rates during immersion

Each otter was fasted for 12 h prior to each metabolic analysis and weighed wet to within 50 g on a platform beam balance. After weighing, each otter was placed into a metabolic chamber 151 cm long and 84 cm wide and holding 1400 L of freshwater. Otters were allowed to come to equilibrium in the chamber for 1 h before data collection began. The chamber was constructed of styrofoam sheets, 9.5 cm thick, covered with fiberglassed wood veneer. Within the lid was a 30-cm-high lucite dome whose base dimensions were 30 cm wide by 60 cm long. This dome was fastened tightly over a neoprene gasket. The chamber was filled up to 2 cm into the dome with freshwater. Opposed ports in the dome functioned as air intake and exhaust. The dome was covered with black plastic to prevent the otter from being disturbed by the personnel conducting the experiment.

Sixty-seven experiments, covering 402 h of metabolic measurements, were made on the five sea otters immersed in water at 5, 10, 15, 20, 25, and 30°C. Resting, active, and average $\dot{V}O_2$ measurements were made. Resting $\dot{V}O_2$ was judged whenever otters were observed quietly floating on their backs and the $\dot{V}O_2$ reading was constant for at least 10 min. Active $\dot{V}O_2$ occurred when otters were swimming, diving, grooming, or otherwise moving about in the chamber. Average $\dot{V}O_2$ was determined as the mean $\dot{V}O_2$ for the entire 6-h measurement independent of the animals activity state. At least two 6-h measurements were made with each otter at each temperature, with the exception of otter 2 for which data were only collected at 5, 20, and 25°C. For some animals and temperatures more experiments were conducted. In order to avoid individual bias between animals and temperatures, statistical comparisons were made between mean $\dot{V}O_2$ for each animal at each temperature. Two mock 6-h experiments were conducted on each animal prior to data collection in order to allow the animals to become familiar with the metabolic chamber.

Flow rate was determined by measuring the total air volume drawn through the chamber divided by the length of the experimental period. Total air flow was measured at the air intake with a Wright respirometer previously calibrated with a Tissot spirometer, accurate to within 1% at the 40 L·min^{-1} flow rate used. A one-way valve was placed after the Wright respirometer to insure unidirectional flow. Humidity was determined with a dial hygrometer, and barometric pressure was determined with an anaeroid barometer calibrated against a mercury barometer. Air and water temperatures were monitored to within ±0.1°C with a thermocouple and a digital mulitimeter. Thermocouple probes were placed at the air intake and on the upper inside portion of the chamber wall 2 cm below water level. Water was slowly and uniformly stirred in the box by a series of manifolds. Water temperature varied less than 0.5°C.

A sample of the dome exhaust was drawn continuously through a series of glass U-tubes. The first was filled with drierite, followed by CO_2 absorber (baralyme), and then drierite before entering the sensor of an Applied Electrochemistry Industries (AEI, Sunnyvale, CA) O_2 analyzer. In experiments with oiled animals, a U-tube of 4- to 12-mesh activated charcoal preceded the first tube to absorb oil fumes.

The AEI O_2 analyzer signal was recorded continuously on a 25-cm chart recorder adjusted to record from 19–21% full scale. The response time of the system was 1 min. At 60-min intervals, the inlet air sample was checked, and the instrument's reference cell was adjusted if it had drifted. The analyzer was calibrated by flushing the sensor with room air presumed to be 20.93% O_2. Recorded curves of O_2 concentration were smoothed by eye and the difference in O_2 concentration from intake and exhaust was determined every minute. Averages for 60-min intervals were collated. Appropriate factors for correction of gas volumes to standard pressure and temperature (dry) were incorporated into a computer program, and $\dot{V}O_2$ values were calculated using Depocas and Hart's (1957) Eq. 8 modified for measurements of fractional O_2 content (Withers 1977).

Deep core and subcutaneous temperature measurements

Deep T_b's were obtained by inserting an encapsulated frequency modulation radio transmitter down the esophagus of anesthetized otters. This procedure was necessary, since the otters would not ingest transmitters hidden inside their food. Measurements were made simultaneously with determination of $\dot{V}O_2$. Transmitters were constructed using the design of Mattison and Seeley (1974). Transmitted pulse rate varied with temperature and was determined by counting the number of pulses in 1 min. Previous to each experiment the telemeters were calibrated in water baths of known temperature. This system was accurate to within ±0.1°C.

