

Thermoregulatory Behavior of the Hawaiian Monk Seal (*Monachus schauinslandi*)¹

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ABSTRACT: The behavior of Hawaiian monk seals at French Frigate Shoals was studied in order to obtain information on their adaptation to a tropical climate. The seals were unable to remain on the dry beach platform during the day except during very high winds, extensive cloud cover, or rain. The seals characteristically moved down to wet sand on the beach slope during the day and returned to the beach platform at night. The frequency with which the seals changed their posture appeared to be related to the prevailing microclimatic conditions. For the most part, the seals lay in postures that exposed their ventral pale-colored hair coat to the atmosphere. The temperature of this surface was significantly lower than that of the darker dorsal coat. The seals were extremely inactive while ashore; their respiratory pattern included long periods of breath-holding, and the heart rate during breath-holding was low. These features were considered to be compatible with a low level of metabolic heat production and to be adaptive to heat exposure.

THE HAWAIIAN MONK SEAL (*Monachus schauinslandi*, Matschie) is the most tropical of all the pinnipeds. It is, in fact, one of the few species to have penetrated the tropics, which are believed to be a major barrier to the geographical distribution of seals (Scheffer 1958). For the most part, the anatomical, physiological, and behavioral features of the adaptation of monk seals to the tropics have not been identified. Although tropical oceans are relatively warm, it is unlikely that monk seals have any difficulty in dissipating metabolic heat when they are in the water. Young harbor seals (*Phoca vitulina*) have been shown to lose heat efficiently in water at 36.7 to 37.5° C, which is close to body temperature (Miller et al. 1976), and there is little evidence that tropical cetaceans are ever heat-stressed (Whittow 1976). When they are ashore, however, monk seals experience high levels of solar radiation and relatively high air

temperatures; there is usually little shade and no fresh water to replace water lost by any physiological evaporative heat-loss mechanisms.

Kenyon and Rice (1959:218), in their pioneer study of the Hawaiian monk seal, reported that the layer of blubber in Hawaiian monk seals is "about as thick as on arctic and antarctic seals," suggesting that a reduction of tissue insulation has not occurred in seals in response to exposure to heat. No evidence has been obtained to show that Hawaiian monk seals become hyperthermic on land, either in their natural habitat in the northwestern Hawaiian Islands (Kridler et al. 1971), or in captivity at the Waikiki Aquarium in Honolulu (Ohata et al. 1972). The hair coat of Hawaiian monk seals would appear to permit maximal convective and conductive heat loss from the skin surface to the air, but the histological structure of the sweat glands did not suggest that they were active (Whittow et al. 1975). Monk seals have been observed to lie in depressions in the sand (Kenyon and Rice 1959), and this may facilitate conductive heat loss to the sand (Ohata and Whittow 1974).

The studies reported here were designed

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to obtain as much information as possible about the thermoregulatory behavior and heat tolerance of the Hawaiian monk seal, within the constraints imposed by the conservation status of the seals. The Hawaiian monk seal is an endangered species, and this precludes all but the simplest measurements and observations.

PROCEDURES AND METHODS

Hawaiian monk seals were studied on Tern and Trig Islands at French Frigate Shoals in the northwestern Hawaiian Islands. French Frigate Shoals is an atoll consisting of a crescent-shaped reef and approximately 12 sand islands. Tern Island is 900 m long, partly man-made, and the site of a Coast Guard Loran Station. Seals haul out on the beaches of Tern Island irregularly and usually singly; they do not breed there. Trig Island is approximately 351 m long, with a resident population of approximately 30 seals. Additional observations were made on the 14-year-old captive animal at the Waikiki Aquarium. This is a male seal, kept in a 359,575-liter pool with a central artificial island 6 m long.

On Trig Island, a group of seals was observed continuously from approximately 8:30 AM to 4:00–6:00 PM on 17 days. The positions and orientations of the individuals in the group were plotted on simple maps constructed at intervals of 30 min. Records were also kept of the temperature of a 15.2-cm black globe, the temperature of the sand surface, and the magnetic compass bearing of the sun and wind. On some occasions, a single seal was observed and a complete dossier kept of its movements, behavior, and postural adjustments. On Tern Island and at the Waikiki Aquarium, the latter type of observation was the only one made. The captive animal hauled out regularly on the artificial island in its pool, following its second feeding period of the day at 2:30 PM. Consequently, records of the behavior of this seal were kept only for part of the day, from 2:30 to 6:00 PM. Occasional measurements were made of the surface

temperature of the seals, their heart rate, and their respiratory frequency. No consistent attempt was made to record the size of the animals observed, other than to note whether they were adult (large) or subadult (small). No observations were made on pups. The designation "subadult" may include animals that DeLong et al. (1976) would classify as "juvenile." Great care was taken to ensure that none of the seals studied was aware of the presence of an observer.

