Effects of Diving and Swimming Behavior on Body Temperatures of Pacific Leatherback Turtles in Tropical Seas

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Accepted 5/26/04; Electronically Published 3/4/05

ABSTRACT

Mathematical models and recordings of cloacal temperature suggest that leatherback turtles (*Dermochelys coriacea*) maintain core body temperature higher than ambient water temperature (T_W) while freely swimming at sea. We investigated the thermoregulatory capabilities of free-ranging leatherbacks and, specifically, the effect that changes in diving patterns and ambient temperatures have on leatherback body temperatures (T_B). Data loggers were used to record subcarapace and gastrointestinal tract temperatures (T_{SC} and T_{GT}, respectively), T_W, swim speed, dive depth, and dive times of female leatherback turtles during internesting intervals off the coast of Guanacaste, Costa Rica. Mean T_{SC} (28.7°–29.0°C) was significantly higher than mean T_W (25.0°–27.5°C). There was a significant positive relationship between T_{SC} and T_W and a significant negative correlation between T_{SC} and dive depth and T_{GT} and dive depth. Rapid fluctuations in T_{GT} occurred during the first several days of the internesting interval, which suggests that turtles were ingesting prey or water during this time. Turtles spent 79%–91% of the time at sea swimming at speeds greater than 0.2 m s^{-1}, and the average swim speed was 0.7 ± 0.2 m s^{-1}. Results from this study show that alterations in diving behavior and T_W affect T_B of leatherback turtles in the tropics. Body temperatures of free-ranging leatherback turtles correspond well with values for T_B predicted by mathematical models for tropical conditions.

Introduction

Most reptiles use behavioral means, such as postural adjustments or movements between different thermal microclimates, to maintain body temperature (T_B) within a preferred range (Avery 1982). In very large reptiles, behavioral adjustments in combination with the effect of large mass and the resultant thermal inertia may contribute to the establishment and maintenance of a large thermal gradient between T_B and ambient temperature (Colbert et al. 1946; Seebacher et al. 1999). For example, saltwater crocodiles (*Crocodylus porosus*; ≤1,010 kg) are able to maintain a high and stable T_B (varying from 27.5° to 35°C seasonally) in relation to ambient water temperature (T_W; 21°–30.5°C) by shuttling between sun and shade and land and water (Seebacher and Grigg 1997; Seebacher et al. 1999). Thermal gradients between T_B and T_W have also been documented for several species of sea turtles, even though the options for behavioral thermoregulation are more limited for these strictly aquatic species than for amphibious species such as *C. porosus*. Sato et al. (1995) found that loggerhead turtles (*Caretta caretta*; 56–107 kg) maintained core T_B (measured via thermistor pills implanted in the stomach) higher than T_W, while freely swimming at sea, and did so primarily through generation of metabolic heat rather than through absorption of solar radiation via basking. The difference between mean T_B and mean T_W for loggerhead turtles in that study was 0.7°–1.7°C (Sato et al. 1995). Adult green turtles (*Chelonia mydas*; 110–121 kg) can elevate T_B 1°–3°C above T_W (Mrosovsky 1980; Standora et al. 1982; Sato et al. 1998), although T_B of smaller juvenile turtles (10–24 kg) is not significantly different from T_W (Read et al. 1996; Southwood et al. 2003*b*).

The leatherback turtle (*Dermochelys coriacea*; ≤1,000 kg) is the largest extant species of sea turtle and achieves the most impressive thermal gradients between T_B and environmental temperatures. Body temperatures of adult female leatherback turtles on tropical nesting beaches, as inferred from egg temperature immediately after deposition, are 2.2°–5.1°C higher than surf T_W (Mrosovsky 1980), and T_B of leatherback turtles captured while migrating off the northeast coast of the United States are up to 18°C higher than ambient air or water temperature (Frair et al. 1972; Standora et al. 1984). Paladino et al. (1990, p. 860) proposed that leatherback turtles were capable of maintaining "constant, high body temperature by means of

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Physiological and Biochemical Zoology 78(2):285–297. 2005. © 2005 by The University of Chicago. All rights reserved. 1522-2152/2005/7802-4022$15.00

Table 1: Summary information for instruments deployed on leatherback turtles nesting at Playa Grande, Costa Rica

Date/Turtle Tag No.	Curved Carapace Length (cm)	Mass (kg)	Instrument	Date Deployed	Date Recovered	Internesting Interval (d)	Documented Returns
1996–1997:							
8866	145.0	244[c]	TDTR	November 9	November 18	8.9	4
7610	166.0	381[c]	TDTR	November 14	November 22	8.9	3
1997–1998:							
3800[a]	155.0	267	TDTR/STT/HTR	November 30	December 18	18.5[d]	3
3800[b]	155.0	267	Mk6 TDR/STT/HTR	December 18	December 27	9.0	2
8364	155.0	310	TDTR/STT/HTR	December 4	December 16	11.5	6
9861	158.0	329	Mk6 TDR/STT/HTR	December 20	December 29	8.1	4
2373	146.0	251	Mk6 TDR/STT/HTR	December 21	December 28	7.1	1

Note. Documented returns are the number of times the turtle returned to the beach to lay eggs after the instruments were deployed.

[a] First monitored internesting interval for 3800. Due to a malfunction of the data logger, data were recorded for only the first 5 d of this internesting interval.

[b] Second monitored internesting interval for 3800.

[c] Mass estimated using length-width regression calculated with data from Eckert et al. (1989) and unpublished mass data from Playa Grande nesting females.

