The effects of oil contamination and cleaning on sea otters (*Enhydra lutris*). II. Metabolism, thermoregulation, and behavior

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The purpose of this study was to develop a method to clean and rehabilitate sea otters (*Enhydra lutris*) that might become contaminated during an oil spill and to determine which physiological and behavioral factors were important in restoring the insulation provided by the fur. Tests were conducted on 12 sea otters captured in Alaska and brought to the Sea World Research Institute in San Diego. Measurements of average metabolic rate, core body temperature, behavior, and squalene (the major lipid of sebum) concentration on the fur were made under three conditions: (*i*) before oiling (base line), (*ii*) 1–3 days after 20% of the body surface area was covered with fresh crude oil, and (*iii*) after cleaning. Under base-line conditions in water at 13°C, average metabolic rate was 8.0 W/kg, core body temperature was 38.9°C, and whole body thermal conductance was 10.7 W/(m^2 · °C). Otters spent 35% of their time grooming, 45% resting, 10% swimming, and 10% feeding. The squalene concentration on the fur averaged 3.7 mg/g fur. Oiling increased thermal conductance 1.8 times. To compensate for the loss of insulation and maintain a normal core body temperature (39°C), the otters increased average metabolic rate (1.9 times) through voluntary activity and shivering; the time spent grooming and swimming increased 1.7 times. Using Dawn detergent, we were able to clean the oiled fur during 40 min of washing and rinsing. Grooming activity by the otters was essential for restoring the water-repellent quality of the fur. Core body temperature, average metabolic rate, and thermal conductance returned to base-line levels 3–6 days after cleaning. Squalene was removed by cleaning and did not return to normal levels in the oiled area after 7 days. Veterinary care was important to keep the otters healthy. At least 1–2 weeks should be allowed for otters to restore the insulation of their fur and for recovery from the stress of oiling and cleaning.

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Nous avons cherché un moyen de nettoyer et de sauver les Loutres de mer (*Enhydra lutris*) qui pourraient être contaminées à la suite d'un déversement de pétrole et nous avons tenté d'établir quels facteurs physiologiques et éthologiques peuvent contribuer à la récuperation des propriétés isolantes de la fourrure. Des tests ont été faits sur 12 Loutres de mer capturées en Alaska et rapportées à l'institut Sea World Research Institute à San Diego. Le taux de métabolisme moyen, la température profonde du corps, le comportement et la concentration de squalène (principal lipide du sebum) sur la fourrure ont été mesurés dans diverses conditions : (*i*) avant la contamination par l'huile (conditions initiales), (*ii*) 1–3 jours après l'enduction de 20% de la surface corporelle avec du pétrole brut frais, et (*iii*) après nettoyage. Dans les conditions initiales, dans l'eau à 13°C, le taux de métabolisme moyen était de 8,0 W/kg, la température profonde, de 38,9°C et la conductance thermique générale, de 10,7 W/(m^2 · °C). Les loutres consacraient 35% de leur temps au toilettage, 45% au repos, 10% à la nage et 10% à l'alimentation. La concentration de squalène dans la fourrure était en moyenne de 3,7 mg/g de fourrure. L'huile multipliait la conductance thermique par un facteur de 1,8. Pour compenser la perte de leurs propriétés isolantes et maintenir une temperature normale (39°C), les loutres devaient augmenter leur métabolisme de base (1,9 fois) en s'adonnant à des activités volontaires et en grelottant; les loutres affectées consacraient 1,7 fois plus de temps au toilettage et à la nage. Nous avons pu nettoyer la fourrure endommagée par l'huile au moyen d'un lavage de 40 min avec du détergent Dawn suivi d'un rinçage. Le toilettage par les loutres elles-mêmes était essentiel à la restauration des qualités isolantes de la fourrure. La température, le taux de métabolisme et la conductance étaient revenus à leurs valeurs initiales 3–6 jours après le nettoyage. Le squalène a été enlevé par le nettoyage et les concentrations n'étaient pas encore parvenues à leur valeurs initiales après 7 jours, dans la région affectée par l'huile. Les soins vétérinaires se sont avérés essentiels pour que les loutres demeurent en bonne santé. Il faut donc au moins 1–2 semaines pour que les loutres récupèrent entièrement les propriétés isolantes de leur fourrure et se remettent du stress causé par les effets du pétrole et par le nettoyage.

[Traduit par la revue]

Introduction

Sea otters (*Enhydra lutris*) live along the coast of the Pacific Ocean with populations in the Soviet Union, Alaska, British Columbia, Washington State, and California. Water temperatures in these areas range from 21 to 38°C below core body temperature (T_b = 39°C; Costa and Kooyman 1982) depending on latitude and season (Estes *et al.* 1986; Garshelis *et al.* 1986). This large thermal gradient and the high heat conductivity coefficient of water, which is 25–100 times that of air, necessitate good thermal insulation to prevent excessive heat loss. Unlike many species of pinnipeds and cetaceans, sea otters lack a subcutaneous fat layer (blubber) and depend, instead, on air trapped within their dense fur for insulation. In addition, they augment thermoregulation with a high resting metabolic rate, which is 2.4 times that predicted for a terrestrial mammal of equivalent size (Costa and Kooyman 1982) and 1.8 times greater than predicted for other mustelids (Iverson 1972). To sustain such a high metabolic rate, sea otters consume approximately 20% of their body weight in food each day (Kenyon 1969; Miller 1974; Costa 1982).