The black globe (Casella & Co., London) was suspended approximately 10 cm above the surface of the sand to approximate the position of the seal. The globe was painted with Nextel Black Velvet Coating (Minnesota Mining Co.) to ensure uniform absorption characteristics of radiation up to wavelengths of 35 μm (Moen 1973). The black globe temperature was selected as the most appropriate single measure of the environmental conditions to which the seal is exposed, compatible with field use. The black globe gains heat by radiation and loses heat largely by convection. Because fluctuations of air temperature in the course of any one day are small at French Frigate Shoals, the black globe temperature varies mainly with solar radiation and wind velocity. In the absence of evidence that evaporative heat-loss mechanisms are important in pinnipeds (Matsuura and Whittow 1974), these are the principal atmospheric environmental factors likely to affect heat gain and heat loss in the Hawaiian monk seal.

Sand surface temperatures were measured with a mercury thermometer, laid almost horizontally, with the bulb and part of the stem just below the surface of the sand. The surface temperature of the seals was measured with a Barnes Portable Infrared Thermometer (Model PRT-10-L).

Respiratory frequency was counted by observation of the nostrils or chest of the seal, in conjunction with a stop watch. Heart rates were counted by observation of the pulsations transmitted to the ventral and lateral chest wall.

Orientations of the seals were recorded with the aid of a sighting pocket compass. The compass was also used to measure the

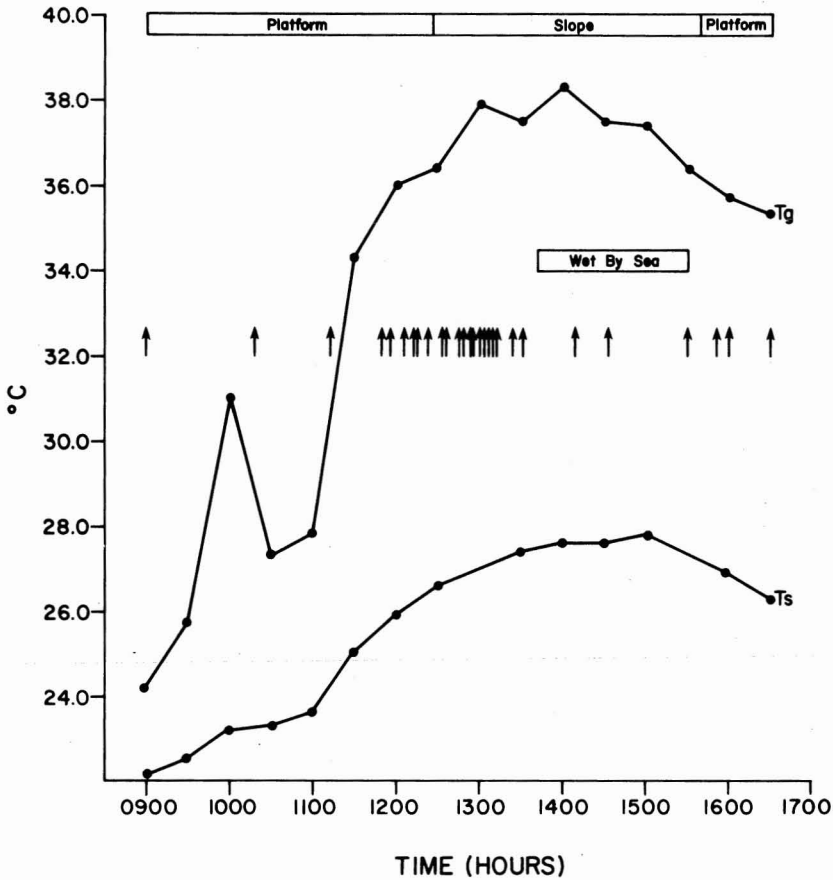


FIGURE 1. Position on beach (top bars) and frequency of postural changes (arrows) of a subadult, male Hawaiian monk seal on Tern Island. Temperatures of the black globe (T_g) and of the sand surface (T_s) refer to conditions on the beach platform.

bearing of the sun and the direction of the wind; the shadow cast by a plumb line provided a bearing of the sun, and a small pennant allowed the direction of the wind to be determined. Data on the air temperature, relative humidity, and wind velocity were extracted from the records of the Coast Guard Station on Tern Island.

RESULTS

Movements

The Hawaiian monk seals at French Frigate Shoals characteristically sleep on dry sand on the level beach platform at night

and move down to moist sand on the beach slope during the day. This pattern of movement was observed both in groups of seals on Trig Island and in single seals on Tern Island. The movements seemed to be related to the prevailing climatic conditions. Although observations were made on 38 individual seals and on 17 groups of seals, in only three instances did the seals not move down the beach. On one of these occasions, the day was generally cloudy, the wind velocity was high (>20 mph), and the air temperature was relatively low (22° C). On the other two occasions, it rained for most of the day. The movement of one other seal down the beach slope was temporarily arrested when the sun was obscured by clouds.