[d] It is likely that this period of time represents two internesting intervals. This turtle may have emerged on the beach to nest at some time during this period, and we may have failed to detect her radio beacon.

large body size, low metabolic rate, and use of peripheral tissues as insulation" and presented a mathematical model to describe theoretical values for T_B under varying physiological and environmental conditions. Their model shows that variations in the level of blood flow between the core and periphery could effectively be used to insulate the core and create large thermal gradients between core T_B and T_W. Other studies have noted that leatherback turtles have a circulatory countercurrent heat exchanger in their flippers (Greer et al. 1973) and large deposits of fat beneath their carapace (Frair et al. 1972; Goff and Stenson 1988), which could also contribute to the leatherback turtle's ability to retain metabolically generated heat in the core.

The ability to elevate T_B above T_W is thought to be an important aspect of the leatherback turtles' biology that allows this species to venture into cold water (Paladino et al. 1990). Leatherback turtles have the widest geographic range of any reptile, with migratory routes that take them from nesting beaches in the tropics to foraging grounds at temperate and subpolar latitudes (Bleakney 1965; Goff and Lien 1988; James and Herman 2001). The maintenance of high, stable T_B may very well be the means by which leatherback turtles exploit high latitude environments that are inhospitable to other species of sea turtles, but to date there have been no recordings of T_B in free-ranging leatherbacks to support this concept. These measurements are necessary in order to validate the models that have been proposed to describe thermoregulation in this species.

Although isolated measurements have shown that leatherbacks can indeed create a large thermal gradient between T_B and T_W, the magnitude of that gradient under free-ranging conditions and the effects of changing environmental conditions on T_B have not previously been investigated. Also, the literature to date has focused on the physiological mechanisms that might contribute to the thermoregulatory abilities of leatherback turtles, with little attention given to the potential role of behavioral adjustments in regulating T_B in this species. Given the importance of behavioral adjustments in thermoregulation in many other reptiles, the possibility that leatherback turtles use behavioral means, such as basking or targeting T_W at specific depths, in combination with physiological means to regulate T_B deserves consideration. Behavioral means of thermoregulation may be particularly important in tropical climates, where heat loss is potentially more important than heat retention for maintaining preferred T_B.

We recorded subcarapace and gastrointestinal tract temperatures (T_{SC} and T_{GT}, respectively), T_W, swim speed, and diving behavior of free-ranging female leatherback turtles in tropical waters. Our primary goals were (1) to determine if leatherback turtles maintained T_B significantly higher than T_W while freely swimming at sea, (2) to determine the degree to which leatherback T_B is affected by alterations in T_W and diving patterns, and (3) to use field data on leatherback T_B to evaluate mathematical models used to describe thermal relations in this species.

Material and Methods

Field Procedures

From late October to early March, leatherback females come ashore to lay eggs on nesting beaches along the Pacific coast of Central America. During the nesting season, a female turtle may lay as many as 10 clutches of eggs on the beach, returning to the offshore waters for an average of 10 d between nesting (Steyermark et al. 1996). The leatherback turtle's instinctive behavior of repeatedly returning to the same beach during a

Table 2: Diving and swimming behavior of leatherback turtles during internesting intervals off the coast of Guanacaste, Costa Rica

Turtle Tag No.	Number of Dives Analyzed	Dive Depth (m)	Dive Time (min)	SI Duration (min)	Time Submerged (%)	Swim Speed ($m\ s^{-1}$)	Maximum Swim Speed ($m\ s^{-1}$)	Time Swimming (%)
8866	936	22 ± 20	8.7 ± 5.9	3.9 ± 2.0	69	…	…	…
7610	1,024	22 ± 21	6.9 ± 4.8	3.9 ± 2.8	64	…	…	…
3800[a]	321	72 ± 32	13.8 ± 5.2	4.3 ± 2.1	76	.9 ± .4	3.8	91
3800[b]	776	41 ± 25	13.0 ± 5.9	2.8 ± 1.4	82	.6 ± .1	1.6	88
9861	859	51 ± 30	10.3 ± 5.3	2.5 ± 1.3	80	.6 ± .1	1.9	89
2373	800	27 ± 15	11.7 ± 6.0	2.4 ± 1.5	83	.6 ± .2	1.8	79
Grand mean ± SD[c]	879 ± 102	33 ± 13	10.1 ± 2.4	3.1 ± .7	76 ± 9	.7 ± .2	2.3 ± 1.0	87 ± 5

Note. Data are presented as the mean ± SD. SI = surface interval.

[a] Dive statistics from the first monitored internesting interval for turtle 3800. Due to a malfunction of the data logger, data were recorded for only the first 4.8 d of this internesting interval.

[b] Dive statistics from the second monitored internesting interval for turtle 3800.

[c] Data from turtle 3800a were excluded from calculation of the grand mean and standard deviation because they do not represent the whole internesting interval.

single nesting season provides the necessary conditions for attachment and retrieval of data-recording instruments.

Our research was conducted at Las Baulas National Park in Guanacaste, Costa Rica, during the 1996–1997 and 1997–1998 nesting seasons. Radio transmitters and data loggers were attached to six leatherback females using procedures described in Southwood et al. (1999). The UBC Committee on Animal Care and the Costa Rican Ministry of Environment (MINAE 41220-5) approved all procedures. Curved carapace length (CCL) and curved carapace width (CCW) were measured for each turtle, and turtles 3800 and 8364 were weighed using a tripod and hanging scale after they completed laying eggs. Mass for turtles that were not weighed was estimated using a regression calculated from mass and curved carapace length from Eckert et al. (1989) and unpublished data from the Las Baulas National Park population of turtles (mass [kg] = 6.517 × CCL [cm] − 700.4; $r^2 = 0.71$; Table 1).

