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Body Temperature and Heat Transfer in the Green Sea Turtle, *Chelonia mydas*

MARTHA E. HEATH AND SAMUEL M. MCGINNIS

The deep body temperature (T_{db}) of adult and juvenile green sea turtles in thermal equilibrium with their environment is consistently 1–2.5 C above ambient temperature (T_a). This gradient and a constant heat loss indicates a degree of endothermy in this species. The heat production, however, is not solely attributable to muscular activity since the temperature gradient between T_{db} and T_a exists even during inactivity. The difference between T_{db} and T_a is greater in a 20 C than in a 30 C environment. This is due to a greater conductivity of the peripheral tissues and therefore greater rate of heat loss at 30 C than at 20 C rather than to a higher rate of heat production at 20 C.

Adult turtles became inactive when presented with warm (26–28 C) water. This is viewed as a mechanism which permits aquatic basking.

ALTHOUGH sea turtles are widely distributed and have been reported to occur in cold as well as warm water, studies on their temperature tolerances and thermoregulatory capacity have been sporadic. Hirth (1962) found that green turtles (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) which were nesting had cloacal temperatures a few degrees above the temperature of the water from which they came. Frair et al. (1972) reported deep body temperature (T_{db}) in leatherback turtles (*Dermochelys coriacea*) to be as much as 18 C above ambient temperature (T_a). Other studies on the effect of T_a on the emergence of hatchlings (Bustard, 1967; Mrosovsky, 1968) and on the rate of O_2 consumption of hatchlings (Mrosovsky and Pritchard, 1971) have been reported. No study, however, has provided continuous comparisons of T_{db} and T_a or measured the rate of heat transfer in a species of sea turtle. The purpose of this work is to investigate the effect of T_a on the T_{db}, heat transfer and behavior of juvenile and adult green sea turtles.

MATERIALS AND METHODS

Experimental animals.—Four adult (50–60 kg) and five juvenile (2–4 kg) green turtles were used. Newly captured adult turtles were obtained from a fishery near Bahia de Los Angeles in Baja California, Mexico. The juvenile sea turtles were obtained from Mariculture Ltd., Grand Cayman Island, British West Indies and maintained in water of 20–24 C when in captivity.

Measurement of T_{db} in adults.—The T_{db} of adult turtles swimming in the large lagoon on Smith Island in the Gulf of California was monitored continuously by radio telemetry for a period of 1.5 days. Each animal was fed a miniature radio transmitter (McGinnis, 1968a) encapsulated in

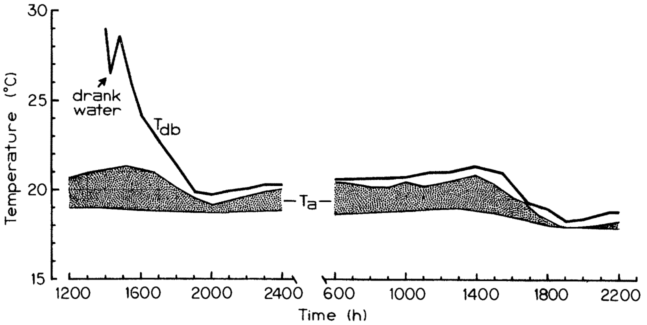

Fig. 1. A 1.5 day diurnal record of the deep body temperature (T_{db}) of an adult green sea turtle freely swimming in a lagoon, and the range of ambient temperatures (T_a) which it would encounter.

a plexiglass container. The signal from the ingested transmitter was received by a circular antenna attached to the periphery of the turtle's carapace with wire clips. A 10 m long coaxial cable carried the signal to a small buoy at the water's surface. The buoy contained a device that boosted the signal so that it could be received on shore (McGinnis, 1970). The temperature of the surface and benthic water was measured with a YSI telethermometer. All temperatures were recorded at 15 min intervals.