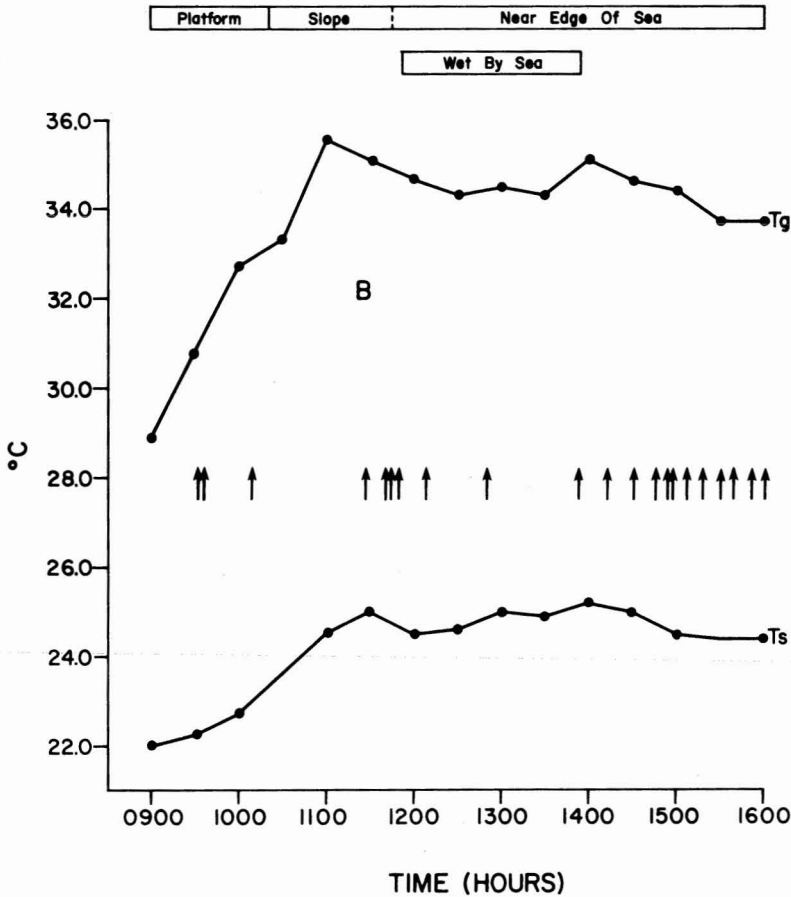


FIGURE 2. Position on the beach (top bars) and frequency of postural changes (arrows) of an adult, male Hawaiian monk seal on Trig Island. At the point marked B, the seal burrowed its muzzle into the sand. Temperatures of the black globe (T_g) and of the sand surface (T_s) were measured in positions corresponding to those of the seal.

The movements of individual seals are illustrated in Figures 1 and 2. In the observations represented in Figure 1, the black globe and sand temperatures were measured on the dry beach platform, which the seal left for moist sand on the beach slope. The seal that provided the data for Figure 2 also left the platform, but, in this instance, the black globe and sand thermometers were moved with the seal. A comparison of Figures 1 and 2 reveals that by moving down the beach, the seal was, in effect, attenuating the increase in the temperature of its environment during the course of the day. The failure of the black globe and sand temperatures to increase appreciably after 11:30 AM

(Figure 2) was due to selection of a different microclimate and not to cloud cover, which was absent on the day recorded in Figure 2. In Figure 3, data from a small group of four seals, each of which could be individually identified, are presented. In the course of this particular day, an additional seal came ashore on the beach under observation, remained on the beach slope for 30 min, and then moved up onto the beach platform at 12:40 PM. The seal remained on the platform until 2:30 PM, when it moved back down to the beach slope.