Instruments were attached to the turtle's shell as she laid eggs and camouflaged her nest cavity. Information for instrument deployment on individual turtles is summarized in Table 1. Custom-built data loggers (time-depth-temperature recorders [TDTRs]) capable of recording dive depth, dive duration, swim speed, water temperature (T_W), and subcarapace temperature (T_{SC}) were attached to the caudal peduncle of four turtles. An epoxy-encapsulated thermistor (Fenwal Electronics, Milford, MA) was used to detect T_{SC}. The thermistor was inserted to a depth of 10 cm with a 14-gauge needle at a point where skin and carapace fused above the right front flipper. Care was taken to position the thermistor along the inner surface of the carapace. Surgical silk sutures (Ethicon, Peterborough, Ontario, Canada) were used to secure the thermistor at the point of insertion. Holes (3.2-mm diameter) were drilled along the dorsal ridges, approximately 1 cm below the margin of the ridge, using a battery-powered, handheld drill so that the leads connecting the thermistor to the data logger could be secured to the shell. Six holes were drilled on the median ridge and two holes were drilled on the second ridge from the lateral ridge on the right side (Southwood et al. 1999). Holes were immediately flushed with Betadine antiseptic (Purdue-Frederick, Pickering, Ontario, Canada) and treated with antibiotic cream (Polysporin; Warner-Lambert, Scarborough, Ontario, Canada). The thermistor lead was secured to the shell using small cable ties passed through the holes.

The TDTRs had a waterproof lead connected to a paddlewheel transducer that could be used to measure swim speed (Andrews 1998). The transducer was positioned on the anterior third of the turtle's carapace on the median dorsal ridge and was secured to the carapace by tygon-coated flexible stainless steel wire passed through the drill holes. The lead connecting the transducer with the data logger was attached to the carapace by small cable ties passed through the drill holes.

Gastrointestinal tract temperature (T_{GT}) was recorded from four turtles using stomach temperature transmitters (STT; Andrews 1998) and receivers. Based on information from necropsies of stranded leatherback turtles, the STTs were designed to be small enough to pass through the pyloric sphincter and the remainder of the digestive tract of the turtle instead of remaining in the stomach indefinitely (R. George, personal communication). This precaution was taken to avoid the possibility of the STT blocking the gastrointestinal tract. STTs were inserted into the turtle's esophagus by hand. Although the STTs were only inserted 0.5 m into the esophagus, and therefore not directly into the stomach, we assumed that peristaltic action and ingestion of food and/or water during the internesting interval would help "push" the STT through the esophagus and into the stomach. The thermistors in the STT sensed T_{GT}, and

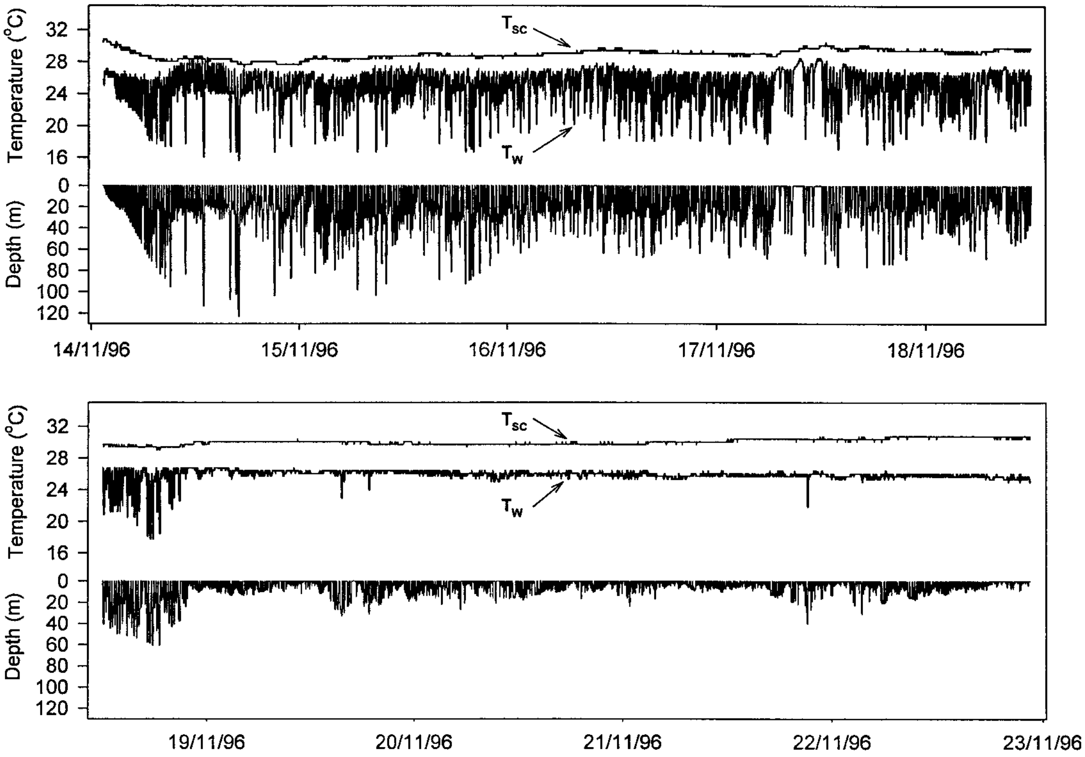

Figure 1. Dive profile, T_W trace, and T_{SC} trace recorded from turtle 7610 during her internesting interval. T_{SC} is maintained higher than T_W for the entire recording period. A shift in diving behavior occurred midway through the internesting interval, such that dives were significantly shorter and shallower during the second half of the interval compared with the first half. The shift in diving behavior was accompanied by an increase in mean daily T_{SC} and mean daily T_W.

this information was then transmitted to a heart-rate/stomach-temperature recorder (HTR, Wildlife Computers, Redmond, WA) for storage. The HTR was attached to the median dorsal ridge on the anterior third of the carapace with tygon-coated flexible stainless steel wire passed through two drill holes.