Effect of solar radiation.—Subsequent to the measurements made in the lagoon, two miniature thermistors were attached to the middle of the carapace of the adult turtles. One probe was positioned on the dorsal surface and the other was attached to the ventral surface of the carapace after being passed through a small hole in the shell. T_{db} was measured via the previously ingested radio transmitter. The turtle was restrained on a sand beach in central Baja California, Mexico during mid-day in late May, thus exposing it to intense solar radiation. T_{db} and carapace temperatures were recorded at 15 min intervals for 2.5 h. Recording continued when the turtles were subsequently released in an aquatic enclosure.

Measurement of T_{db} and heat flow in juveniles.—As in the adults, the T_{db} of juvenile turtles were monitored by miniature radio transmitters. Heat flow (HF) from the carapace, plastron, scaled area of the head and flippers, and soft skin of the neck and proximal flippers was measured with Hatfield HF discs (Hatfield, 1950). The discs were held in place with an elastic band, and a heat conducting paste (Thermopath) was applied between the disc and tissue. Measurements of T_{db} and HF were made while the subjects were a) inactive and actively swimming, b) warming in water after being transferred from 20 C water to 30 C water, and c) cooling in water after being transferred from 30 C water to 20 C water. These experiments were carried out indoors and thus not affected by solar radiation.

The conductance (K) of each epidermal covering was calculated using the equation:

$$K = \frac{HF}{T_{db} - T_a} \quad \text{(Mount, 1968)}$$

where HF = W/m² and T_{db} and T_a = °C. The rate of total heat loss from the turtles was estimated by multiplying the rate of heat flow from each type of epidermal covering by the surface area of that covering and then sum-

TABLE 1. THE CONDUCTANCE ($\bar{x}$ ± SD) OF THE SOFT WHITE SKIN, PLASTRON, CARAPACE AND SCALED SKIN WHEN TURTLES (N = 5) ARE AT THERMAL EQUILIBRIUM IN 20 C WATER AND 30 C WATER.

Ambient temperature	Conductance (W/m²·C)			
	Soft white skin	Plastron	Carapace	Scaled skin
20 C	0.0976 ± 0.000007	0.0389 ± 0.00003	0.0149 ± 0.00004	0.0136 ± 0.00018
30 C	0.1400 ± 0.00009	0.0707 ± 0.00007	0.0683 ± 0.00085	0.0784 ± 0.00385