Contamination of the fur with crude oil eliminates the air layer, allows water to penetrate to the skin, and reduces insu-

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TABLE 1. Division of otters into experimental study groups

Study	Protocol	Otter
Pilot study 1	Base line, oiled 6 days, cleaned	Gold tag
Pilot study 2	Base line, oiled 1 day, cleaned	White tag*
Base line	Without radiotransmitters	Red tag, orange tag, dark green tag
Main study (after implantation of radiotransmitters)	Group 1: base line, oiled 1 day, cleaned	Orange tag, gold tag, navy blue tag†, purple tag†
	Group 2: base line, oiled 3 days, cleaned	Pink tag, dark green tag, light blue tag, red and white tag†

*Data included in 1-day oiled group in main study.
†Unable to complete experimental protocol because of peritonitis.

lation up to 70% (Williams *et al.* 1988*a*). To balance increased heat loss and maintain a normal body temperature, oiled otters must further increase their metabolic rate and food consumption, or they will become hypothermic and possibly die.

Although all marine mammals are protected under the Marine Mammal Protection Act, the southern sea otter was afforded additional protection in 1977 as a "threatened" population under the Endangered Species Act. This status was based primarily on the population's vulnerability to a spill resulting from an oil tanker accident in California (Marine Mammal Commission Annual Report 1984, p. 92). The purpose of this study was to develop a method to clean and rehabilitate otters that might become contaminated during an oil spill. Tests were first conducted on pelts (Williams *et al.* 1988*a*), but these were insufficient to determine the effectiveness, practicality, and safety of the cleaning procedure for live otters. Therefore, sea otters were oiled and cleaned, and data on average metabolic rate (AMR), core body temperature, behavior, visual appearance, squalene concentration on the fur, and overall health of the animals were used to evaluate the procedure.

Methods

Animals

Twelve male sea otters (body mass = 15–32 kg) were captured with modified gill nets in Prince William Sound near Cordova, Alaska, in May 1985 and transported by air to the Sea World Research Institute, Hubbs Marine Research Center, in San Diego. Sea otters were obtained from Alaska rather than California because of restrictions on the capture and study of otters from the small population in California. They were held in a cement pool (12 × 12 × 3 m deep) that was divided with netting into four quadrants (6 × 6 cm), each containing an experimental group of two to four animals. About 36 m^2 of haul-out space was available around the perimeter of each quadrant. Filtered, dechlorinated seawater chilled to 13°C was circulated through the pool 3 days before and during the experiments. At other times, the water temperature was allowed to increase to 18°C. Otters were fed five to seven times daily on a diet of fresh frozen clams, crab, shrimp, and sea urchins. Standard hematological and clinical chemistry tests were conducted throughout the study to monitor the health of the otters, and flipper tags were used for identification. These experiments were conducted in accordance with standard guidelines for the care and use of laboratory animals established by the National Institutes of Health (publication No. 85-23).

Experimental design

Otters were studied under three conditions: (*i*) before oiling (base line), (*ii*) for 1–3 days after a single oiling, and (*iii*) after cleaning. Data were obtained from six healthy otters; of the remaining six, some died and some developed peritonitis and could not be used for the complete experimental protocol. The division of otters into experimental groups is shown in Table 1.

Before the main experiments, two otters were used in pilot studies to verify that the cleaning procedure developed for pelts (Williams *et al.* 1988*a*) would be effective on live otters. We chose to oil 20% of the body surface area on the basis of previous tests in which the metabolism of otters oiled to this extent increased an average of 41% in water at 10–20°C (Costa and Kooyman 1982). We considered this to be an adequate thermoregulatory stress to test the cleaning procedure without unduly jeopardizing the health of the animals. Oil was applied in a band around the chest to mimic the effects of oil contamination on the dorsal and ventral surfaces of the otter. The ventral surface is exposed to air when the otter is resting at the surface, whereas the dorsal surface remains submerged much of the time. In addition, the ventral surface and head appear to be groomed more frequently than the dorsal surface (R. W. Davis, unpublished observation), which could influence the effects of oil contamination and restoration of the fur after cleaning.

In addition to the pilot studies, base-line studies were conducted on three otters to assess the effects of the subsequent surgery and implantation of radiotransmitters on behavior and metabolic rate.

The main study group consisted of eight otters (including a fully recovered otter used in the first pilot study) divided into two groups of four animals (Table 1). Each otter had a radiotransmitter implanted in its abdomen 2–4 weeks before the experiments. After base-line measurements, oil was applied to all eight otters (details below) and left on the fur of animals in group 1 for 1 day and on animals in group 2 for 3 days before cleaning. After cleaning (details below), the behavior, AMR, and squalene concentration in the fur of both groups were monitored for 7–8 days before surgical removal of the radiotransmitters. However, two otters in group 1 and one in group 2 developed peritonitis and were unable to complete the experiment. Data were obtained from three otters in each group by including data from pilot study 2 (this otter did not have a transmitter). After the removal of the transmitters, the appearance of the fur was monitored for an additional 5 weeks, and behavioral observations were made during the 7th week after cleaning.

Oiling procedure

Otters were lightly anesthetized with halothane and fresh crude oil (ARCO 3120-9, Holly platform, Monterey Zone; a "sour crude" containing highly volatile sulfur; Fry and Lowenstine 1985) was applied in a band around the chest with a paint brush. The area to be covered was calculated for each otter as 20% of the body surface area determined by the following equation:

$$s = aW^{0.66}$$

where s = total surface area (m^2), a = the surface area constant (0.087) determined from pelt and carcass measurements by Costa and Kooyman (1982), and W = mass of animal (kg). The width of the oil banded around the chest was calculated as follows:

$$b = 0.2s/c$$

where b = the width of the band (cm), s = body surface area (cm^2), and c = the circumference of the chest (cm). The amount of oil applied was determined from tests on pelts and scaled to equal 0.1 mL/cm^2; this amount penetrated the fur down to the skin when the otter began grooming. After oiling, the otters were allowed to recover from anesthesia and were returned to the holding pool.

