CONTRIBUTION OF SPECIFIC DYNAMIC ACTION TO HEAT BALANCE AND THERMOREGULATION IN THE SEA OTTER ENHYDRA LUTRIS[1]

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Specific dynamic action (SDA), measured in three sea otters using indirect calorimetry, is 10.0%–13.2% of the ingested clam or squid energy. Sea otter SDA is intermediate in magnitude and shorter in duration than reported for marine mammals that were fed fish. The postprandial peak increase in resting $\dot{V}O_2$ was 54% higher than postabsorptive values. This peak occurred 82 min after the otter ate 0.84 kg of squid or clam. The $\dot{V}O_2$ returned to postabsorptive levels 4–5 h after feeding. The short duration rise in metabolism attributable to SDA may contribute to thermoregulation at rest and correlates with field observations of resting and foraging behavior.

INTRODUCTION

The sea otter, *Enhydra lutris*, the smallest marine mammal, must maintain a high body temperature in the cold water of the North Pacific Ocean (Kenyon 1969). Its metabolic rate is 2.5–3.0 times that of a terrestrial mammal of equal size, and its body temperature varies as a function of heat production (Costa and Kooyman 1982). At rest when heat production is low, its body temperature declines as much as 1 C. When heat production is high during activity, its body temperature rises, allowing for the storage of heat, which is then lost during rest periods. These observations have been made on postabsorptive animals, and the contribution of the specific dynamic action (SDA) to thermoregulation may be quite profound.

The postfeeding increase in resting metabolism, known as the specific dynamic action, has been well described (Lusk 1917; Benedict 1938; Brody 1945; Hoch 1971; Kleiber 1975; Simek 1975, 1976; Krieger 1978). In some mammals, SDA increases resting heat production as much as 30% (Kleiber 1975). In hot or thermally neutral environments the increased metabolic heat from SDA is in excess, for the animals need to maintain constant body temperature and it must be dissipated. In a cool environment, it may be conserved and used to maintain homeothermy (Brody 1945; Kleiber 1975; Simek 1975, 1976). In this report we show that SDA results in a supplement to heat production that aids in maintenance of body temperature in sea otters resting in water at temperatures that normally occur in nature.

MATERIAL AND METHODS

ANIMALS AND FACILITIES

Three female sea otters with a mean mass of 18.4 kg (range 17.4–19.2 kg) were captured near Pacific Grove, California, by the California Department of Fish and Game and were flown to the Physiological Research Laboratory, Scripps Institution

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of Oceanography, San Diego, California. The time from capture to release in an outdoor holding pool was 5 h. Animals were maintained 1–2 yr in a holding pool 6 m wide, 12 m long, and 3 m deep filled with seawater to a depth of 1.2 m. A flow of 110 liters/min of new seawater was continuously added to the pool, and water temperature varied with ambient ocean water (mean temperatures: 20 C, summer; 16 C, winter). Otters were fed five times a day with 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 (*Strongylocentrotus franciscanus*).

METABOLIC MEASUREMENTS

The contribution of SDA to thermoregulation during rest was estimated by monitoring the increase in oxygen consumption and changes in activity level after feeding 0.8–1.5-kg meals consisting of either squid or clam. Since otters would not eat in the metabolic chamber, they were first fed, weighed wet to within 50 g on a platform beam balance, and then placed in the chamber. Thirty minutes elapsed between the end of feeding and initiation of metabolic measurements. Metabolic measurements were made in a water-filled chamber equipped with a small "breathing space." It was 151 cm long and 84 cm wide and held 1,400 liters of fresh water. 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 × 60 cm long. This dome was fastened tightly over a neoprene gasket. The chamber was filled up to 2 cm into the dome with fresh water. Opposed ports in the dome functioned as air intake and exhaust. Air was drawn through the "breathing space" and its O_2 content measured. The dome was covered with black plastic to prevent the otter from being disturbed by the personnel conducting the experiment. Frequent observations of the animal's activity state 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.

Airflow rate was determined by measuring the total volume drawn through the chamber divided by the length of the experimental period. Total airflow was measured at the air intake with a Wright respirometer previously calibrated with a Tissot spirometer, accurate to within 1% at the 40 liters/min 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 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 multimeter. 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 exhaust entered the sensor of an Applied Electrochemistry Industries (AEI, Sunnyvale, Calif.) oxygen analyzer. The O_2 analyzer signal was recorded continuously on a 25-cm chart recorder adjusted to record from 19% to 21% full scale. The response time of the system was 1 min. At 30-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 between intake and exhaust O_2 concentrations was determined every minute. Averages for 30-min intervals were collated. Appropriate factors for correction of gas volumes to STPD were incorporated into a computer program, and oxygen consumption rates ($\dot{V}O_2$) were calculated using Depocas and Hart's (1957) equation 8 modified for measurements of fractional O_2 content (Withers 1977).

Seventeen SDA and 17 control measurements were made while the otters were in water: three at 5 C, eight at 15 C, four at 25 C, and one each at 20 C and 30 C.