Posture

While ashore, Hawaiian monk seals lie in

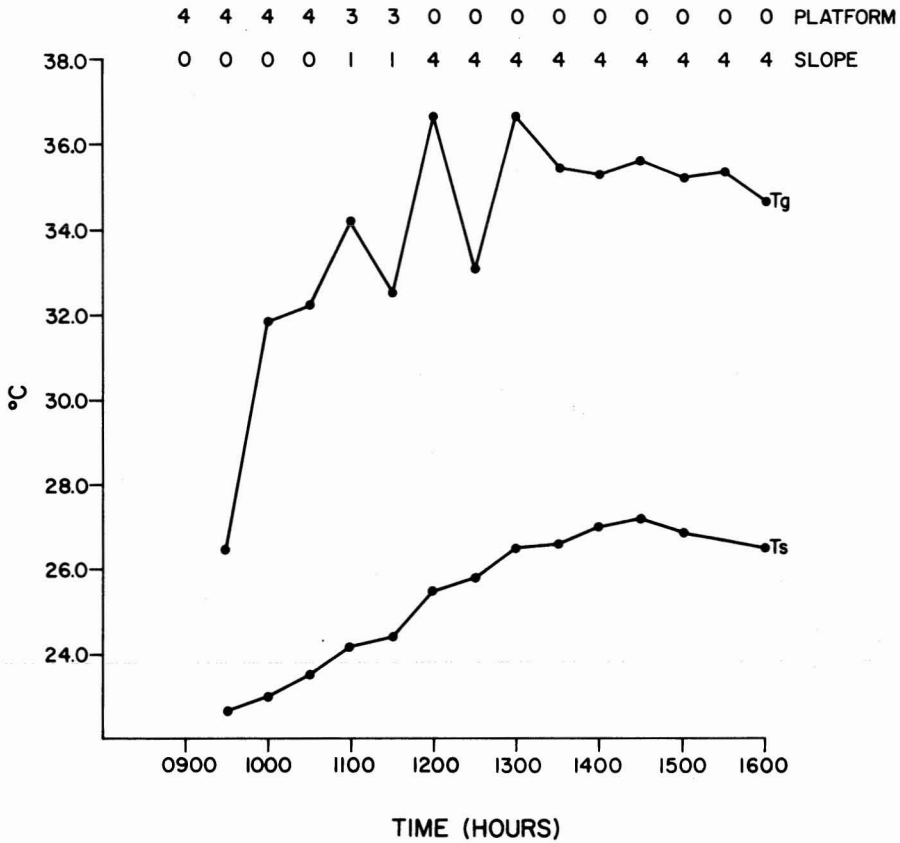


FIGURE 3. Position on the beach of a small group (four) of Hawaiian monk seals on Trig Island. Temperatures of the black globe (T_g) and sand surface (T_s) were measured on the beach platform. The numbers at the top of the graph refer to the number of seals on the beach platform or slope.

a prone position (on their ventral surfaces), completely supine (on their backs), on either flank (side), or in an intermediate position between the flank and either the supine (semisupine, Figure 4) or the prone (semi-prone) positions. Analysis of detailed records of the behavior of seven seals at French Frigate Shoals revealed that during the day the length of time the seals lay on their flanks was greater than times spent in other postures. However, this included time on both flanks, and the most favored single posture was the prone position (Table 1). This posture was obligatory when the animals moved up or down the beach. Observations of the captive monk seal at the Waikiki Aquarium, which did not execute such movements, indicated a lower mean per-

centage (21.1 percent) of time in the prone position, although the range of four separate days of observation was wide (4.2–57.1 percent). On one occasion, seal number 3 (Table 1) did not move from its overnight position on the beach. The seal lay in the prone position for 12.1 percent of the time on this day. The following day, the same seal moved down the beach, and its percentage of total time in the prone position was 25.4. However, it is apparent from Table 1 that although the prone position was the most favored single posture, the seals lay for most of the time in postures (supine, semisupine, and flank) that left the greater part of their light-colored ventral surface exposed to the atmosphere. Table 1 indicates that there is no simple relationship between the posture



FIGURE 4. Monk seal lying in a semisupine position on Trig Island.

TABLE 1
POSTURE OF SEVEN HAWAIIAN MONK SEALS DURING THE DAY*

ANIMAL			POSTURE (PERCENTAGE OF TIME)					PERCENTAGE OF TIME WET OR ON WET SAND	THERMAL CONDITIONS ON THE BEACH PLATFORM [†]	
NUMBER	SEX	AGE	PRONE	SEMI- PRONE	FLANK	SEMI- SUPINE	SUPINE		\bar{T}_g (°C)	\bar{T}_s (°C)
1	Male	Adult	59.1	4.7	36.2	0	0	54.7	37.2	28.0
2	Female	Adult	40.5	1.9	24.8	14.0	18.8	78.6	33.7 [‡]	24.3
3	Female	Adult	12.1	2.0	45.5	40.4	0	89.9	26.4	23.7
			25.4	4.4	42.4	15.0	12.8	44.1	33.9	28.0
4	Male	Subadult	41.9	9.3	14.4	13.1	21.2	84.6	37.3	27.6
5	Male	Subadult	38.7	1.6	48.0	11.8	0	79.3	42.9 [§]	29.4
6	Male	Subadult	34.3	0	56.0	7.7	2.1	37.4	36.1	25.7
			21.1	0	40.9	18.7	19.3	54.4	33.7	25.6
7	Female	Subadult	54.1	0	45.4	0	0.5	86.9	45.2	33.0
Mean			36.4	2.7	39.3	13.4	8.3	67.8	36.3	27.3

* Between 8:15 AM and 5:30 PM. Each seal was observed continuously for 254–540 min. The mean duration of observations was 431 min.

[†] \bar{T}_g , mean black globe temperature; \bar{T}_s , mean sand surface temperature.

[‡] Black globe thermometer was moved down the beach with the seal.

[§] Seal, but not the black globe thermometer, in partial or complete shade of seawall for 37.1 percent of time.

of the seal and the wetness of the seal and its substrate. Nor did the postures of the seals seem to be connected with the black globe and sand temperatures on the beach platform (Table 1).

The frequency of changes in posture appeared to be related to the environmental conditions, as well as the duration of exposure to these conditions. Thus, as the temperatures of the sand and black globe thermometers increased, the dry seal changed its posture more often (Figure 1). However, when a seal was wet by rain or sea, its rate of change of posture diminished. This is strikingly illustrated by data from seal number 3 (Table 1). On the first day this animal was observed, it rained for most of the time and the seal changed its posture only four times in 495 min. On the following day, which was dry and sunny, the same seal changed its posture 48 times in 540 min.