Cleaning procedure

Each oiled otter was immobilized with an intramuscular injection of meperidine hydrochloride (11 mg/kg) and diazepam (0.3 mg/kg) and placed on a trough with a bottom of 0.25-in (0.635-cm) wire mesh screen that allowed water to drain. The otter was only lightly sedated to minimize the side effects of meperidine hydrochloride, which causes peripheral vasodilation and increased heat loss. As a result, mild physical restraint was required to prevent the animal from moving. The otter was washed with a solution of Dawn dishwashing detergent (Proctor & Gamble Inc.) which was diluted (1:16 in water) to facilitate rinsing and thereby shorten the cleaning procedure. Four to eight litres of the detergent solution were normally required. A small splash panel was placed in front of the otter's face to prevent it from aspirating water. After detergent was applied and massaged into the oiled fur, the otter was dipped up to the neck in an 80-L tank of water and rinsed thoroughly using the same massaging action. This procedure removed a large portion of the initial oil and detergent. The otter was returned to the trough and successive applications of detergent were applied to the oiled area and massaged by hand. Between each application of detergent, the fur was rinsed under moderate pressure (30–40 psi; 1 psi = 6.89 kPa) with a shower head. After 40 min of washing, there was no indication of oil residue on the fur or in the rinse water. An additional 40 min of rinsing removed all traces of detergent and restored the loft and water repellency of the fur; air entrained in the rinse water may help restore the air layer. After being rinsed, the otters were dried with towels and the sedative antagonist Narcan (naloxone) was administered intramuscularly to reverse the effects of the meperidine hydrochloride. When they were fully recovered from sedation, the otters were returned to the pool.

Time budgets

The activity of each otter was documented at 15-min intervals during the experiments to determine the percentage of time spent grooming, swimming, feeding, resting, and hauled out (sum of the percent time spent in each of these activities equals 100%). Shivering and immersing the hind flippers were recorded as occurring concurrently with the other activities.

Average metabolic rate

AMR, which was used to assess changes in heat production after oiling and cleaning, was calculated from carbon dioxide production using the doubly labeled water method (Lifson and McClintock 1966). On the 1st day of an experiment, an otter that had been fasted for 3–4 h was removed from the holding pool, placed in a cage, and weighed. A blood sample was taken from the femoral vein for determination of background levels of oxygen-18 and deuterium followed by an intramuscular injection of oxygen-18 labeled water at a dose of 0.02 mol/kg body weight (95+% [^{18}O]H_2O, Monsanto Corporation, Miamisburg, OH) and deuterium oxide at a dose of 0.02 mol/kg (99% [^{2}H]H_2O, ICN-KOR Corporation, Cambridge, MA). This level of enrichment enabled us to obtain metabolic measurements for 4 days. Syringes were weighed to 0.01 g before and after use to precisely determine the amount of labeled water injected. The otter was isolated in a small seawater pool (7.5 × 3.8 × 2 m deep) for 3 h without food to permit the isotopes to equilibrate with the total body water (Costa 1987). After a second blood sample was taken, the animal was returned to the main pool. Subsequent blood samples were taken after 2 and 4 days, which completed a single measurement period. Each experimental protocol, with a base-line period of 4 days, an oiled period of 1–3 days, and a cleaned period of 7–8 days, required four separate injections of doubly labeled water for each otter.

TABLE 2. Composition of the edible portion of clams, shrimp, and crab consumed by sea otters

	Clams	Shrimp	Crab	$\bar{x}$
Composition (g/100 g fresh wt.)				
Water	83.1	78.2	77.2	79.5
Protein	10.5	18.7	17.4	15.5
Fat	1.3	2.2	2.5	2.0
Carbohydrate	3.1	0	1.1	1.4
Energy content (kJ/100 g)	293	423	430	382

NOTE: Food composition from Diem and Lentner (1970); energy content calculated assuming protein = 18.0 kJ/g, fat = 39.4 kJ/g, carbohydrate = 17.0 kJ/g (Schmidt-Nielsen 1979).

Blood samples were centrifuged and the plasma stored at −50°C until analysis. Ultrafiltrates of the plasma, obtained using a centrifugal microconcentrator (Amicon Corp.) that removes all macromolecules with a molecular weight greater than 10 000, were sent to Global Geochemistry (Los Angeles, CA) for mass spectrometric analysis of the oxygen-18 and deuterium enrichments. Total body water (TBW, litres) was calculated from both oxygen-18 and deuterium enrichment using eqs. 2 and 3, respectively, of Schoeller *et al.* (1980). Carbon dioxide production (litres CO_2/day) was calculated from eq. 35 of Lifson and McClintock (1966). The metabolic rate was calculated from the rate of carbon dioxide production (litres CO_2/day) and the energy equivalent for carbon dioxide of 23.8 kJ/L CO_2 for a diet containing equal amounts of clams, shrimp, and crab (Tables 2 and 3).

Core body temperature

T_b was monitored in eight otters by radiotelemetry. Epoxy-coated transmitters (Cedar Creek, Minnesota) each with a temperature thermistor were gas sterilized and surgically implanted in the abdomens of the otters 2–4 weeks before the experiments. Each transmitter weighed 200 g and had dimensions of 9.5 × 5 × 2.5 cm. Power was provided by a single lithium battery.