Of the four turtles from which T_{GT} was recorded, two of the turtles (3800 and 8364) were also equipped with TDTR data loggers so that dive variables, swim speed, and subcarapace temperatures could be monitored. The other two turtles (9861 and 2373) were equipped with Mk6 time-depth recorders (TDRs, Wildlife Computers) that recorded dive depth, dive duration, swim speed, and T_W. Mk6 TDRs were attached to the median dorsal ridge on the anterior third of the carapace in the same manner as the HTRs and swim-velocity transducers for the TDTRs.

Instruments

TDTRs (12.5 cm × 6 cm × 1.5 cm, 200 g) were deployed on two turtles (8866 and 7610) during the 1996–1997 nesting season and on two turtles (3800 and 8364) during the 1997–1998 nesting season. A full description of the instruments used with these four turtles can be found in Andrews (1998). TDTRs recorded dive depth every 5 s, swim speed every 10 s, and T_{SC} and T_W every 2 min. These instruments had 512 kilobytes (kb) of memory and recorded data for 9.5 d with the specified sampling intervals. Depth resolution of the TDTRs was 1 m over a range of 0–500 m. Swim-speed transducers were calibrated before use by placing them on a fiberglass model of a leatherback turtle in a swim flume. This calibration was checked and corrected for each individual turtle by comparing speed with the derivative of the scaled depth signal for every sampling interval (Andrews 1998). The transducers were calibrated over the range of 0.4–1.2 m s^{-1}. Stall speed for the swim-speed transducers was 0.2 m s^{-1}. Thermistors used to detect T_{SC} and T_W were calibrated in a water bath over the range of 10° to 35°C. Resolution of the temperature readings was 0.2°C.

Mk6 TDRs (7.4 cm × 5.7 cm × 3.0 cm, 70 g) were deployed on three turtles (3800, 9861, and 2373) during the 1997–1998 nesting season. Turtle 3800 was initially tagged with a TTDR on November 30, 1997. The TTDR was replaced with an Mk6 TDR when this turtle returned to nest on December 18, 1997. The first monitored internesting interval for turtle 3800, during which time the TTDR was deployed, will be referred to as 3800a. The second monitored internesting interval for turtle 3800, during which time the Mk6 TDR was deployed, will be referred

Table 3: Subcarapace temperature (T_{SC}), gastrointestinal tract temperature (T_{GT}), and water temperature recorded from leatherback turtles during the internesting interval off the coast of Guanacaste, Costa Rica

		Body Temperature (°C)			Water Temperature (°C)		
Turtle Tag No.	Hours Analyzed	Mean	Maximum	Minimum	Mean	Maximum	Minimum
T_{SC}:							
8866	213.8	29.0 ± 1.0	30.9	26.7	25.0 ± 2.3	28.1	15.7
7610	213.1	29.5 ± .8	31.1	27.3	25.2 ± 1.9	28.5	15.7
3800[a]	115.1	28.7 ± .4	29.7	27.8	27.5 ± 1.9	29.8	18.3
Mean ± SD	180.7 ± 56.8	29.1 ± .4	30.6 ± .8	27.3 ± .6	25.9 ± 1.4	28.8 ± .9	16.6 ± 1.5
T_{GT}:							
3800[a]	115.1	29.8 ± .6	34.4	24.5	...	...	...
8364	207.9	29.6 ± .5	33.9	28.2	...	...	...
9861	190.9	31.1 ± 1.2	33.1	27.6	...	...	...
2373	189.9	30.1 ± .8	31.5	28.0	...	...	...
Mean ± SD	176.0 ± 41.4	30.2 ± .7	33.2 ± 1.3	27.1 ± 1.7	...	...	...

Note. Data are presented as the mean ± SD.

[a] Dive statistics from the first monitored internesting interval for turtle 3800. Due to a malfunction of the data logger, data were recorded for only the first 4.8 d of the interval.

to as 3800b (Table 1). Dive depth and swim speed were sampled every 10 s, and the instrument had a depth resolution of 1 m over a range of 0 to 500 m.

STTs (diameter = 3.1 cm, length = 6.5 cm) and HTRs (1 cm × 5 cm × 7 cm, 60 g) were used to record T_{GT} from four turtles (3800, 8364, 9861, and 2373) during the 1997–1998 season. The STT consisted of four thermistor probes interfaced with a 5 kHz transmitter (Andrews 1998). STTs transmitted signals to the HTRs at a rate that varied with the temperature at the sensing thermistors, with higher temperatures corresponding to higher pulse rates (Andrews 1998). HTRs could record transmitted T_{GT} over a range of 0° to 40°C with a resolution of 0.2°C. STT thermistors were calibrated in the same manner as thermistors used for monitoring T_{SC} and T_W.

Statistics and Analysis

Dive data from the TDTRs and Mk6 TDRs were analyzed using the Dive Analysis (DA) program (Wildlife Computers). Submergence to depths of 4 m or greater were considered to be dives and were analyzed for maximum depth, dive duration, and postdive surface interval. Although the depth resolution of the data loggers was 1 m, we conservatively set the dive criterion at 4 m to account for the effects of wave action. Dive profiles recorded from Playa Grande leatherback turtles in the past show that turtles from this population typically make dives of 10 m or greater (Southwood et al. 1999).

A dive cycle was defined as an individual dive and the accompanying postdive surface interval. Dive depth was defined as the maximum depth attained during the dive. The turtle was considered to be at the surface if depth readings were less than the minimum dive criterion of 4 m. If turtles made a dive or a series of dives to depths less than 4 m, the analysis program would not be able to distinguish these dives from a surface interval. Dive cycles with surface intervals three times longer than the mean surface interval of the individual turtle were excluded from analysis to account for the possibility that turtles might have made shallow dives to depths above the dive criterion during these periods. Elimination of exceptionally long surface intervals also ensured that basking periods between dive bouts did not inflate the mean value for surface intervals occurring during a dive bout. Depending on the individual turtle, 1%–11% of all surface intervals were excluded from the dive cycle analysis by this criterion. Because we were interested in the effects of basking periods on body temperature, we looked at the extended surface intervals and associated body temperatures on an individual basis. The paired *t*-test was used to test for significant differences between mean T_{SC} and T_{GT} during extended surface intervals compared with periods of continual diving.