Orientation

To reveal any orientation of the seals with respect to the sun and wind, relatively long periods of time were needed in which the seals did not change their positions on the beach. Because of the movements of the seals between the beach platform and slope, this was not possible. Examination of segments of the records revealed an instance in which a seal's bearing remained unchanged for as long as 176 min. During this time the bearing of both the sun and the wind changed by 25°. The group of four seals that provided the data for Figure 3 retained their orientation on the beach slope essentially unchanged for 180 min, while the bearings of the individual seals differed from one another by as much as 180°. Although many maps were constructed depicting the position and approximate orientation of larger groups of seals, throughout the day, these maps were of little value in determining the orientation of the seals because individual animals could not always be identified and it was extremely difficult to record the movements of individuals in a large group of seals. In the absence of knowledge of the recent thermal history of individual animals

in a group, their orientation at any particular time could be misleading. Plots of the bearings of individual seals observed on separate days, together with those of the sun and wind throughout the day, did not reveal any readily discernible pattern.

Wallows

As reported by Kenyon and Rice (1959), some of the seals lay in depressions (wallows) in the sand. In part, the wallows appeared to be formed inadvertently as the seals changed their posture. In addition, the seals sometimes actively burrowed into the sand with their muzzles as they moved forward. If the sand was wet, this resulted in the adherence of a considerable amount of sand to the face of the animal. There seemed to be little relationship between the incidence of wallows and the meteorological conditions. Wallows were excavated by some seals in dry sand on the beach platform, in the evening, or at night. In addition, they were formed in wet sand on the beach slope, either by seals that had moved down from the platform, or by animals that had recently come ashore. In one instance, a seal lay in a wallow on a cloudy, rainy day on Tern Island, when heat stress was clearly not a factor in the wallowing behavior. The deepest wallows seemed to be produced by adult seals, and the incidence of wallow formation seemed to be highest among adults. (A heavy animal is more likely to disturb the sand when it moves.) The incidence of wallowing during the day was relatively low; in 26 records of groups of seals consisting of 7 to 23 individuals, the mean percentage of seals in wallows was 10.1 percent. The highest number (7) was recorded from a group of 20 seals on the wet sand of a sandspit attached to Trig Island. Measurements made on two wallows revealed depths of 16 and 16.5 cm, respectively. Surrounding each wallow was a ridge of sand 6.0 to 10.5 cm, respectively, above the level of the adjacent sand. It may be seen from Figure 5 that the temperature of the sand at a depth of 7.5 cm was as much as 5° C lower than that at the surface, although the temperatures varied with the time of day, the meteorolog-

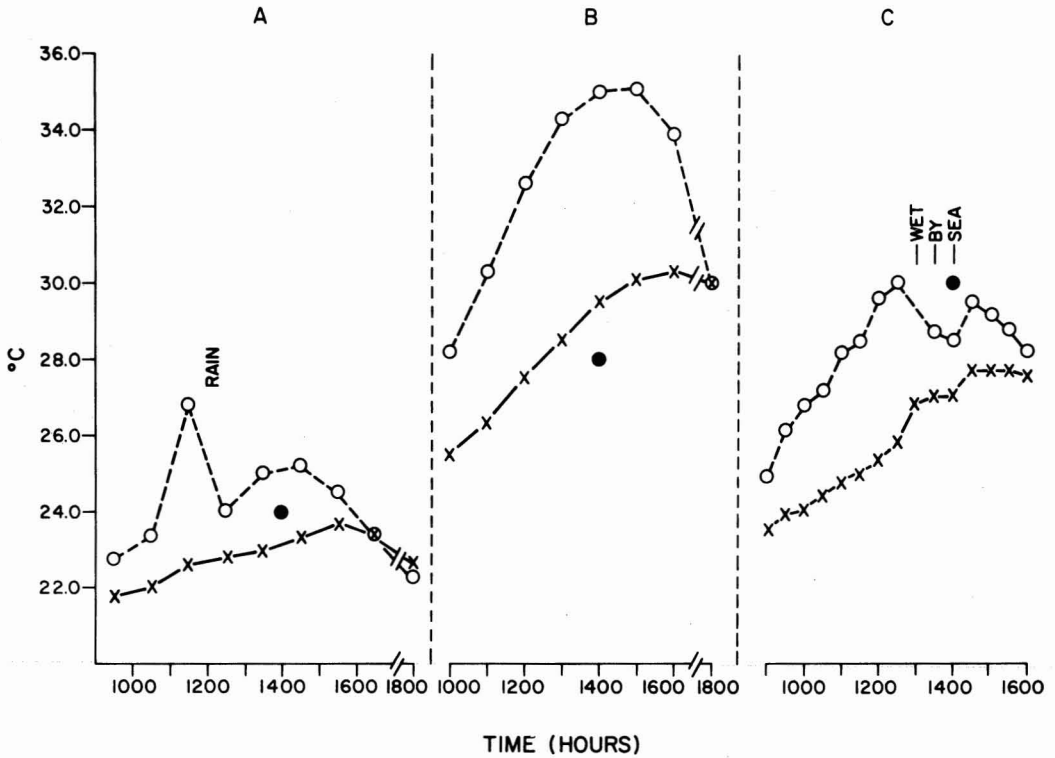


FIGURE 5. Sand temperatures on the surface (o---o) and at a depth of 7.5 cm (x---x) on the beach slope. A, Tern Island, March 1977; B, Tern Island, August 1976; C, Trig Island, October 1976. ● = dry-bulb air temperature recorded by U.S. Coast Guard, Tern Island.

ical conditions, and probably other features of the beach.