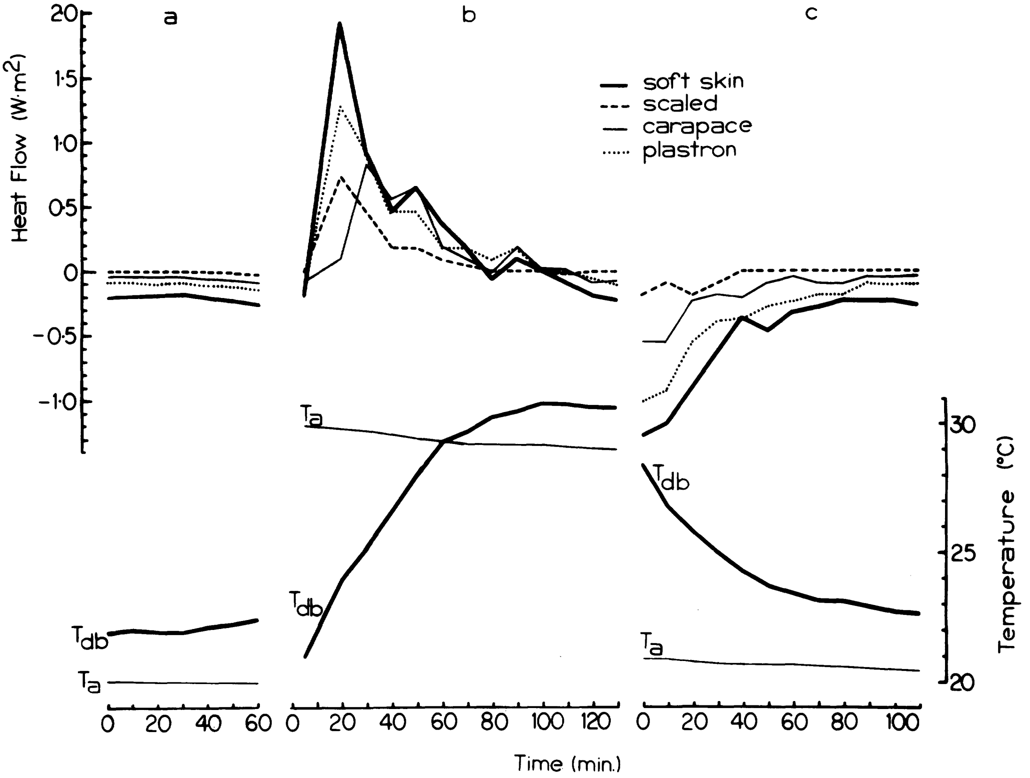

Fig. 2. The deep body temperature (T_{db}) and rate of heat transfer across the different epidermal coverings of a juvenile green sea turtle (positive values = heat flowing into turtle). In 2a, during the first 30 min the turtle was inactive and during the subsequent 30 min it was swimming continually. In 2b the turtle was transferred from 20 C water to 30 C water and in 2c the turtle was transferred from 30 C water to 20 C water.

ming these values. The surface area of each epidermal covering was estimated by outlining the surface on a paper and determining its area with a planimeter. This estimate assumed that the rate of heat flow was uniform throughout each epidermal covering.

T_a and activity.—Three adult and one subadult turtles were tested for their behavioral response to rising water temperature. The turtles were placed individually in a tank, 1.7 m in diameter, of 20 C water. The respiratory frequency and amount of activity of the turtles were monitored visually while the temperature of the water was raised slowly and subsequently lowered.

RESULTS

T_{db} of free-swimming adult turtles.—Fig. 1 shows a 1.5 day diurnal record of the T_{db} of a 50 kg pacific green sea turtle and the range of T_a of which it could come in contact. The abnormally high T_{db} at the beginning of the experiment was due to heat acquired while the turtle was held on the beach before being released. The rapid drop and subsequent rise in gut temperature shortly after release could have resulted only from the intake of water or food. The T_{db} of this and other turtles never fell below the temperature of the surface water and was as high as 2.5 C above the temperature of the benthic water. The animals swam slowly during most of the recording period and only contacted the surface water when breathing.

T_{db} and HF in captive juvenile turtles.—The T_{db} and rate of HF from a juvenile turtle in 20 C water is shown in Fig. 2a. During the first 30 min when the turtle was inactive at the water's surface its T_{db} was 2 C above T_a and heat was being lost to the environment. For the remain-

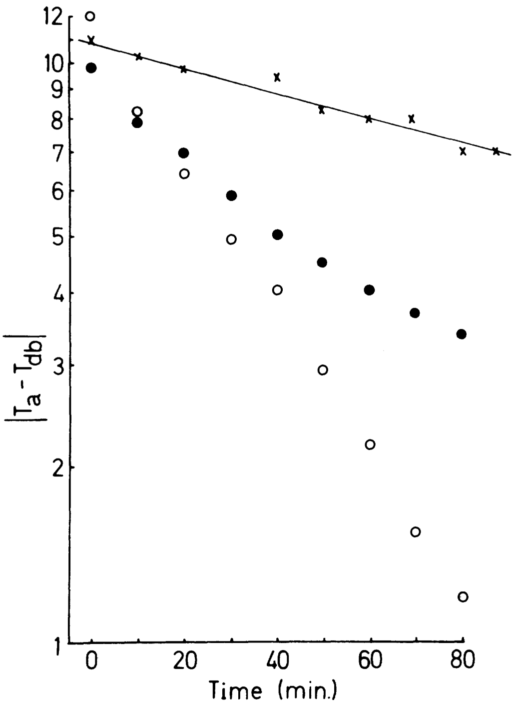

Fig. 3. The mean $|T_{db} - T_a|$ of three live juvenile green sea turtles during heating (o) and cooling (•) experiments and the rate of cooling in one dead turtle of similar mass (2–4 kg) as the live turtles.