Spearman rank correlation was applied to time-series data to determine if there was a significant relationship between depth and $T_{W.}$ The relationship between mean daily depth and mean daily body temperature was also investigated using Spearman rank correlation. For the turtles from which both T_W and T_{SC} were successfully recorded (8866, 7610, and 3800), Spearman rank correlation was used to test for a significant relationship between mean daily T_W and mean daily T_{SC}, and the Student's *t*-test was used to determine if there was a statistically significant difference between mean T_W and mean T_{SC} for the entire internesting interval. Linear regression was used to investigate the relationship between body mass and mean body temperature. Differences were considered significant at $P<0.05$.

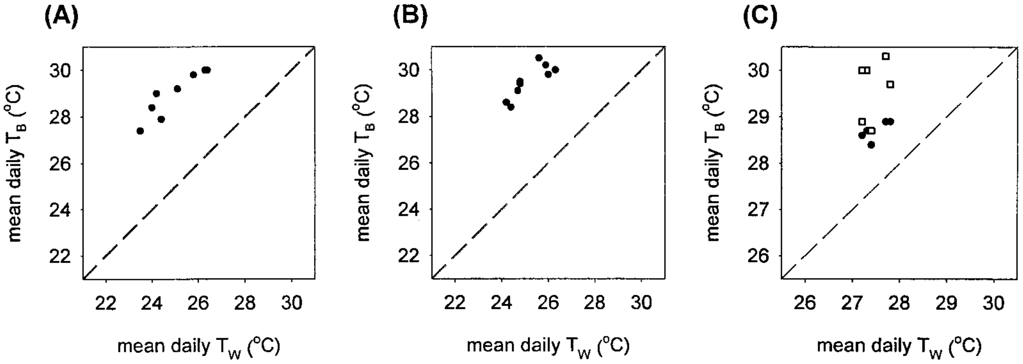

Figure 2. Spearman correlations showed a significant relationship between mean daily T_W and mean daily T_{SC} (*filled circles*) for (*A*) turtle 8866 ($r_S = 0.92$, $P < 0.001$) and (*B*) turtle 7610 ($r_S = 0.83$, $P < 0.001$), but not for (*C*) turtle 3800 ($r_S = 0.63$, $P = 0.103$). There was no correlation between mean daily T_W and mean daily T_{GT} (*open squares*) for turtle 3800 (*C*). Dashed lines represent the line of unity. Mean T_{SC} was significantly higher than mean T_W ($t = 3.791$, df = 4, $P = 0.019$).

Paired *t*-test was used to compare diurnal (0500–1759 hours) and nocturnal (1800–0459 hours) means for dive depth, dive duration, and surface interval so that diel patterns in dive behavior could be discerned. Additionally, the paired *t*-test was used to look for significant differences in these dive variables between the first and second half of the internesting interval.

Swim-speed records were divided into periods of swimming and inactivity. The turtle was considered to be inactive if the swim speed was below the paddle-wheel transducer's stall speed of 0.2 m s^{-1}. Mean, median, and maximum swim speed were determined for the periods of activity. All values for means in the "Results" are presented as the mean ± SD.

Results

Diving Behavior and Water Temperature

Dive profiles were successfully recorded from five turtles (Table 2). Data were collected during two consecutive internesting intervals for turtle 3800; however, only data from the second monitored interval (3800b) were included in the calculation of means, as the data set from the first interval was incomplete due to instrument failure. Mean dive depth for turtles during the internesting interval ranged from 22 ± 20 to 51 ± 30 m with maximum depths of 64–146 m. Mean dive duration was 6.9 ± 4.8 to 13.0 ± 5.9 min (maximum durations of 19.2 to 67.3 min), and the mean dive bout surface interval was 2.4 ± 1.5 to 3.9 ± 2.8 min. Maximum surface intervals for individual turtles ranged from 13.7 to 80.3 min. Extended surface intervals generally occurred toward the end of the internesting interval when turtles were making shallow dives, but there was no significant difference in routine surface intervals between the first and second halves of the internesting interval ($t = -0.513$, df = 4, $P = 0.635$). The majority of extended surface intervals (68%) occurred during the daytime (0500–1759 hours). Turtles spent 64%–83% of the time at sea submerged. A significant shift in diving behavior was observed midway through the internesting interval (Fig. 1). Maximum dive depths were deeper ($t = 5.638$, df = 4, $P = 0.005$) and dive durations were significantly longer ($t = 5.924$, df = 4, $P = 0.004$) during the first half of the internesting interval compared with the second half.

T_W measurements were obtained from three turtles equipped with TDTRs. T_W varied predictably with depth. There was a significant inverse relationship between ambient T_W and dive depth for turtles 3800 ($r_S = -0.880$, $P < 0.001$), 8866 ($r_S = -0.853$, $P < 0.001$), and 7610 ($r_S = -0.908$, $P < 0.001$).

Subcarapace Temperatures

Subcarapace temperature (T_{SC}) was recorded from three turtles equipped with TDTRs (8866, 7610, and 3800). Temperature data were collected from turtle 3800 during her first monitored internesting interval only. Mean T_{SC} for all turtles was significantly higher than mean ambient T_W ($t = 3.791$, df = 4, $P = 0.019$). Mean T_{SC} for individual turtles ranged from 28.7° to 29.5°C, and mean T_W over the entire recording period was 25.0°–27.5°C (Table 3). Minimum T_{SC} was 9.5°–11.6°C higher than minimum T_W. Subcarapace temperature remained relatively stable throughout the recording period, despite wide fluctuations in T_W experienced by turtles during dives to various depths (Fig. 1). Subcarapace temperature of individual turtles varied by 1.9° to 4.2°C, whereas T_W experienced by turtles varied by 11.5° to 12.8°C.