Control measurements were the same as SDA measurements, except the animals were not fed. Resting, active, and average oxygen-consumption measurements were made. Resting $\dot{V}O_2$ measurements were made while the otters floated quietly and the $\dot{V}O_2$ recording was constant for a minimum of 8 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 each 30-min measurement independent of the animals' activity state. SDA was measured as the area between postprandial resting $\dot{V}O_2$ (plotted against time) and the postabsorptive levels attained toward the end of the experiment (fig. 1). By the first resting measurements at $t = 45-60$ min, $\dot{V}O_2$ was already elevated and was, therefore, extrapolated to the prefeeding (postabsorptive) level at $t = 0$. Average $\dot{V}O_2$ was calculated for each resting period and was plotted as the midpoint of each measurement period. All measurements were subdivided into 30-min periods. Increased $\dot{V}O_2$ was converted to watts by multiplying by 0.335 $W \cdot ml^{-1} \cdot O_2^{-1} \cdot min^{-1}$. The SDA for clams and squid was calculated from

$$SDA = M/(FE * ME), \quad (1)$$

where M = increased energy produced from SDA (KJ), FE = gross food energy, and ME = metabolizable energy to ingested energy ratio. The metabolizable energy ($ME = 0.72$) and caloric content of clam, *Spissula solidissima* (4.98 kJ/g wet weight), and squid, *Loligo opalescens* (3.60 kJ/g wet weight), were derived from Costa (1982). There were sufficient resting periods in eight of the 17 metabolic experiments to estimate SDA.

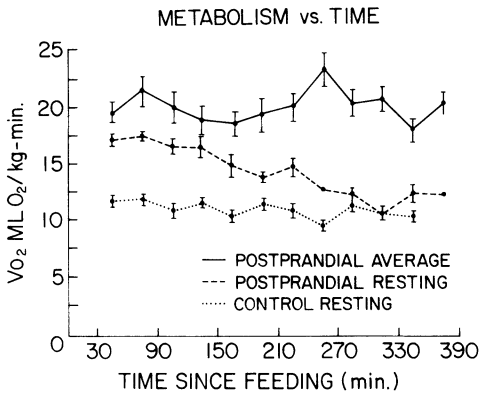

FIG. 1.—The elevation in postprandial $\dot{V}O_2$ due to SDA significantly decreased with time after feeding, reaching control levels within 318 min, whereas there was no change in control resting or postprandial average metabolism with time. Total SDA was determined as the area between the control resting and postprandial resting $\dot{V}O_2$ curves.

RESULTS

SDA was 13.2% ± 1.4% SD ($n = 6$) of the ingested squid energy and 10% ($n = 2$) of the ingested clam energy. Since the magnitude and duration of SDA did not correlate with water temperature, the data were pooled for all temperatures. The $\dot{V}O_2$ in postabsorptive control otters did not change with time (fig. 1). In fed otters, $\dot{V}O_2$ approached control postabsorptive levels within 250–320 min after feeding. The highest postprandial $\dot{V}O_2$ was 102% greater than control levels measured 68 min after the consumption of 1.5 kg of squid. Mean peak increase in resting $\dot{V}O_2$ was 54% ± 20% ($n = 10$) higher than postabsorptive values. This peak occurred 82 ± 26 min ($n = 10$) after feeding 0.84 ± 0.3 kg of squid or clam (fig. 1). Maximum increase in $\dot{V}O_2$ was significantly correlated with food intake (Pearson product moment correlation; $r = .94$, $n = 8$, $P < .05$) and followed the equation $Y = -531 + 1.64X$, where Y = the increase in $\dot{V}O_2$ above resting in ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ and X = the mass in grams of squid or clam consumed. The amount of time spent active (and therefore the heat produced from activity) increased significantly as the heat contribution of SDA decreased (Pearson product moment correlation; $r = .56$, $n = 67$, $P < .01$). Resting time significantly decreased (Pearson product moment correlation; $r = .334$, $n = 140$, $P < .01$) in a manner that directly corresponded to the decrease in the relative contribution of SDA to metabolism above control levels (fig. 2). The time spent resting by control animals also decreased with time. However, the effect was less than that observed for fed animals, and this may be a consequence of handling, reflecting the time required for the animals to come to thermal equilibrium in the chamber (fig. 2). There was no significant relationship between average metabolism and time after eating or being handled.

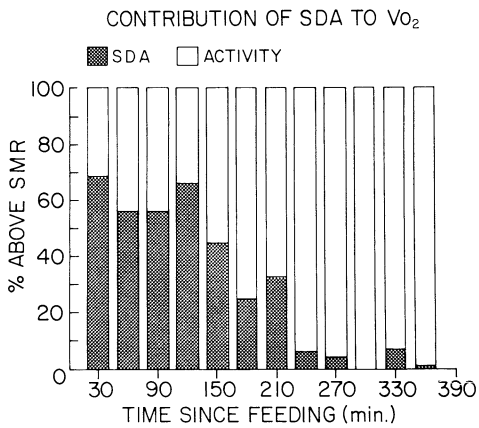

FIG. 2.—The relative contribution of SDA above control resting levels significantly declined with time after feeding and was compensated by an increased heat production from activity.