Squalene concentrations on the fur

Fur samples (about 300 mg) were taken from the abdomen (unoiled) or the sternum (oiled) of restrained otters. They were weighed to the nearest 0.1 mg and placed in 2-mL vials containing 1 mL of methanol:benzene (1:1 ratio) and 200 μg of methyl heinicosanoate (C-21 internal standard) for 1 h. Squalene concentration (mg/g fur) was determined by gas chromatography with reference to the standard (C-21) peak.

Statistics

Results are reported as the mean ± 1 standard error (SEM). Data for AMR, T_b, and the average percentage of time that otters spent hauled out were analyzed using repeated measures one-way ANOVA with posterior comparisons using Dunnet's method at $\alpha = 0.05$ to compare base-line values with those after oiling and cleaning (Keppel 1982). A t-test at $\alpha = 0.05$ was used to compare TBWs measured with oxygen-18 and deuterium oxide. The linear regression analysis of body mass and percent TBW was tested using the Pearson product–moment correlation (r). Because of the small sample size, squalene data were analyzed using the nonparametric sign test at $\alpha = 0.05$ (Conover 1971).

TABLE 3. Energy equivalent of carbon dioxide production for sea otters consuming a diet containing equal amounts of clams, shrimp, and crab

	Composition of diet (g/100 g fresh wt.)	Energy content (kJ)	CO_2 production (L CO_2)
Protein	15.5	279	12.1
Fat	2.0	79	2.8
Carbohydrate	1.4	25	1.2
Sum	18.9	383	16.1

NOTE: Composition of diet and energy production from the oxidation of protein, fat, and carbohydrate from Table 2; carbon dioxide production from complete oxidation calculated assuming protein = 0.78 L CO_2/g, fat = 1.42 L CO_2/g, and carbohydrate = 0.84 L CO_2/g (Schmidt-Nielsen 1979). Energy equivalent of carbon dioxide = 383/16.1 = 23.8 kJ/L CO_2.

Results

Activity–time budgets

During the base-line period, the activity–time budgets of all six otters were similar: ca. 35% of the total time grooming, 10% swimming, 10% feeding, and 45% resting in water (Figs. 1*a*, 1*b*). Hind flippers, which may be an important source of heat loss, were immersed 49% of the time. Only the smallest animal (body mass = 18 kg) shivered occasionally after a long rest period at night.

Five of the otters oiled for 1 or 3 days behaved similarly, so their time budgets were combined (Fig. 1*a*): grooming increased to 61%, swimming increased to 17%, and resting decreased to 12% of the total time. As a result of the increased grooming and swimming, the hind flippers were immersed 95% of the time. Shivering increased slightly (3%) in occurrence. The behavior of one otter (orange tag) differed from that of the others after oiling (Fig. 1*b*): swimming increased to 56% and grooming decreased to 32% of the time; hind limbs were continuously immersed.

During the first 8 days after cleaning, five otters decreased grooming to 49% and increased resting in water to 28%. Three began to haul out along the edge of the pool, but the average percentage of time for the entire group (13%) was not significantly different ($F_{1,4} = 5.49$, $p > 0.05$) from base-line conditions, when they never hauled out. The occurrence of shivering increased to 34% and varied among individuals, but was most pronounced in otters that did not groom well. The percentage of time spent with the hind flippers immersed remained high at 73%. The otter with the orange tag continued to groom 32% of the time, but decreased its swimming to 18% after cleaning. Resting in water and hauling out increased to 29 and 12%, respectively; shivering occurred 38% of the time and hind flippers were immersed 85% of the time.

By the 6th week after cleaning, the activity–time budgets of five otters had returned to base-line values (Fig. 1*a*); the otter with the orange tag died of peritonitis during the 5th week.

Average metabolic rate

In the first pilot study, the AMR of the otter (gold tag) increased 59% after oiling from 7.1 to 11.3 W/kg. Metabolic measurements were obtained for 3 days although the oil was left on the fur for 6 days. After cleaning, the otter began to shiver and become lethargic. To reduce further stress, water temperature was increased to 21°C and metabolic measurements were discontinued. The fur regained its normal appearance, and the otter was fully rehabilitated after 2–3 weeks.