There was a significant positive relationship between mean daily T_{SC} and mean daily T_W for turtles 8866 ($r_S = 0.92$, $P < 0.001$) and 7610 ($r_S = 0.83$, $P < 0.001$), but not for turtle 3800 ($r_S = 0.63$, $P = 0.103$; Fig. 2). However, temperatures for turtle 3800 were only recorded during the first 4.8 d of the internesting interval, and the ranges of mean daily T_{SC} and mean daily T_W were very narrow (28.4°–28.9°C and 27.2°–27.8°C,

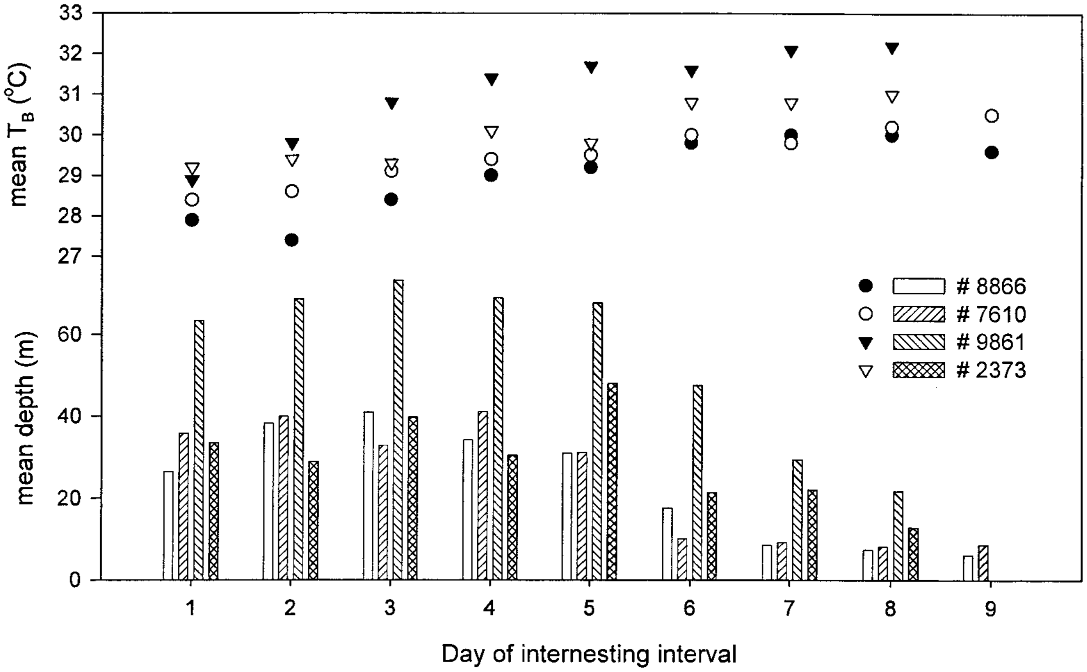

Figure 3. Mean dive depth and mean body temperature (T_B) for each day of the internesting interval for four leatherback sea turtles. Subcarapace temperatures (T_{SC}) are depicted for turtles 8866 and 7610, and gastrointestinal tract temperatures (T_{GT}) are depicted for turtles 9861 and 2372. Spearman correlations showed a significant relationship between mean daily T_{SC} and mean daily dive depth for both turtle 8866 and turtle 7610. There was also a significant relationship between mean daily T_{GT} and mean daily dive depth for turtle 2373 ($r_S = 0.78$, $P = 0.015$), but not for turtle 9861($r_S = 0.64$, $P = 0.072$).

respectively). As the internesting interval progressed, dives became shorter and shallower for turtles 8866 and 7610. This shift in diving behavior was accompanied by a concurrent increase in mean daily T_W and T_{SC} (Fig. 3). There was a significant negative correlation between mean daily depth and mean daily T_{SC} for both turtle 8866 ($r_S = -0.76$, $P = 0.012$) and turtle 7610 ($r_S = -0.85$, $P < 0.001$).

Mean T_{SC} during prolonged surface intervals was not significantly higher than mean T_{SC} during routine dive cycles ($t = -2.25$, df = 2, $P = 0.153$). There was no significant relationship between mass and T_{SC} ($r^2 = 0.738$, $P = 0.342$).

Gastrointestinal Tract Temperature

Measurements of gastrointestinal tract temperature (T_{GT}) were obtained for all four turtles (3800, 8364, 9861, 2373) that were equipped with STTs and receivers. The TDTR for turtle 8364 failed at sea, so there are no depth measurements for this animal. Unfortunately, simultaneous recordings of ambient T_W were only obtained for turtle 3800. Mean daily T_{GT} for this animal was 1.3°–2.8°C higher than mean daily T_W (Fig. 2). There was no significant correlation between mean daily T_{GT} and mean daily T_W ($r_S = 0.10$, $P = 0.803$; Fig. 2).

Mean T_{GT} for individual turtles ranged from 29.6° to 31.1°C (Table 3). As with T_{SC}, there was a trend for the mean daily T_{GT} to increase as mean daily dive depth decreased during the second half of the internesting interval (Fig. 3). This trend was significant for turtle 2373 ($r_S = 0.78$, $P = 0.015$) but not for turtle 9861 ($r_S = 0.64$, $P = 0.072$).