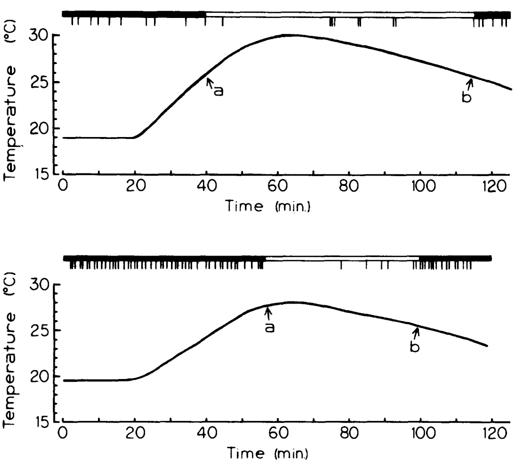

Fig. 4. The effect of water temperature (solid line) on the activity of the turtles (activity = black bar, inactivity = white bar) and their respiratory frequency (vertical lines). Arrow "a" is the ambient temperature at which each turtle became inactive as the water was heated, and arrow "b" is the ambient temperature at which each turtle resumed activity as the water was cooled.

ing 30 min when the turtle swam continuously its T_{db} rose by 0.4 C and the rate of heat loss increased. This indicates the extent to which activity contributes to heat production in turtles.

The HF data show that at 20 C (Fig. 2a) the rate of heat loss is greatest through the soft white skin of the neck and proximal area of flippers, followed by the plastron, carapace and scaled epidermis on the distal areas of the flippers, respectively.

In Figs. 2b and 2c are shown the effects of transferring a turtle from 20 C water to 30 C water and vice versa on T_{db} and HF. Subsequent to each transfer turtles were kept at the new T_a until thermal equilibrium (heat production + heat gain = heat loss) between the animal and the environment occurred. Again it is clear that the soft white skin is the interface of greatest heat flow while the scaled epidermis of the flippers plays a minimal role in heat transfer.

The rate at which the T_{db} of the turtles rose after they were transferred from 20 C to 30 C water was greater than the rate at which it fell after they were transferred from 30 C to 20 C water (Fig. 3). In contrast the heating and cooling rates were equal, and slower, in a dead turtle than in live turtles of similar mass (2–4 kg).

When the turtles were in thermal equilibrium with the environment, the difference between T_{db} and T_a was greater in 20 C water (2.20 ± 0.16 C; $\bar{x} \pm$ SD) than in 30 C water (1.68 ± 0.17 C; $\bar{x} \pm$ SD). In spite of this larger temperature gradient at 20 C, the rate of total heat loss was greater ($P < 0.02$; paired *t*-test) in 30 C water (0.02668 ± 0.000054W; $\bar{x} \pm$ SD) than in 20 C water (0.01482 ± 0.000007W; $\bar{x} \pm$ SD). Examination of the conductance of the different epidermal tissues at the two T_a (Table 1) shows that the conductance is greater in all tissues when the turtles are in 30 C water than when they are in 20 C water.

Behavioral responses to T_a.—When the temperature of the water was raised from 20 C towards 30 C, adult and subadult turtles became inactive (arrow a, Fig. 4) and markedly decreased their respiratory frequency when the temperature of the water reached 25–28 C. The turtles then floated at the surface of the water with at least half of their carapace exposed to air. The only movement during this period of inactivity was the raising of the nares above the water's surface during breathing. As the temperature of the water was subsequently lowered the turtles resumed activity when the temperature reached 27–28 C (arrow b). Of the four turtles tested, inactivity occurred at a water temperature of 26.9 ± 0.95 C ($\bar{x}$ ± SD). These temperatures correspond closely to the temperature of the surface water (27–28 C) in the southern Gulf of California from June to October. This range is also about 10 C below the lethal temperature of 37.5 C determined for two juvenile turtles by slowly warming their ambient water. This allows for a substantial increase in T_{db} from the onset of inactivity until a lethal temperature is reached.