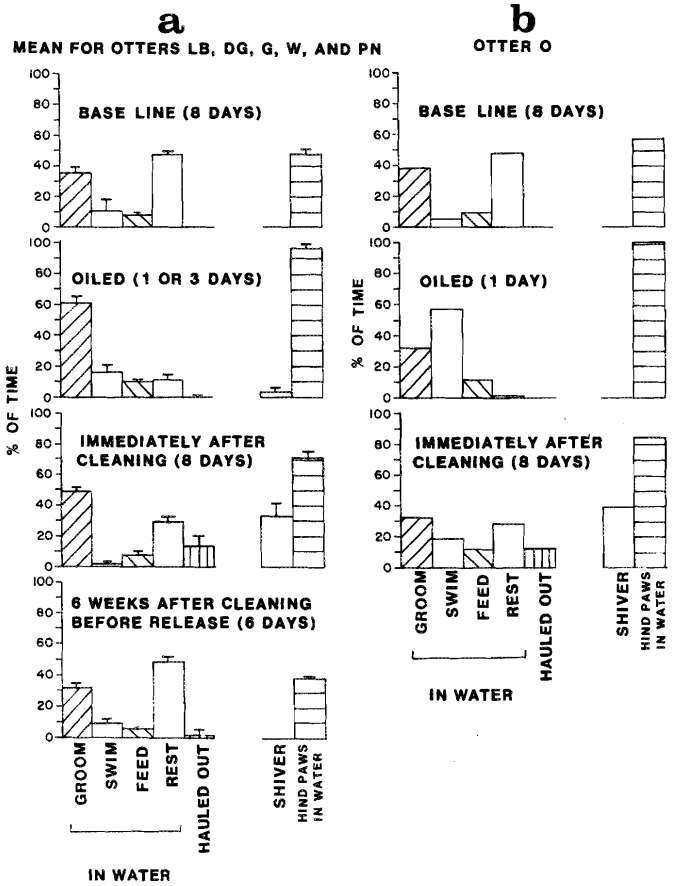

FIG. 1. Average percent time spent in different activities for sea otters under base-line, oiled, and cleaned conditions. Vertical lines represent 1 SEM. The results for five otters are combined in Fig. 1*a* (LB, light blue tag; DG, dark green tag; G, gold tag; W, white tag; PN, pink tag). Figure 1*b* shows the results for the otter with the orange tag (O). The sum of the percent time spent grooming, swimming, feeding, resting in water, or hauled out equals 100%, while shivering and immersing the hind flippers were behaviors that occurred concurrently with the other activities.

This otter may have been able to tolerate being left in water at 13°C, but a cautious approach was used during the initial testing. The AMR of the second pilot animal (white tag) increased 240% after oiling and then decreased to about base-line levels 4–8 days after cleaning (Table 4). This otter showed a rapid rehabilitation with full restoration of the fur

TABLE 4. AMR for sea otters under base-line, oiled, and cleaned conditions

Otter	Mass (kg)	Average metabolic rate (W/kg)					
		Base line, 6 days	Oiled, 1–3 days	After cleaning			
				Days 1 and 2	Days 3 and 4	Days 5 and 6	Days 7 and 8
Gold tag	18.9	10.4	19.2	16.9	13.3	14.2	14.7
White tag (pilot)	28.1	7.7	18.8	11.0	9.8	9.6	9.6
Pink tag	28.7	6.9	14.1	13.3	12.3	12.5	7.7
Dark green tag	29.6	7.7	8.9	9.6	6.9	10.1	—
Light blue tag	34.7	6.0	10.8	11.2	9.2	6.4	7.1
Orange	22.5	7.3	14.0	13.7	12.4	13.3	11.4
Mean ± SE	27.1±2.3	7.7±0.6	14.3±1.7*	12.6±1.1*	10.7±1.0	11.0±1.2	10.1±1.4

NOTE: All of the otters had implanted radiotransmitters except for the one with the white tag (pilot study).
*Significantly different from base-line values.

TABLE 5. AMR for sea otters under base-line conditions before implantation of radiotransmitters

Otter	Mean mass (kg)	AMR (W/kg)
Gold tag (pilot)	18.9	7.1
Orange tag	22.5	7.7
Dark green tag	29.6	8.9
White tag (pilot)	28.1	7.1
Red	24.9	10.4
Mean ± SE	24.8±1.9	8.4±0.6

within 1 week. The results from the pilot studies showed that (*i*) oiling 20% of the body surface produced an adequate thermoregulatory stress with which to assess the effectiveness of the cleaning procedure and (*ii*) the cleaning procedure enabled the otter to restore the water-repellent and insulatory qualities of oiled fur. Based on these results, the main experiments were begun.

Base-line AMRs averaged 8.4 ± 0.6 and 7.7 ± 0.6 W/kg before and after implantation of the radiotransmitters, respectively (Tables 4 and 5). After oiling, the AMR increased significantly to 14.3 ± 1.7 W/kg ($F_{1,4} = 53.1$, $p < 0.05$) (Table 4, Fig. 2). Despite standardization of the area oiled and the amount of oil applied, the increase in metabolism among the six otters was variable and ranged from 1.2 to 2.4 (mean = 1.9) times base-line levels.

The AMR decreased after cleaning and was not significantly different from base-line levels ($F_{1,5} = 10.9$, $p > 0.05$) after the 2nd day (Table 4, Fig. 2). However, the metabolic response to cleaning was variable, with some otters showing marked declines immediately after cleaning and others showing little change. The AMR of the otter with the white tag (pilot study) returned rapidly to about base-line levels after cleaning, associated with consistent grooming and restoration of the air layer in the fur (Fig. 3). In contrast, the otter with the orange tag did not groom after cleaning and spent much time swimming, an activity that increases heat production but does not restore insulation of the fur. Consequently, its AMR remained elevated 8 days after cleaning to offset increased heat loss through the wet fur. The metabolic response of the other otters to cleaning ranged between those of the otters with the white (pilot study) and orange tags.

Total body water

The average TBWs for seven sea otters measured with oxygen-18 and deuterated water were not significantly different ($t = 0.67$, df = 6, $p > 0.5$) and equaled about 71% of body mass (Table 6). There was no significant linear relationship ($r = 0.69$, $n = 7$, $\alpha = 0.05$) between body mass and the percent TBW.

Core body temperature

T_b averaged 38.9 ± 0.2°C ($n = 3$) under base-line conditions and 39.0 ± 0.3°C ($n = 5$) after oiling. During 2 h of cleaning and rinsing, the T_b of sedated otters decreased by about 2°C (Fig. 4), but increased to normal levels after 1–2 h of recovery in a cage. When the otters were returned to the pool, T_b decreased significantly ($F_{1,4} = 9.27$, $p < 0.05$) by about 1°C during the first 4 days (days 1 and 2, T_b = 37.9 ± 0.02, $n = 5$; days 3 and 4, $T_b = 38.0 \pm 0.3$, n = 5), but increased and was not significantly different by the 5th day ($T_b = 38.3 \pm 0.3$, $n = 4$).