Shade

On some of the islands at French Frigate Shoals, there is no shade. On others, shade is provided only by one or two low bushes (*Tournefortia argentea*). On Tern Island, there is more extensive natural shade and also the artificial shade provided by seawalls and buildings. In only one instance was a seal observed to seek shade in the middle of the day. However, this animal (number 5, Table 1) was wet when it sought shade at 1:13 PM, and it was returning to a position that it had occupied overnight. As far as could be determined, therefore, this seal was not seeking shade to ameliorate heat stress. However, probably because of the shade, the animal was able to remain in this position

for the rest of the day, in spite of the fact that the black globe temperature in the sun remained above 40°C for the next 3 hr.

On one occasion on Trig Island, it was observed that the last seal to leave the platform in the morning was a large adult in the shade of a small bush. The animal was also molting and this may have been a factor in determining its behavior. However, a similar phenomenon has been observed by Karl W. Kenyon (personal communication) on Laysan Island, where there is extensive natural shade from *Scaevola* bushes. In the area of observation on Laysan Island, the first seals to leave the beach platform, at 8:45 AM, were an adult female seal and her pup, which were between the bushes but not shaded from the sun. The last seal to leave was an adult male animal that had slept in the shade of a bush.

Radiometer readings of the temperature

TABLE 2

MEAN SURFACE TEMPERATURE \bar{T}_{cs} OF THE HAIR COAT OF HAWAIIAN MONK SEALS UNDER DIFFERENT CONDITIONS

CONDITION OF COAT	\bar{T}_{cs} (°C)	RANGE (°C)	NUMBER OF MEASUREMENTS, <i>n</i>
Dry coat on dorsal surface exposed to sun	40.6	36–47	32
Dry coat on ventral surface exposed to sun	35.5	30–40	13
Wet or damp coat on dorsal surface exposed to sun	37.4	32–42	8
Wet or damp coat on ventral surface exposed to sun	31.0	28–34	8

of the sand between *Tournefortia* bushes on Tern Island often indicated surface temperatures in excess of 50° C. There was less air movement among the bushes, and the sand was darker than that on the beach slope, due to admixture with guano.

Other Behavior

The seals made some movements that did not result in a change of posture or position on the beach. These included raising the hind flippers and caudal part of the abdomen off the sand and rubbing the flippers together. Occasionally, a seal raised the greater part of its body off the sand and flopped back into the same position. Another activity consisted of rubbing the face and flank with one of the front flippers. Seals seemed to do this when they were dry and apparently uncomfortable. Sometimes, seals turned completely around on the long axis of their body and then resumed their original position. While in the prone position, seals had the choice of tucking their front flippers in close to the body or spreading them. Insufficient data were obtained to indicate a firm relationship between the position of the front flippers and other variables. However, in several seals, including the captive specimen, the front flippers were spread when a wet animal lay in the prone posture. As the seal dried, it tucked its front flippers in close to its flanks, possibly as a response to evaporative cooling of the skin.

Apart from brief moments of alertness when the seals changed their posture, moved down to the beach slope, or executed the other movements described above, they were completely inactive when ashore, and slept for the entire time. Although it was not an objective of the present study to record how long seals were ashore, several animals were observed on consecutive days, and the approximate times of their arrival and departure revealed that the seals may stay ashore for 2 to 3 days. More extensive observations by Karl W. Kenyon and Mark J. Rauzon and by B. W. Johnson and P. A. Johnson (personal communications) have established the duration of the seals' stay ashore.

Coat Temperatures

The surface temperature of the dark fawn hair on the dorsal surface, and also that of the very light fawn hair on the ventral surface of the seals, was measured in a number of animals under a variety of conditions. In spite of variations in the length of time a particular surface had been exposed to solar radiation, in the intensity of radiation, in wind velocity, and other factors, the mean temperature of the dry dorsal surface was significantly higher ($t = 4.77$; $p < 0.001$) than that of the dry ventral hair (Table 2). Data from individual animals in which the temperatures of the dorsal and ventral surfaces were measured simultaneously disclosed that the light ventral hair coat was cooler

TABLE 3
BREATHING PATTERN AND HEART RATE IN THE HAWAIIAN MONK SEAL

	MEAN	RANGE	NUMBER OF OBSERVATIONS, <i>n</i>
Duration of one breath-holding period (sec)	236.7	66-453	50
Duration of breathing period (sec)	155.9	76-343	25
Number of breaths during breathing period	13.5	7-23	25
Heart rate during breath-holding period (beats per minute)	49.8	40-80	51

than that of the darker dorsal hair, even when the latter was exposed less directly to the sun. The coat temperatures were lower when the hair was wet, as might be expected, and although the dorsal hair was again warmer than that of the ventral surface, variations in the degree of wetness, which were difficult to assess, may also have contributed to these differences. For comparison with these data, the temperature of the dorsal surface of a seal that remained in the shade of a seawall on Tern Island for 150 min was measured. The seal remained in the prone position for the entire period, and it was intermittently wet by the sea. The temperature of the wet dorsal surface was 23 to 24° C throughout the 150-min period.