Marked fluctuations (0.9°–3.6°C) in T_{GT} occurred for all four turtles. Most of these fluctuations were characterized by a rapid decrease in T_{GT} followed by a gradual return to the previous temperature over the course of 40–105 min (Fig. 4). There were also fluctuations in which the decrease and subsequent increase in T_{GT} were both rapid and the entire event took 10–25 min to be completed. All of these fluctuations occurred within the first 3 d of the internesting interval, and for turtles 8364 and 9861 these fluctuations only occurred during the first few hours after the turtle had returned to the sea following nesting. Maximum T_{GT} (31.5°–34.4°C) for three turtles was recorded while turtles were still on the nesting beach before entering the surf. Gastrointestinal tract temperature dropped quickly after turtles returned to the ocean. Turtles 8364 and 9861 showed marked fluctuations in T_{GT} during this initial cooling period (Fig. 5), but turtles 2373 and 3800 did not show any marked fluctuations in T_{GT} until after T_{GT} had already dropped by 1.3° and 3.9°C, respectively.

Paired *t*-tests showed no significant difference in dive depth ($t = 1.832$, df = 4, $P = 0.141$), dive duration ($t = 2.135$, df = 4, $P = 0.100$), or surface interval ($t = 1.960$, df = 4,

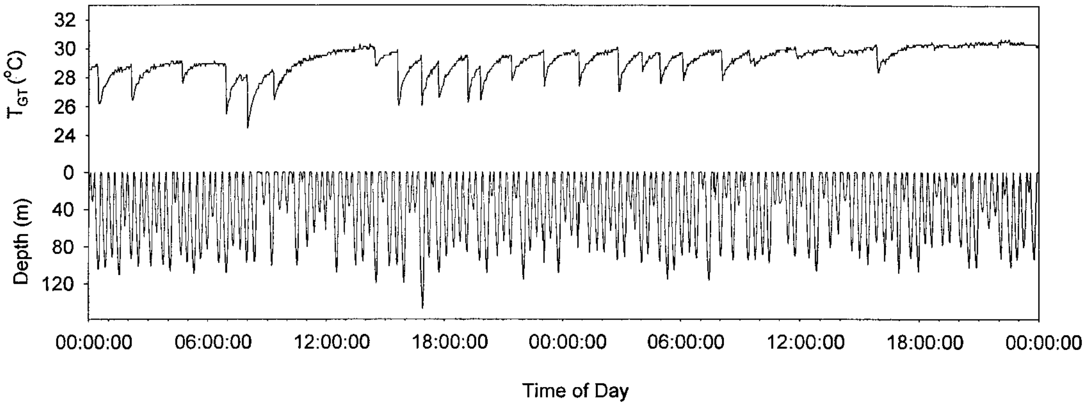

Figure 4. Gastrointestinal tract temperature (T_{GT}) and dive depth for leatherback turtle 3800a during the second and third days of her internesting interval. Numerous rapid fluctuations in T_{GT} occurred during this period of the recording. Fluctuations were 0.9°–3.6°C in magnitude and were characterized by a rapid decrease in T_{GT} followed by a gradual return to previous temperature over the course of 40–105 min.

$P = 0.122$) between day and night. However, dive profiles from some individual turtles (9861 and 2373) showed a distinct diel pattern emerging midway through the internesting interval, with deeper and longer dives and longer surface intervals occurring during the daytime (Fig. 5). Gastrointestinal tract temperature of turtle 9861 fluctuated with the diel changes in dive pattern, such that T_{GT} was lower during diurnal periods of deep diving compared with nocturnal periods of shallow diving (Fig. 5). However, T_{GT} of turtle 2373 did not fluctuate with diel changes in depth. Overall, there was no significant difference in T_{GT} between day and night ($t = -0.620$, df = 3, $P = 0.579$).

Gastrointestinal tract temperature during extended surface intervals was not significantly higher than T_{GT} during routine dive cycles ($t = -2.278$, df = 2, $P = 0.150$). There was no significant relationship between mass and T_{GT} ($r^2 = 0.246$, $P = 0.504$).

Swim Speed

Swim speed was successfully recorded from turtles 3800 (both her first and second internesting intervals), 9861, and 2373. Figure 6 shows the frequency distribution of swim speed for these three turtles. The data for individual turtles was nonnormally distributed (Kolmogorov-Smirnov distance 0.174–0.259, $P < 0.001$). Faulty connections between the swim-speed transducer and the TDTR prevented us from obtaining swim-speed measurements from turtles 8866 and 7610.

Turtles spent 79% to 91% of the time at sea moving faster than 0.2 m s^{-1}. Mean swim speed for individual turtles ranged from 0.6 to 0.9 m s^{-1}, and the mean speed for all turtles was 0.7 ± 0.2 m s^{-1}. Maximum swim speed was 1.6–3.8 m s^{-1} (Table 2). Figure 7 shows typical swimming behavior along with diving behavior and T_{GT} measurements for two turtles (9861 and 2373). During periods of deeper diving characterized by V-shaped dive profiles, turtles moved continuously while submerged and did not swim at the surface. During dives with square-shaped profiles, turtles alternated between periods of movement and inactivity while at maximum depth and did not swim at the surface. In contrast, turtles swam both while submerged and at the surface during the periods of short shallow diving that frequently occurred during the second half of the internesting interval.

Discussion

Elevated Body Temperatures and Thermal Stability in the Leatherback Turtle

Leatherback turtles maintained T_B higher than T_W throughout the internesting interval. The minimum observed T_{SC} was 26.7°C and the minimum observed T_{GT} was 24.5°C, despite the fact that T_W dropped as low as 15.7°C during deep dives. The magnitude of the mean temperature gradient maintained between T_{SC} and T_W during the internesting interval (1.2°–4.3°C) was similar to the thermal gradient between core T_B of nesting leatherback turtles and surf T_W (2.2°–5.1°C; Mrosovsky 1980). Leatherback T_B remained relatively stable in the face of changing T_W; however, T_B was not entirely independent of T_W and was affected by shifts in diving and swimming patterns.