Squalene analysis

The squalene concentration under base-line conditions averaged 3.7 ± 1.1 mg/g fur and did not change significantly after oiling ($t = 1$, $p = 0.625$) (Fig. 5). However, cleaning removed the squalene almost completely from both oiled (sternum) and unoiled (abdomen) fur ($t = 5$, $p = 0.0625$). The concentration returned to base-line levels after 7 days ($t = 2$, $p = 0.75$) in unoiled fur that had been cleaned, but remained at about 10% of the base-line concentration ($p = 0.0625$) in the fur that had been oiled and then cleaned.

Discussion

Base-line thermoregulation and behavior

The average T_b for sea otters measured in this study (38.9 ± 0.2°C) was similar to that reported by Morrison *et al.* (1974) and Costa and Kooyman (1982). The AMR with and without implanted transmitters (8.0 W/kg) was 2.1 times that of resting, postabsorptive metabolism (3.8 W/kg, Morrison *et al.* 1974) and higher than values (5.1–6.5 W/kg) measured for active otters in water at 15°C by indirect calorimetry (Costa and Kooyman 1982). However, the measurements of active metabolism were made for less than 6 h in a small metabolic chamber that prevented a full range of daily activities from being monitored. In addition, the otters were postabsorptive so that the measurement period did include the specific dynamic action of food digestion, which raises AMR by 10–15% (Costa and Kooyman 1984). In contrast, Costa (1982) estimated that the AMR of active otters during feeding studies

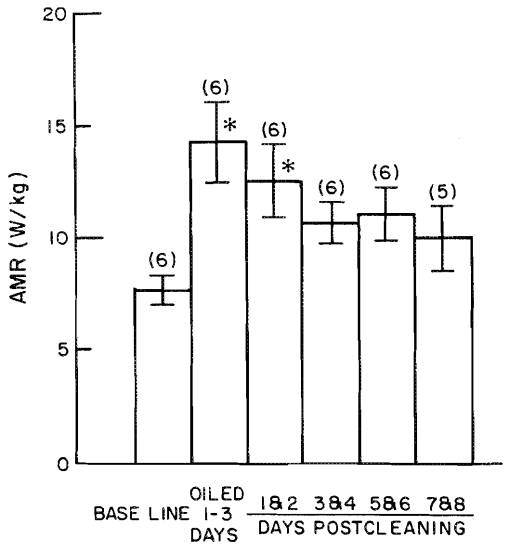

FIG. 2. AMR for sea otters under base-line, oiled, and cleaned conditions. Vertical lines represent ± 1 SEM. Number of animals monitored is shown in parentheses. Asterisks indicate AMRs that are significantly different from base-line values.

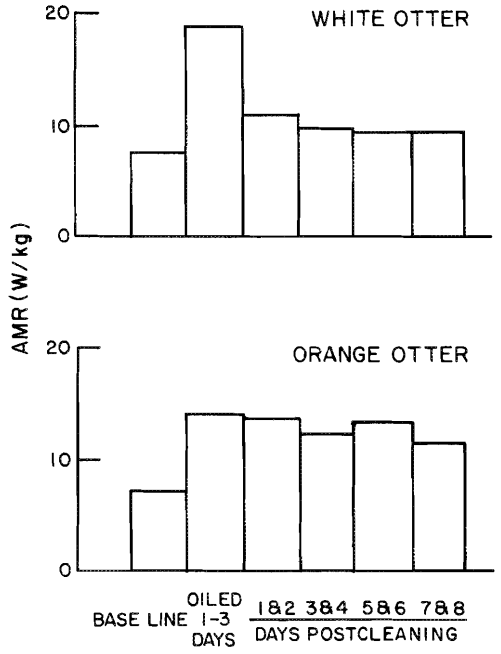

FIG. 3. AMR for otters with white and orange tags under base-line, oiled, and cleaned conditions. The former groomed well and showed rapid recovery whereas the latter did not groom and showed poor recovery of a normal AMR.

(material flux and composition of food, feces, and urine) in a small outdoor pool was 8.2 W/kg. This value is nearly identical with ours and similar to the estimated energy metabolism of free-ranging sea otters (8.4 W/kg) in Prince Williams Sound, based on observations of the type and quantity of prey consumed (Garshelis *et al.* 1986).

The average whole-body thermal conductance for sea otters in water was 10.7 W/(m^2 · °C), determined from the following equation:

$$C = \text{AMR}/[s \times (T_b - T_a)]$$

where C = whole body conductance (W/(m^2 · °C)), AMR = average metabolic rate (8.0 W/kg × 27 kg), s = body surface area (0.78 m^2), T_b = core body temperature (38.9°C), and T_a = ambient water temperature (13°C). This value is about 40% greater than that determined for sea otters resting in water (7.4 W/(m^2 · °C); calculated from data by Costa and Kooyman, 1982), and probably results from the difference in metabolism between resting and normal, diel activity.

TBW measured with oxygen-18 labeled water or deuterated water averaged 71% of body mass, similar to the value of 72% measured by Costa (1982) using tritiated water. If it is assumed that fat-free mass (FFM) is 73% water (Schoeller and van Santen 1982), then a 27-kg otter would have a FFM of 26.3 kg. The fat mass (FM) equals the difference between body mass and FFM, which in this case is 0.7 kg (3% of body mass). These calculations of FM are in agreement with previous measurements (Tarasoff 1974) and emphasize how little adipose tissue sea otters have as an energy reserve or as insulation. In comparison, FM is about 13% of body mass for ringed seal (*Phoca hispida*) pups and ranges from 27 to 50% for juvenile and adult northern (*Mirounga angustirostris*) and southern elephant seals (*Mirounga leonina*), ringed seals, and harbor seals (*Phoca vitulina*) (Depocas *et al.* 1971; Ortiz *et al.* 1978; Bryden 1968; Stirling and McEwan 1975).