Effect of exposure to solar radiation.—In Fig. 5 the effect of intense solar radiation on T_{db} and the temperature of the ventral and dorsal surfaces of the carapace are shown. During the first 30 min of exposure to intense solar radiation the temperature of the carapace rose by 6–7 C but subsequently rose more slowly so that a total increase of 9–10 C occurred over the entire 2.5 h period. In contrast, the T_{db} rose by only 1.2 C during the first 30 min and by only 4.6 over the entire 2.5 h. Since the sand on which the turtle was restrained was warm, some of the rise in T_{db} may be attributable to heat gain by conductance from the warm sand. The large difference in the rate at which the temperature of the carapace and the T_{db} rose shows that considerable insulation is present. The similarity of the temperature of the dorsal and ventral surfaces of the carapace indicates that the carapace per se is a good conductor of heat whereas the great difference in T_{db} and carapace temperature suggests that the insulation lies in the tissues below the carapace.

DISCUSSION

Previous studies where individual recordings of T_{db} made on adult green, ridley, leatherback and hawksbill sea turtles (Hirth, 1962; McGinnis, 1968b, Mrosovsky and Pritchard, 1971, Frair et al., 1972) have shown T_{db} to be above T_a. The present study confirmed this observation both for juvenile and for adult green turtles with continuous records of T_{db} and T_a. This elevation of T_{db} above T_a (Figs. 1, 2) and the continuous loss of heat during thermal equilibrium (Fig. 2) indicates a small degree of endothermy in this species.

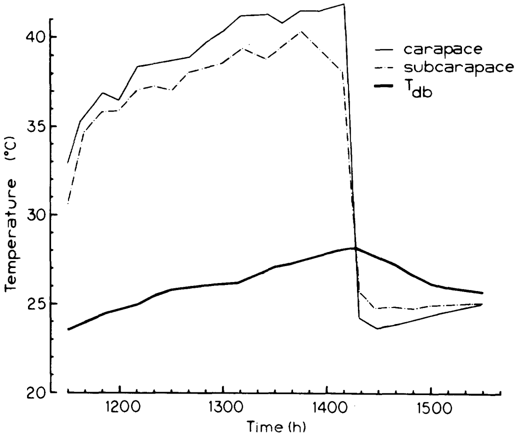

Fig. 5. The temperature of the deep body and the dorsal and ventral surfaces of the carapace when the turtle was beached and exposed to intense solar radiation for 2.5 h and subsequently released into an aquatic enclosure.

It has been suggested (Hirth, 1962; Frair et al., 1972) that the heat is produced by muscular activity. In the present study, however, it is shown that the elevation of T_{db} above T_a is maintained even during prolonged (2 h) periods of inactivity and that the difference is increased by activity (Fig. 2a). Thus the heat produced internally is not due solely to muscular activity.

Alternatively, it has been suggested (Mrosovsky and Pritchard, 1971, Frair et al., 1972) that the elevation of T_{db} above T_a is the result of thermal inertia and that turtles of greater mass retain more heat than turtles of lesser mass. This was not found to be the case in the present study in which the temperature difference was similar in juvenile (2–4 kg) and adult (50–60 kg) turtles in a T_a of about 20 C.

Although the green turtle appears to have some degree of internal heat production it does not necessarily follow that this species actively thermoregulates. The discovery, however, that the difference between T_{db} and T_a was greater at 20 C than at 30 C may suggest active thermoregulation. This difference can only be explained by the turtles a) losing heat more rapidly at 30 C, b) producing heat more rapidly at 20 C, or both. Likewise, the finding that the turtles heat faster than they cool (Fig. 3), which may indicate active thermoregulation, can be explained by either or both of these hypotheses.

That the rate of heat loss is greater at 30 C than at 20 C, and that the conductance (Table

1) of the peripheral tissues is greater at 30 C than at 20 C supports hypothesis a). On the other hand, since at thermal equilibrium heat loss is equal to heat production (Kleiber, 1975), heat production must be greater at 30 C than at 20 C which disproves hypothesis b). Thus if the turtles are actively thermoregulating they appear to be doing so by vascular changes which affect the conductance of the tissues. This is supported by the fact that in dead turtles in which blood flow is not a factor, heating and cooling rates are equal.