T_{sq}'s were determined with small (approximately 2 cm × 1 cm) amplitude modulation radio transmitters using the design of McKay (1970). These transmitters were surgically implanted immediately below the dermis in the dorsal region between the shoulders. The transmitted signal and temperature measurements were similar in procedure to those used for core body temperature.

Experiments with oiled and washed otters

Four oiling experiments were conducted on three of the five otters (once each on otters 3 and 5 and twice on otter 1). Sea otters were oiled under light anesthesia maintained by placing the otter's head in a plastic cylinder through which gas at a known concentration of halothane was flowing. Gas flow rate and concentration were maintained with a Bird MK 5 respirator and a Fluotec vaporizer. From 38 to 60 mL of Prudhoe Bay crude oil, a low-viscosity oil, was brushed over the back covering an average of 17.5% of the animal's body surface (Table 1). This process took no more than 15 min. After oiling and recovery from anesthesia the animals were permitted to swim in a clean pool of water for 30 min prior to the metabolic test. After measurement of $\dot{V}o_2$ in the oiled animals they were washed with Amber Lux (Lever Brothers), an anionic surfactant-type detergent. This was accomplished by anesthetizing the animal and washing the oiled area with a 1–8% solution of Amber Lux in water. The fur was washed and rinsed until the rinse was oil free. Control measurements were made upon otters which had been anesthetized for placement of temperature telemeters. These animals were treated the same as experimentals except that they were not oiled or washed.

Surface area measurements

Surface areas of five fresh pelts from otters with a mean weight of 26.7 kg were measured by tracing the flattened pelt, less feet, paws, and tail, on an acetate sheet. The appendages were traced separately. The outline was then transferred to tracing vellum where it was cut out and weighed. The surface area to weight ratio of the tracing material was then used to calculate surface area. Total surface area of one pelt was measured by planimetry and by weighing; both procedures agreed to within 1%. Surface area of feet, paws, and tail were measured separately by planimetry. Hind feet were measured while expanded and while closed. A surface area constant (a) was derived from these measurements and used in Eq. 1 to calculate surface area of the experimental otters (Iverson and Krog 1973):

$$[1] \quad S = aW^{2/3}$$

where S = total surface area (square metres), a = constant derived from pelt measurements, and W = animal mass (kilograms).

During metabolic measurements frequent observations of posture (position of the feet and height of the body in the water column), appearance and texture of fur, and activity were made through a small opening in the black plastic. Observations were aided by a 40-W orange light which remained on throughout the experiment.

Results

Mean resting $\dot{V}o_2$ measured in these sea otters at all temperatures was 11.7 ± 0.3 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ (4.0 ± 0.1 $W \cdot kg^{-1}$; $\bar{x}$ ± SE, n = 27) (Fig. 1). Control telemetered otters had metabolic rates similar to unanesthetized, untelemetered otters. There was no significant difference between resting $\dot{V}o_2$ from 5 to 30°C (F = 0.74, ν = 5,21, analysis of variance). However, there was a significant increase in both average (F = 7.314) and active (F = 5.933) $\dot{V}o_2$ as the water temperature declined ($P < 0.01$, ν = 5,21, analysis of variance) (Fig. 1).

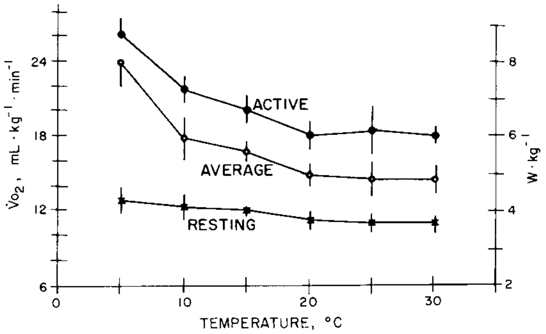

FIG. 1. Mean resting, average, and active $\dot{V}o_2$ plotted against chamber water temperature for the five sea otters studied. Bars equal ± 1 SE. These mean values were derived from the mean $\dot{V}o_2$ for each otter at each temperature. Data for otter 2 were not collected at 10, 15, and 30°C.