The six otters devoted a similar amount of time to grooming (35%), resting (45%), and swimming (10%). Very little time (10%) was spent feeding, probably because food was thrown to the animals and foraging was unnecessary. Wild otters in California and Alaska spend about the same proportions of their time resting (50%) and swimming (2−15%), a smaller proportion grooming (6%), and a greater proportion foraging (California, 21−34%; Alaska, 17−69%), depending on the season (higher proportion in winter) and whether the area is close to equilibrium density for otters (Loughlin 1977, 1980; Estes *et al.* 1982, 1986; Garshelis *et al.* 1986).

Effects of oil

Oiling increased whole-body thermal conductance 1.8 times. To compensate for the loss of insulation and to maintain a normal T_b, the otters increased AMR through voluntary activity and shivering. Costa and Kooyman (1982) observed that oiled sea otters respond to increased heat loss by increasing activities such as grooming and swimming, which are energetically demanding and produce additional heat. In this study, five otters increased the time spent grooming and swimming 1.7 times; the sixth increased swimming activity 10 times but decreased grooming. The increased activity occurred throughout the day and may have disrupted the normal, nocturnal resting periods. In theory, otters could partially compensate for the increased thermal conductance of the oiled fur by keeping their flippers out of the water. However, we observed that they immersed their flippers 95% of the time because of increased grooming and swimming activity. By reducing blood flow to the flippers, or possibly through counter-current heat exchange in the pelvic vasculature (Tarasoff 1974), heat flux could still be reduced, although to what extent remains uncertain.

The increased metabolism necessary to balance increased heat loss after oiling must be provided by ingested food because an otter's energy reserves are very small. To double AMR, an oiled otter in the wild would have to increase its daily food intake to 40−50% of its mass, which would require

TABLE 6. Total body water (TBW) measurements for sea otters determined from the injection of oxygen-18 labeled water and deuterated water

Otter	No. of measurements (*N*)	Mean mass (kg)	TBW determined from $[^{18}O]H_2O$		TBW determined from $[^{2}H]H_2O$	
			Litres	% mass	Litres	% mass
Gold tag	3	18.7	14.2	75.9	13.4	71.7
Orange tag	4	22.6	16.3	72.1	15.9	70.4
Red tag	1	25.5	16.9	66.3	19.2	75.3
White tag	3	28.0	20.0	71.4	21.0	75.0
Pink tag	4	28.5	19.6	68.8	20.5	71.9
Dark green tag	4	29.3	21.6	73.7	20.9	71.3
Light blue tag	4	35.3	22.8	64.6	23.0	65.2
Mean ± SE	7	26.8±2.0	18.8±1.2	70.4±1.5	19.1±1.3	71.5±1.3

NOTE: TBW is shown in litres and as a percentage of body mass.

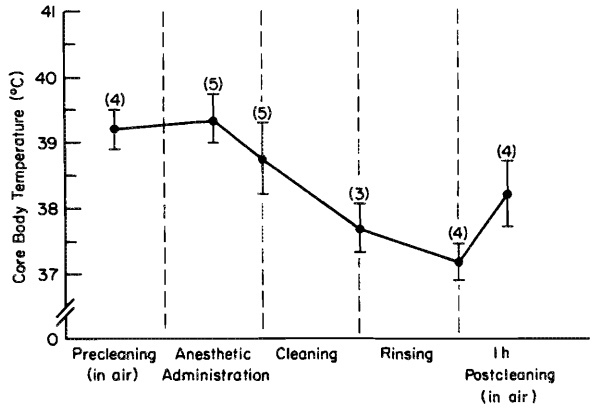

FIG. 4. T_b of sea otters before and during cleaning. Vertical lines represent ± 1 SEM. The number of animals monitored is shown in parentheses.

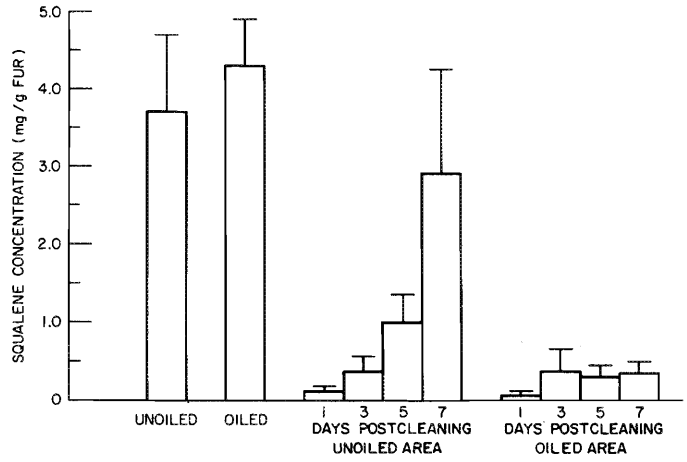

FIG. 5. Squalene concentration on the fur of five otters under base-line, oiled, and cleaned conditions. Vertical lines represent ± 1 SEM. Samples for oiled and unoiled areas were taken from the thorax and from the abdomen, respectively.

it to spend 40–100% of its time foraging, depending on the location and season. It may be impossible for otters to capture and digest this much food in 24 h. If the otter goes into negative energy balance, then body protein will be metabolized, leading to rapid weight loss, increased susceptibility to disease, and eventually death. In cases of severe oiling (e.g., greater than 20% coverage), the otter may be unable to consume and assimilate enough food energy, even in captivity, to balance heat loss in water at 13°C. As a result, it may be necessary to increase the water temperature (e.g., 25°C) or to remove the otter from the water to reduce heat loss.