In addition to the green turtle, the agamid lizard (Bartholomew and Tucker, 1963), Australian skink (Bartholomew et al., 1965), marine iguana (Bartholomew and Lasiewski, 1965), alligators (Smith, 1976), fish (Spigarelli et al., 1971) and pond turtles (Spray and May, 1972) heat faster than they cool. This difference in heating and cooling rates has often been attributed to active thermoregulation in these species (Bartholomew et al., 1965; Smith, 1976). It has been shown, however, that peripheral blood vessels respond directly to increases and decreases in temperature by dilating and constricting, respectively (Cowles, 1958; Heath et al., 1968; Morgareidge and White, 1969). Thus, as pointed out by Crawshaw (1979), the differences in heating and cooling rates may not be due to responses by the thermoregulatory center but to the direct response of vascular tissue to changes in temperature.

It is also possible that the vascular arrangement in the limbs of green turtles is like that found in the leatherback turtle (Greer et al., 1973) and function as a counter current heat exchange system. Such a mechanism would account for the lack of heat loss from the limbs in 20 C water. In addition, it is obvious from the present study that the carapace per se of the green turtle is a good conductor of heat and that it is the tissues between the carapace and the visceral cavity which provides insulation (Fig. 5). A counter current heat exchange may also occur in these tissues. It is obvious that more study of the anatomy and physiology of the vascular system of sea turtles is necessary to determine the extent to which they use vascular control to thermoregulate.

The observation (Fig. 4) that sea turtles become inactive in warm (25–28 C) water is interesting since it is the opposite of the response of increased activity at high temperatures observed in many ectotherms (Templeton, 1970). Native fisherman in the Gulf of California have reported large flotillas of green turtles during the summer months in the southern gulf. These observations correspond to the June to October period when the surface water in the southern gulf is 27–28 C. This behavior contrasts with their normal behavior of surfacing only briefly for breaths of air. Although this inactivity could be viewed simply as resting at the surface, we consider it a thermoregulatory behavior since it occurs in response to warm water (25–28 C). Indeed, lingering in warm water and absorbing solar radiation via the carapace are the only means by which a turtle at sea can bask.

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Thermal Influences on the Swimming Speed of Loggerhead Turtle Hatchlings

JAMES O'HARA

Loggerhead turtle hatchlings in laboratory tanks had a sustained swimming speed of approximately 20 cm/sec at temperatures between 25.6 and 28.9 C. Test temperatures of 30.0 and 33.0 C significantly reduced this speed. The swimming speed of hatchlings exposed to fluctuating temperatures varied with the temperature. A temperature of 33.0 C eliminated phototactic orientation.

ATLANTIC loggerhead turtles (*Caretta caretta*) nest on the barrier islands along the southeastern United States. One of the last major nesting rookeries is on Hutchinson Island, Florida, where resort motels, condominiums, restaurants and an electric generating facility are located.

Despite commercial development, large tracts of uninhabited beach still remain on the island. During summer nights, adult females crawl up the beach to deposit about 120 eggs in a 60 cm-deep nest hole. The eggs hatch 50–70 days later. The hatchling turtles dig out of the nest at night, then rapidly crawl across the beach and into the sea. Once there, the turtles must be able to swim rapidly to an area offering both food and shelter. They spend the rest of their lives in the sea, except for the mature female's beach nesting periods.

Hendrickson (1958) examined nest emergence of green turtles (*Chelonia mydas*) and suggested that temperatures over 33 C inhibit nest chamber activity and that hatchlings resume activity only with the return of lower nocturnal temperatures. Mrosovsky (1968) substantiated Hendrickson's observations, but specified 28.5 C as the temperature at which green turtles become lethargic in the nest. Both authors agree that thermal inhibition of activity is a major factor limiting the emergence of hatchling sea turtles. Nocturnal emergence can enhance hatchling sea turtle survival, therefore, by protecting them from the high surface temperatures on tropical beaches and by reducing both water loss and attacks from visually-oriented predators.

Studies on green turtles indicate the sea-finding process to be primarily visual and the brighter portion of the environment (under natural conditions, over the ocean) attracts the