In an attempt to elucidate further the thermal properties of the coat, the surface temperature of a shallow dish (diameter, 14.0 cm; depth, 2.4 cm) of dry sand from the beach slope on Tern Island was compared with that of a similar dish covered with a section of the dark molted pelt of a seal. When both were simultaneously exposed to solar radiation under identical conditions, the temperature of the coat was 13 to 15° C higher than that of the sand. In another test, the internal temperature of two identical small metal globes (diameter, 44.6 mm) was measured during exposure to solar radiation. One globe was painted with Nextel Black Velvet Coating, while the other was covered with molted seal pelt. The temperature of the pelt-covered globe was higher than that of the black globe by 4.3° C. This was not due to the greater insulation of the pelt, with a corresponding reduction in convective heat loss from the globe, because, when the pelt-

covered globe was covered with several thicknesses of black cloth, which increased its insulation further, the temperature of the globe decreased by 5.6° C.

Breathing Pattern

In none of the seals observed was there any evidence of thermal polypnea or open-mouth panting. On the contrary, in all the animals studied, the pattern of breathing was similar, consisting of periods of apnea (breath-holding) alternating with periods of breathing. The duration of the period of breath-holding was as long as 453 sec; in general, the periods of breathing were shorter than the periods of apnea (Table 3).

The seals were more alert when they were breathing, but during the periods of apnea they could be approached without awakening them, and they appeared to be sleeping deeply. The captive seal at the Waikiki Aquarium frequently rested on the bottom of the pool and, while there, seemed to be asleep. The duration of its submergence, measured on four occasions, was found to vary from 267 to 342 sec. These voluntary dives were, therefore, of a similar order of magnitude to the periods of breath-holding of seals on land (Table 3). Between dives, the seal took 10 or 11 breaths in 96 to 120 sec; these values also were within the range of data for the breathing cycles of seals on land.

Heart Rate

The heart rate was relatively easy to count when the seals were breath-holding (apnea); the mean heart rate of the seals thus measured

was 49.8 beats per minute (Table 3). It was difficult to measure the heart rate when the seals were breathing; in the few instances in which counts were made, they were higher than the values during breath-holding.

DISCUSSION

The most important component in the Hawaiian monk seal's repertoire of thermoregulatory behavior is the movement of the seals during the day from dry sand on the beach platform to either wet sand on the beach slope or the edge of the surf itself. The cooler wet sand provides increased opportunities for both conductive heat loss to the sand and evaporative cooling from a wet seal. In addition, the mean radiant temperature of the environment on the beach slope may be less than on the platform because of the lower temperature of the wet sand and ocean. There is no doubt about the effectiveness of this behavior; the seals may stay on the beach slope all day, even when they are not wet by the ocean. A similar movement of Hawaiian monk seals on Laysan Island was reported by Butler and Udvardy (1966), who explained the movement of the seals in terms of evasion of flies on the beach platform. The progression of the seals down the beach at French Frigate Shoals cannot be attributed to flies, because there were very few flies on Tern or Trig Islands. The movement of northern elephant seals (*Mirounga angustirostris*) to the surf on Guadalupe Island, Mexico, was also clearly correlated with weather conditions (White and Odell 1971). Similar behavior has been reported for the California sea lion (*Zalophus californianus*) (Peterson and Bartholomew 1967), Steller sea lion (*Eumetopias jubatus*), Australian fur seal (*Arctocephalus forsteri*) (Gentry 1973), and others (White and Odell 1971). The movements of the seals provide some insight into their level of thermal comfort. Seals that moved down to the beach slope and were then wetted by the sea, often moved back up the beach onto dry sand. This occurred on sunny, warm days and, subsequently, the seals moved back down onto wet sand. The

most likely explanation for this behavior is that the seals had lost sufficient heat by evaporation and conduction to warrant their return to a warmer microclimate. They were, in fact, regulating their body temperature and comfort level by behavioral means.

Next in importance are the changes in posture. Turning over promotes heat loss from a seal in a number of different ways. Exposure of a moist surface on which it has been lying, permits evaporative cooling to occur. At the same time, a warm, dry area of the coat is brought into contact with cool, moist, or wet sand. By directing the light-colored ventral surfaces and parts of the flanks to the sun, a seal may also reduce solar heat gain (see below). However, the thermal benefits of changes of posture alone are not sufficient to permit a seal to remain on dry sand throughout the day, except during cloudy or exceptionally windy conditions. As the sand temperature rises, when the sun is not obscured by clouds, heat loss from a seal will diminish, so that it derives less benefit from each change of posture. This will tend to lead to an increase in the rate of change of posture. However, the changes in posture may be of little value, or even become self-defeating, if their frequency increases to the point where the metabolic heat generated by turning may equal or exceed the enhanced heat loss secured by turning over. It is presumably at this point, or before this point, that a seal moves to the beach slope.