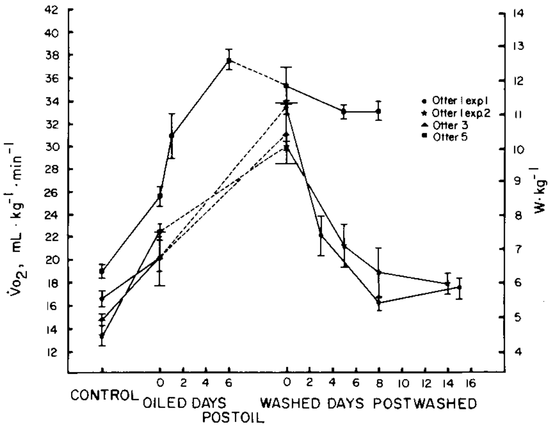

FIG. 2. Mean average $\dot{V}o_2$ for control, oiled, and washed animals. Days postoiled refers to treatment of otter 5 only, which was oiled for 8 days prior to washing. Otherwise, all animals were washed 8 h after oiling. Bars equal ± 1 SE. The number of 1-h control measurements were 18 for otter 1, experiment 1, 12 for otter 1, experiment 2, 16 for otter 3, and 24 for otter 5. There was one 6-h measurement for each oiling and washed metabolic measurement.

Mean average $\dot{V}o_2$ for the three animals prior to oiling in 15°C water was 16.0 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$. After oiling, average $\dot{V}o_2$ increased 41% to 22.2 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$. Upon washing, $\dot{V}o_2$ increased 106% to 32.6 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ (Fig. 2). In animal 5, oil was left on the fur for 8 days, and on day 6 the average metabolic rate had increased 98% above control levels to 37.6 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$. This was the highest $\dot{V}o_2$ recorded for any animal under any treatment (Fig. 2). Resting $\dot{V}o_2$ measurements after oiling are presented in Table 1. Maximum sustained (10 min or longer) $\dot{V}o_2$ was 37.9 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ measured in oiled otter 1 and washed otter 3.

After the first oiling experiments on otter 1 and otter 5

TABLE 1. Changes in resting $\dot{V}O_2$ after oiling and washing the fur with a known quantity of oil over a prescibed surface

Otter	Surface area oiled		Amount of oil, mL	Resting $\dot{V}O_2$, mL $O_2 \cdot kg^{-1} \cdot min^{-1}$			
	%	m^2		Control	Oiled	6-day oiled	Washed
1	14	0.074	38	12.5	51.9(27%)	—	31.2(150%)
1	11	0.060	60	10.0	16.3(63%)	—	27.7(177%)
3	25	0.125	60	10.9	14.8(36%)	—	26.0(139%)
5	20	0.117	35	12.7	13.5(6%)	23.1(82%)	28.8(127%)
$\bar{x}$	17.5	0.094	48.3	11.5	15.1		28.4

TABLE 2. Surface area with the corresponding mass for five sea otters

Sex	Mass, kg	Hind flippers, m^2		Paws, m^2	Tails, m^2	Maximum total surface area, m^2
		Expanded	Closed			
F	16.6	—	—	—	—	0.5
M	20.0	1.020	0.782	0.331	0.238	0.805
M	24.9	1.649	0.453	0.209	0.340	0.657
F	35.8	1.386	1.120	0.440	0.378	0.902
M	36.3	1.067	0.774	0.425	0.648	0.965

the animals were washed and returned to holding tanks with a summertime water temperature of 20°C. They quickly returned to their normal behaviour and the fur resumed a normal appearance. Following the second oiling experiment (after washing) otter 1 shivered constantly in the holding tank, which was at a winter water temperature of 16°C. Twenty-four hours of intermittent exposure to air and 25–30°C water allowed her to groom her fur sufficiently so as maintain T_b without further shivering in the holding tank. Otter 3 also shivered upon return to the holding tank at a winter temperature of 16°C. However, she did not respond to similar treatment, and she died 11 days postoiling while under treatment of an experienced marine mammal veterinarian. A necropsy was performed and pneumonia was found to be the cause of death.