Otters that were oiled for 3 days showed no signs that they could reduce the extent of contamination by grooming; in fact, grooming may have rubbed oil deeper into the fur. The inclination to groom oiled fur varied among the otters; some avoided the oil and groomed more vigorously in unoiled areas. Others groomed the oiled area and contaminated other parts of their body, especially the forepaws, chest, face, and back of the head. This secondary contamination was usually restricted to the surface of the fur, but occasionally could be severe in the highly groomed areas around the chest.

Effects of cleaning

Using Dawn detergent, we were able to remove all visible traces of oil from the fur during 40 min of washing. An equal period of rinsing was essential to remove residual detergent and to restore the water-repellent quality of the fur. Failure to rinse out the detergent, which lowers the surface tension on the hair, allows water to penetrate and prevents restoration of the air layer. As a result, the otter is clean but thermoregulation is compromised because the insulating properties of the fur have not been restored.

The decrease in T_b that occurred while the otters were sedated and washed probably resulted from (*i*) the additional loss of insulation because detergent and water penetrated into areas of clean fur adjacent to the oiled area, (*ii*) decreased heat production associated with inactivity, and (*iii*) peripheral vasodilatation caused by meperidine hydrochloride. Hand-held hair dryers were used to warm the otters if T_b decreased below 37°C. During recovery from sedation in a cage, T_b increased to normal levels. However, when the otters were returned to the pool, T_b decreased about 1°C. T_b, AMR, and whole body thermal conductance returned to base-line levels in 3–4 days; another week elapsed before otter activity approached base-line levels. Otters continued to shiver mildly 25–30% of the time 8 days after cleaning, although this did not increase AMR. Some reduced heat loss by hauling out, which minimized the loss of insulation and allowed the fur to dry if it had not been fully restored.

Grooming activity by the otters was very important for restoring the water-repellent quality of the fur. After cleaning, fur that had been oiled retained an insulating air layer for several hours. It was noted, however, that many air bubbles emerged from the fur as the otter swam and dived, and the fur gradually began to wet. In some cases, only the outer surface wetted, but in others the fur became wet down to the skin. This result contrasted with the results from the pelt studies (Williams *et al.* 1988*a*) in which the cleaned fur retained the air layer. The difference resulted from agitation and movement that dislodged air trapped within the fur of an active animal. Vigorous grooming by a cleaned otter as soon as it was returned to the holding pool prevented or slowed the wetting process. For example, the otter with the white tag (pilot study) groomed during the initial post-cleaning period and restored the fur to normal appearance 4 days after cleaning; the underfur was dry and AMR was almost at normal levels. In contrast, the otter with the orange tag did not groom after cleaning and the fur gradually wetted, resulting in a high thermal conductance and metabolic rate. The behavior of this otter demonstrated the importance of grooming for the cleaning procedure to be successful. Complete restoration of the fur to normal appearance was as short as 4 days but averaged about 2 weeks; in some cases (orange tag), full recovery never occurred.

One of the principal functions of grooming appears to be aeration of the fur. The mechanical effects of grooming may also align the underhairs so that they overlap and interlock, and it has been suggested that the scale patterns on the hair contribute to the interlocking and maintenance of entrapped air (Tarasoff 1974). Oiling and cleaning may disrupt or prevent normal alignment of the underhair, thereby allowing water to penetrate. This condition may be analogous to the disruption of feather imbrication when birds become oiled and are cleaned (Berkner *et al.* 1977).

The importance of sebum, squalene being the major component (Williams *et al.* 1988*a*, 1988*b*), in maintaining the water-repellent and insulating quality of the fur remains uncertain. Squalene was not reduced by the oiling but was almost completely removed by washing. After cleaning, there was a gradual increase in the squalene concentration in fur that had not been oiled. In contrast, squalene was not restored in the oiled and cleaned fur after 7 days. Whether the residual effects of oiling inhibited sebaceous secretion remains uncertain. Fur that was oiled and cleaned took longer to regain a normal appearance than fur that was only washed, an observation that correlates with their respective sebum concentrations. However, this result did not correlate with the time required for a return to a normal AMR (4 days). The otters were able to thermoregulate without elevating heat production before the full restoration (based on appearance) of the fur. Although squalene measurements were not made beyond the 7th day after cleaning, the fur regained its normal appearance after 1–2 weeks depending on how well the otter groomed.

In conclusion, the results show that sea otters that have had 20% of their surface area oiled can be successfully cleaned and rehabilitated using techniques developed in this study. Oil contamination increases thermal conductance and requires an increase in metabolism that may exceed the ability of a wild otter to remain normothermic and in positive energy balance. Therefore, an oiled animal needs to be captured and taken to a rehabilitation center within 1–2 days to insure the greatest chance of survival. Proper cleaning procedures and normal grooming by the otter restore the insulation of the fur and allow metabolism to return to normal levels. If the otter fails to groom, then the fur wets and thermal conductance remains high. Veterinary care is important to prevent the development of secondary infection such as pneumonia. At least 1–2 weeks should be allowed for restoration of the fur and recovery from the stress of oiling and cleaning, provided no medical problems such as disease, aphagia, or dehydration develop.

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