The coat occupies a strategic position in the monk seal's efforts to mitigate the effects of heat stress. The relatively low surface temperatures of the pale hair on the ventral surface may indicate a high reflectance for solar radiation, although this can only be determined with certainty by precise measurements of the reflectance of a monk seal pelt (using a solarimeter). A low coat surface temperature does not necessarily imply a low rate of solar heat gain by the animal. It has been demonstrated both in the ox (*Bos taurus*) (Hutchinson and Brown 1969) and in the harp seal (*Pagophilus groenlandicus*) (Ortsland 1971) that solar radiation penetrates the hair coat by reflection from hair to hair toward the skin and that penetrance is

greater for light-colored coats. This might explain the higher temperature of the globe covered with monk seal pelt in the present study, although it may have been an artifact resulting from the small radius of curvature of the globe. However, Ray and Smith (1968) note that the surface temperature of the pelt of the Weddell seal (*Leptonychotes weddelli*) exceeded the black globe temperature in the sun, and they discuss the possibility of a greenhouse effect of the coat, permitting more thermal radiation to penetrate the coat than to escape through it. While this effect would be to the advantage of a seal in the Antarctic, it would clearly not benefit a tropical seal. A more extensive study of the properties of the Hawaiian monk seal's coat, with regard to the absorption of solar radiation, is warranted. It would be interesting also to obtain information on the reflective properties of the black coat of the pup (Kenyon and Rice 1959). White and Odell (1971: 762, 773) reported that the northern elephant seal's "usual posture, prior to sand flipping, was supine or semi-supine." They believed this exposed the "most reflective area of the body." It would be interesting to know the degree of penetration of solar radiation into the coat of this species also.

The metabolic heat production of seals during spontaneous breath-holding on land has never been determined. However, by analogy with the diving response (Irving 1973), the long periods of apnea and relatively low heart rate in the monk seal raise the possibility that the metabolic rate diminishes during breath-holding. A similar pattern of breathing was noted in the northern elephant seal by Bartholomew (1954). Other features of the monk seal's behavior are also consistent with a low level of metabolic heat production while it is ashore. Thus, the absence of any territorial or social behavior of the seals while on land, the prolonged sleep, and the absence of dramatic, but energy-consuming, behavior such as sand-flipping or flipper-waving, all point to a low heat production. The complete inactivity of the seals when they are ashore may well be one of their most efficacious adaptations to the hot environment in which they live. However,

this also implies that much of their social and reproductive behavior must take place in the sea, with a correspondingly increased risk of predation by sharks. In contrast, may other pinnipeds have elaborate patterns of behavior and activity on land (Peterson 1968).

The wallowing behavior of the seals is, in some ways, an enigma. There is no doubt that a wallow is beneficial to a seal, in the sense that it exposes cool, wet sand and thereby promotes conductive heat loss. At the same time, a smaller surface area of the seal is exposed to solar radiation so that solar heat gain is presumably reduced. The advantage of this is offset to some extent by the lower surface area available for convective heat loss. The fact that much of the excavation of the wallow is incidental to changes of posture does not detract from the thermal advantages of a wallow to a seal. However, the proportion of seals that occupy wallows is not large and the construction of some wallows is not warranted by the environmental conditions. This raises the question whether the active component in the construction of a wallow—the gouging of sand with the muzzle—may be for reasons unconnected with heat transfer, such as altering the level of the sand on which the muzzle rests. The only other seal known to excavate wallows is the northern elephant seal (White and Odell 1971). Wallowing is easier to explain in this species than in the monk seal, because sand surface temperatures are higher on Guadalupe Island, where the elephant seals breed, than in the northwestern Hawaiian Islands. The exposure of cool, wet sand may also be allied with the sand-flipping behavior of the elephant seals. In addition, elephant seals have a complex social structure on land.

Although air temperatures in the northwestern Hawaiian Islands are relatively high, and the levels of solar radiation are very high, the overall heat stress imposed by the environment is attenuated by the strong tradewinds and the high reflectance of the white coral sand to solar radiation, which result in lower sand surface temperatures than might be expected. Nevertheless, Hawaiian monk seals are unable to tolerate these conditions

without behavioral augmentation of conductive and evaporative heat loss. Hawaiian monk seals also haul out on the rocky substrate of Necker Island in the northwestern Hawaiian Islands. The temperature of the black lava rock surface would be expected to be considerably higher than that of coral sand. It is noteworthy, therefore, and consensual with conclusions drawn from the seals at French Frigate Shoals, that monk seals on Necker Island make frequent use of rock pools (G. H. Balazs, personal communication). In addition, seals have been observed to haul out on coral rock surfaces on Laysan Island, and here, also, they utilize rock pools (B. W. Johnson and P. A. Johnson, personal communication).

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