T_b averaged 37.3 ± 0.3°C (n = 5, range = 36.7–37.9). After oiling, the T_b was 37.7 ± 0.23 (n = 3). However, T_{sq} was lower in 5°C water (T_{sq} = 24.3 ± 0.3, n = 9, one experiment) than in 15°C water (T_{sq} = 36.5 ± 0.1, n = 8). T_{sq} beneath oiled fur declined in all animals (control T_{sq} = 35.1 ± 1.4, n = 3); oiled T_{sq} = 26.3 ± 0.8, n = 4). One day after oiling, T_{sq} increased under the oiled area of otter 5 (oil T_{sq} = 24.6 ± 0.4, n = 37; 1 day postoil T_{sq} = 33.7 ± 0.5, n = 4). T_{sq} approached control levels after washing in all animals (control T_{sq} = 35.1 ± 1.4, n = 3; washed T_{sq} = 34.6 ± 0.02, n = 3). Changes in T_b correlated with changes in T_{sq} in otter 5 after washing. Lowest T_b's were coincident with initiation of activity. As the otter became active, T_b rose, leveled off, and then declined as the otter rested (Fig. 3).

The surface area constant a = 0.087 in Eq. 12 was determined from the five otter pelts. Appendages, including the tail, accounted for 21.4% of the total body surface (Table 2). Closing the hind flippers resulted in a 25% reduction in total flipper surface or a 3% reduction in total body surface.

Otters in 30°C water rested with their abdomen level

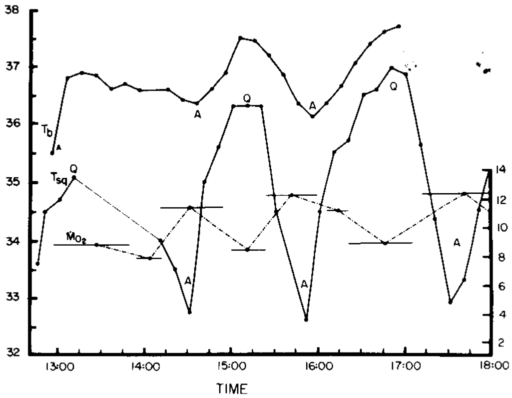

FIG. 3. T_b, T_{sq}, and $\dot{V}O_2$, plotted against time, measured on otter 5 after being washed. A, active periods; Q, quiet periods. Broken line in T_{sq} indicates a break in the data. The horizontal bars of $\dot{V}O_2$ represent the time periods over which mean $\dot{V}O_2$ was obtained.

to the water surface, with only the head, feet, and paws out of the water. In 5°C water they floated with approximately one-third of their body above the water surface. During rest, flippers were always held out of the water and the tail was always submerged.

Discussion

Metabolism

Our estimates of resting $\dot{V}O_2$ (11.7 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) are slightly different from the 11.2 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ in air and the 14.2 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ in water reported by Morrison *et al.* (1974). However, the variability of our results is much less than Morrison *et al.* (1974) possibly due to our larger sample size and because animals had more experience with the metabolic chamber.

Metabolic rates reported in this study were taken on mature, postabsorptive, resting sea otters within their thermoneutral zone (at least 20–30°C). Measurements of specific dynamic action in these otters confirm that they were postabsorptive (D. P. Costa and G. L. Kooyman, unpublished data). Furthermore, these measurements were not complicated by the presence of blubber or by changes in metabolism during diving, since sea otters rest floating on their backs with their heads above water. Therefore, valid interspecific comparison can be made. The standard metabolic rate measured in this study is 2.4 times the predicted rate for a terrestrial mammal of equal size (Kleiber 1975) and is 1.8 times greater than predicted for other mustelids (Iverson 1972). Surface area to volume relationships may have a greater influence upon heat loss due to the higher thermal conductivity of water (25 times that of air (West 1977)). Increased heat production may be necessary in small aquatic endotherms, such as the sea otter, to offset the greater heat loss of their small size.

The maximum $\dot{V}O_2$ measured in this study was 3.2 times the resting rate. This is close to the 43.4 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ or four times the resting rate measured for a brief period in Alaskan sea otters (Morrison *et al.* 1974). These $\dot{V}O_2$ values if compared with resting rates extracted from the Kleiber (1975) curve would be equivalent to metabolic scopes of 7.6–8.7.