DISCUSSION

In an attempt to explain the high SMR measured in sea otters, Morrison, Rosenmann, and Estes (1974) proposed "that the SDA is not expended in a metabolic 'bulge' following the meal as in other carnivores but rather is rationed out over the day." However, our results indicate that the opposite occurs. In sea otters SDA is a short and intense metabolic bulge that is over within 6 h. Previous measurements of SMR (Iverson and Krogh 1973; Morrison et al. 1974; Costa and Kooyman 1982) were taken 12–15 h after a meal and should not have been influenced by SDA. It is therefore unlikely that SDA could account for the elevated SMR reported for sea otters (Iverson and Krogh 1973; Morrison et al. 1974; Costa and Kooyman 1982).

The proportion of SDA to the gross energy ingested by the sea otter is intermediate to the 4.7% reported for harbor seal (Ashwell-Erickson and Elsner 1981) and the 17% reported for harp seal (Gallivan and Ronald 1981), both fed fish. However, sea otter SDA is shorter in duration (3 h) and is intermediate in magnitude (54%) above basal than that reported for these marine mammals. In harp seal the peak increase in metabolism was 67% and lasted at least 7 h (Gallivan and Ronald 1981). In harbor seal it lasted 10–12 h but increased only 28% above the basal rate (Ashwell-Erickson and Elsner 1981).

The short duration of the metabolic increase in the sea otter may be related to its rapid (3 h) food passage rate (Stulken and Kirkpatrick 1955). Also a sea otter may use its short and intense metabolic "bulge" to offset heat loss during rest (or to maintain T_b at rest). A postabsorptive resting sea otter is not thermally neutral at water temperatures below 20 C (Costa and Kooyman 1982). Although their resting metabolic rate does not significantly increase at these lower water temperatures, their body temperature does not remain constant and fluctuates as much as 1 C. Otters achieve thermoneutrality by augmenting their overall metabolic rate by periodic bouts of activity (Costa and Kooyman 1982). This heat is stored (resulting in up to a 1 C rise in body temperature) and is later lost during rest. This mode of thermoregulation would not allow for the periods of uninterrupted rest observed for wild otters (Loughlin 1979). Postprandial otters may utilize heat produced from SDA to replace heat otherwise generated from activity. This would allow longer rest periods while the food is being processed and digested. The presence of such a mechanism in sea otters is supported by the lack of a trend in average metabolism with time and the relationships between SDA and activity after feeding (figs. 2, 3): its correspondence between the reduced time spent resting and the decline in SDA. As the heat produced from SDA declined, otters compensated by increasing the amount of time spent active. The relative contribution of SDA to average metabolism in fed animals versus postabsorptive animals further supports this hypothesis (fig. 3).

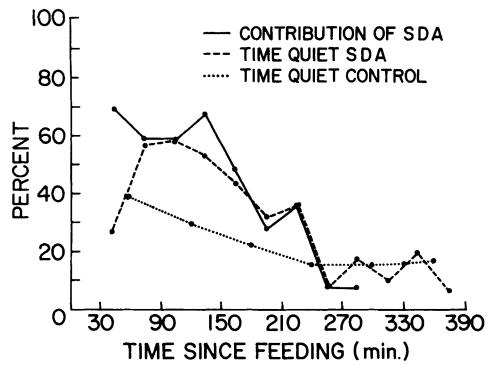

FIG. 3.—The decline in the contribution of SDA to heat production above control resting rates correlated with a decrease in the time spent resting and an increase in the time spent active.

Previous studies have shown that postabsorptive resting sea otters periodically increase their heat production by increasing the amount of time spent active. Postprandial otters apparently decrease periodic activity bouts by using the heat produced from SDA to offset heat loss during rest. This hypothesis correlates well with behavioral observations, indicating that this mechanism operates in wild sea otters as well. Free-ranging sea otters usually forage three times a day and spend about 4.6 h resting after each foraging bout (Loughlin 1979). These periods closely correspond to the 4.2–5.3-h duration of increased metabolism due to SDA (fig. 1).

The evolution of such a thermoregulatory mechanism might be understood if we consider the biology of this animal. Wild sea otters are rarely postabsorptive without being active. They feed throughout the day, consuming (Loughlin 1979) at least 23% of their body mass (Costa 1982). Furthermore, rafting periods (Loughlin 1979) coincide with the length of time required for the passage of food through the gut (Stulken and Kirkpatrick 1954). Since otters have an elevated SMR to meet the thermal demands of the aquatic environment, it seems reasonable to incorporate SDA as part of resting heat production. This would maximize energy conservation by reducing the amount of waste heat. We believe this may be an important thermoregulatory mechanism in other animals as well.

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