Thermal conductance

Sea otter fur is quite an efficient insulator. A thermal gradient of 20°C exists between the ambient water temperature and subcutaneous tissue immediately below the fur. This observation and the similarity of the T_{sq} to T_b indicates that the fur supplies almost all of the insulation at 15°C. However, in 5°C water T_{sq} drops, indicating vasoconstriction and peripheral shell cooling. For comparison we can estimate whole body thermal conductance for sea otters resting in water if we assume (1) T_b remains constant, (2) evaporative heat loss is insignificant compared with overall heat flux, (3) heat loss through the appendages is no different from the rest of the surface area, and (4) 1 mL $O_2 \cdot min^{-1} \cdot kg^{-1} = 0.335$ $W \cdot kg^{-1}$ based on 4.8 $kcal \cdot L^{-1}$ O_2 (1 kcal = 4.1855 kJ). Total conductance can then be calculated from the following expression:

$$[2] \quad C = M/(S)\,(T_b - T_a)$$

where T_b = body temperature (degrees Celsius), T_a = ambient temperature (degrees Celsius), M = metabolic rate (watts), C = total thermal conductance (watts per Celsius degree), and S = surface area (square metres).

Thermal conductance varied 4.3-fold from 3.6 ± 0.4 $W \cdot m^{-2} \cdot degree^{-1}$ ($n = 4$) for otters resting in 5°C water to 15.5 ± 0.9 $W \cdot m^{-2} \cdot degree^{-1}$ ($n = 4$) in 30°C water. Other aquatic endotherms that rely on fur or feathers for insulation have similar conductances at comparable temperatures: polar bear, 6.0 $W \cdot m^{-2} \cdot degree^{-1}$ (Frisch *et al.* 1974); Adelie penguin, 3.3 $W \cdot m^{-2} \cdot degree^{-1}$; and Gentoo penguin, 2.2 $W \cdot m^{-2} \cdot degree^{-1}$ (Kooyman, Gentry, Bergman *et al.* 1976); fur seal, 16 $W \cdot m^{-2} \cdot degree^{-1}$ (Kooyman, Gentry, and McAlister 1976). Of these species only polar bears do not retain an air layer in the fur but rely on a stagnant water layer for insulation (Frisch *et al.* 1974).

Sea otter fur offers similar insulation as blubber and in a thinner insulating layer. Conductance measurements on live harbor seals, *Phoca vitulina*, (2 $W \cdot m^{-2} \cdot degree^{-1}$ in 0–27°C water (Hart and Irving 1959)) and on excised blubber of elephant seals, *Mirounga leonina*, (3.0–3.6 $W \cdot m^{-2} \cdot degree^{-1}$ in 0°C water (Bryden 1964)) are nearly equivalent to the values in otters. Blubber thickness of these animals was 2.0–2.4 cm (Hart and Irving 1959; Bryden 1964). Otter fur is the same length as the blubber is thick (2.3–2.4 cm (Kenyon 1969)). However, in water the fur lays against the body creating a very thin insulating layer (D. P. Costa, personal observation). One of the primary differences between these two types of insulation is that fur requires grooming and is susceptible to contamination. This conclusion is based on the higher conductances in excised pelts of sea otters and fur seals than measured in live animals (Kooyman *et al.* 1977). Sea otters spend 12% of their time grooming their fur (Loughlin 1977) and we believe that this is necessary to maintain the fur's water repellency and insulation.

Sea otters employ at least four methods of conserving heat in cold-water environments. (1) As indicated by our metabolic measurements sea otters do not increase resting heat production in response to decreased water temperature; rather, they increase average heat production by increasing active heat production (Fig. 1). These adjustments may be accomplished by allowing T_b temperature to fluctuate. Otters may store heat during periods of activity, such as grooming and swimming, thus increasing T_b. While resting they appear to lose heat steadily, as indicated by the declining T_b (Fig. 3). It should be noted that this was a washed otter and is the best example of this relationship; this trend was also observed in otter 1 in 5°C water. Therefore, excess heat produced during activity is stored and lost slowly during inactivity, reducing the need to increase resting heat production. We propose that average $\dot{V}O_2$ better indicates thermal tolerance in sea otters. (2) Widespread peripheral vasoconstriction, as indicated by the low T_{sq} in 5°C water, would reduce heat loss at lower temperatures. (3) The lung volume of sea otters is 2.5 times that of similar-sized mammals (Lenfant *et al.* 1970) and variations in this volume would have substantial effects upon buoyancy. We noted that our otters floated much higher in the water at 5°C than at 30°C. It appears likely that this buoyancy adjustment was used by the otters to increase and decrease the surface in contact with water and thus alter conductive and convective heat loss. Morrison *et al.* (1974) noted similar changes in buoyancy in relation to water temperature. They concluded that reduced buoyancy in warm water was due to infiltration of water into the fur. The physical appearance of the fur (such as the slick even appearance when wet) in our otters remained the same before, during, and after experiments. Therefore, we do not agree that the reduced buoyancy was due to wetting of the fur. (4) Thermal conductance could also be modified by using the flippers and paws to regulate heat loss. The flippers and paws are highly vascularized and are the least insulated parts of the body (Tarasoff 1974). During periods of activity when heat production is high, sea otters could use their flippers and paws as radiators to unload excess heat. When heat production is low, otters can close their flippers reducing exposed flipper surface by 25%. Furthermore, prior to rest, otters groom their head, feet, and paws by licking them dry, thereby reducing evaporative heat loss (D. P. Costa, personal observation). During rest sea otters hold their flippers and paws out of the water which would minimize heat loss (Loughlin 1977).

Fur contamination

A reduction in insulation after oiling appeared to be the result of fur clumping and subsequent loss of the entrapped air layer. Other aquatic mammals which depend upon fur for insulation also exhibited marked increases in metabolism after oiling and washing of their fur (Kooyman, Gentry, and McAlister 1976; McEwan *et al.* 1974). Removal of natural fur oils during washing would explain the loss of the fur's water repellency. The magnitude of this effect is also indicated by the increase in $\dot{V}O_2$ after washing. This increase is a conservative measure of the change in metabolism after washing the fur, since only the oiled area was washed (however, it was not possible to prevent detergent contamination of other fur as well). The loss of insulation after oiling may be partially compensated for by peripheral vasoconstriction beneath the oiled area, as indicated by the reduction in T_{sq}. However, this response is transitory, as indicated by the increase in T_{sq} 1 day postoiling and after washing. This effect may be similar to the cold-induced vasodilation associated with the immersion of human subjects' extremities in cold water (Hellstrøm 1965).

Changes in insulation can be estimated by calculating whole body conductance in control, oiled, and washed animals with Eq. 2. Whole body conductance increased from 5.3 ± 0.3 $W \cdot m^{-2} \cdot degree^{-1}$ in control animals to 6.7 ± 0.2 $W \cdot m^{-2} \cdot degree^{-1}$ in initially oiled animals and 10.8 $W \cdot m^{-2} \cdot degree^{-1}$ in otter 5 oiled for 6 days. Maximum conductance was 12.9 ± 0.3 $W \cdot m^{-2} \cdot degree^{-1}$ measured in washed animals. Mean whole body conductance of live otters is lower than the 27 $W \cdot m^{-2} \cdot degree^{-1}$ measured on excised pelts (Kooyman *et al.* 1977). This is not surprising, since only 20% of the animal's surface was oiled. The increase in conductance 6 days after oiling indicates that grooming had probably spread the oil over the fur and worsened its insulative properties. Although washing was initially harmful to the otter, since it increased conductance by about 2.5 times, it was transitory and by about 8 days the fur's insulating qualities were normal. Therefore, treatment of oil-fouled otters by washing with a detergent would be successful if the otters were held in water warmer than 20°C until they could reestablish and maintain the hydrophobic quality of their fur. It is unlikely that an otter could sustain a metabolism sufficient to offset the heat loss resultant from oil fouling of the entire body, especially at the water temperatures where they occur, and for the extended period that the soiling would persist in the fur.

Thermoregulation in sea otters depends upon efficient insulation and increased metabolism. The maintenance of an air layer within the fur is of utmost importance in reducing heat loss, with an increased metabolism making up the difference. Changes in body posture as well as changes in peripheral circulation and heat stored during activity may also aid in thermoregulation. Compared with other marine mammals which depend upon blubber for insulation, sea otters' dependence upon a nonwetting fur is energetically expensive due to the large maintenance component in the form of grooming. Furthermore, the fur is highly sensitive to envirnomental contamination, which in the past has probably not been a serious liability but may be so now and in the foreseeable future with the increased need for offshore oil development and transportation within the sea otters range.

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