There was a significant positive correlation between T_{SC} and T_W (Fig. 2). Relatively low T_W, such as experienced during prolonged periods of deep diving, was associated with decreased T_B (Figs. 3, 5, 7). This is well illustrated by the shift in T_W and T_B that occurs concurrent with the drastic shift in diving behavior midway through the internesting interval (Figs. 1, 3). During the first half of the internesting interval, T_W fluctuated greatly as turtles made dives to various depths down to 146 m. Routine dives during the second half of the internesting interval were significantly shallower compared with dives made during the first half, and T_W experienced by turtles was warmer and

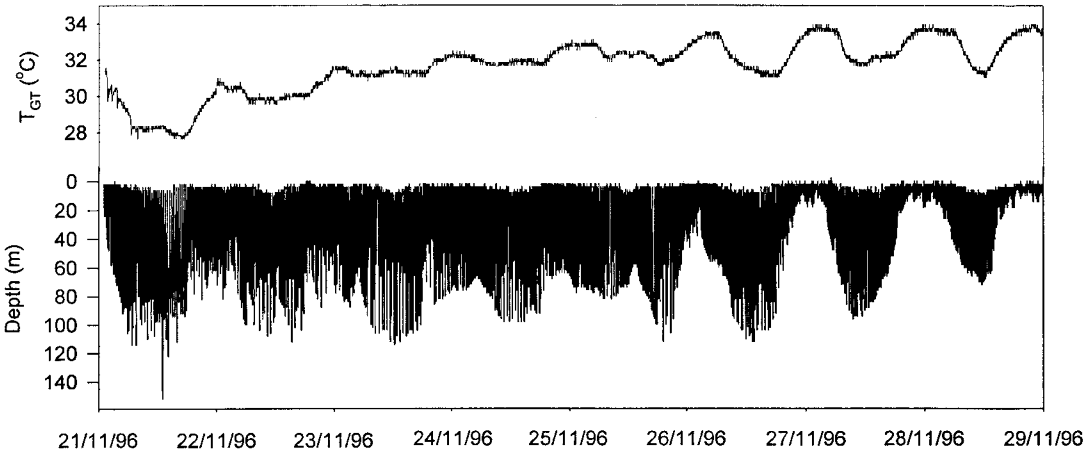

Figure 5. Gastrointestinal tract temperature (T_{GT}) and dive depth for leatherback turtle 9861 during her entire internesting interval. There is a progressive increase in T_{GT} over the first several days of the interval. This may be due to metabolic heat generation and retention or movement of the STT pill from cooler to warmer sections of the gastrointestinal tract. The second half of the internesting interval was characterized by a distinct diel pattern, with short shallow dives occurring at night and long deep dives occurring during the day. T_{GT} during periods of shallow diving was several degrees higher than T_{GT} during periods of deep diving.

more stable (Fig. 1). The trend toward warmer T_{SC} and T_{GT} at the end of the internesting interval suggests that turtles allow T_B to fluctuate with T_W to some degree while in the tropics (Fig. 3). A correlation between T_B (specifically stomach temperature) and T_W has also been noted for loggerhead sea turtles (Sato et al. 1994). As with leatherback turtles, loggerhead turtles maintain T_B higher than T_W but also experience fluctuations in T_B that correspond to long-term shifts in their thermal environment.

It is also possible that increased metabolic heat production due to higher activity levels contributed to the increase in T_B as the internesting interval progressed. Swim-speed data show that turtles swam continuously both while submerged and at the surface during the periods of short, shallow diving, which characterized the second half of the internesting interval (Fig. 7). This is in contrast to the pattern typical of periods of deep diving, in which turtles swam while submerged but not at the surface. A similar dichotomy in swimming behavior was observed for female leatherback turtles during the internesting interval at St. Croix, U.S. Virgin Islands (Eckert 2003). Eckert (2003) described two distinct swim patterns for leatherback turtles from this population. Type 1 behavior consisted of intermediate periods of swimming (lasting 5–15 min) bordered by rapid drops to very low speed. Type 2 behavior consisted of continuous swimming with very little variation in speed and without the rapid drops in speed characteristic of type 1 behavior. Leatherback turtles from the St. Croix population displayed type 2 behavior with greater frequency during the last few days of the internesting interval, which is consistent with the behavior we observed for leatherbacks from the Playa Grande population. Swim speeds observed in our study (0.7 ± 0.2 m s^{-1}) were comparable to speeds recorded from leatherback turtles in the Caribbean Sea (0.62 ± 0.24 m s^{-1}; Eckert 2003).

Mean T_B (T_{SC} and T_{GT}) during extended surface intervals was not significantly higher than mean T_B during periods of routine diving. If climatic conditions at the surface are favorable, then leatherbacks could conceivably increase T_B by basking. How-

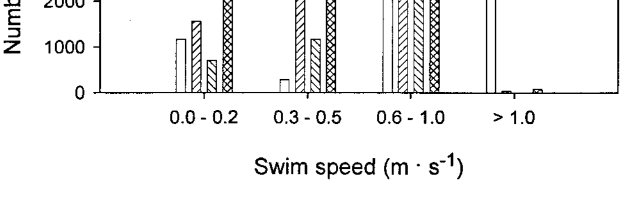

Figure 6. Frequency distribution of swim speed measurements for leatherback turtles 3800, 9861, and 2373. For turtle 3800, the bar labeled 3800a represents the first monitored internesting interval, and the bar labeled 3800b represents the second monitored internesting. Turtles spent the majority of time swimming at speeds between 0.6–1.0 m s^{-1}. The mean swim speed for all turtles was 0.7 ± 0.2 m s^{-1}.

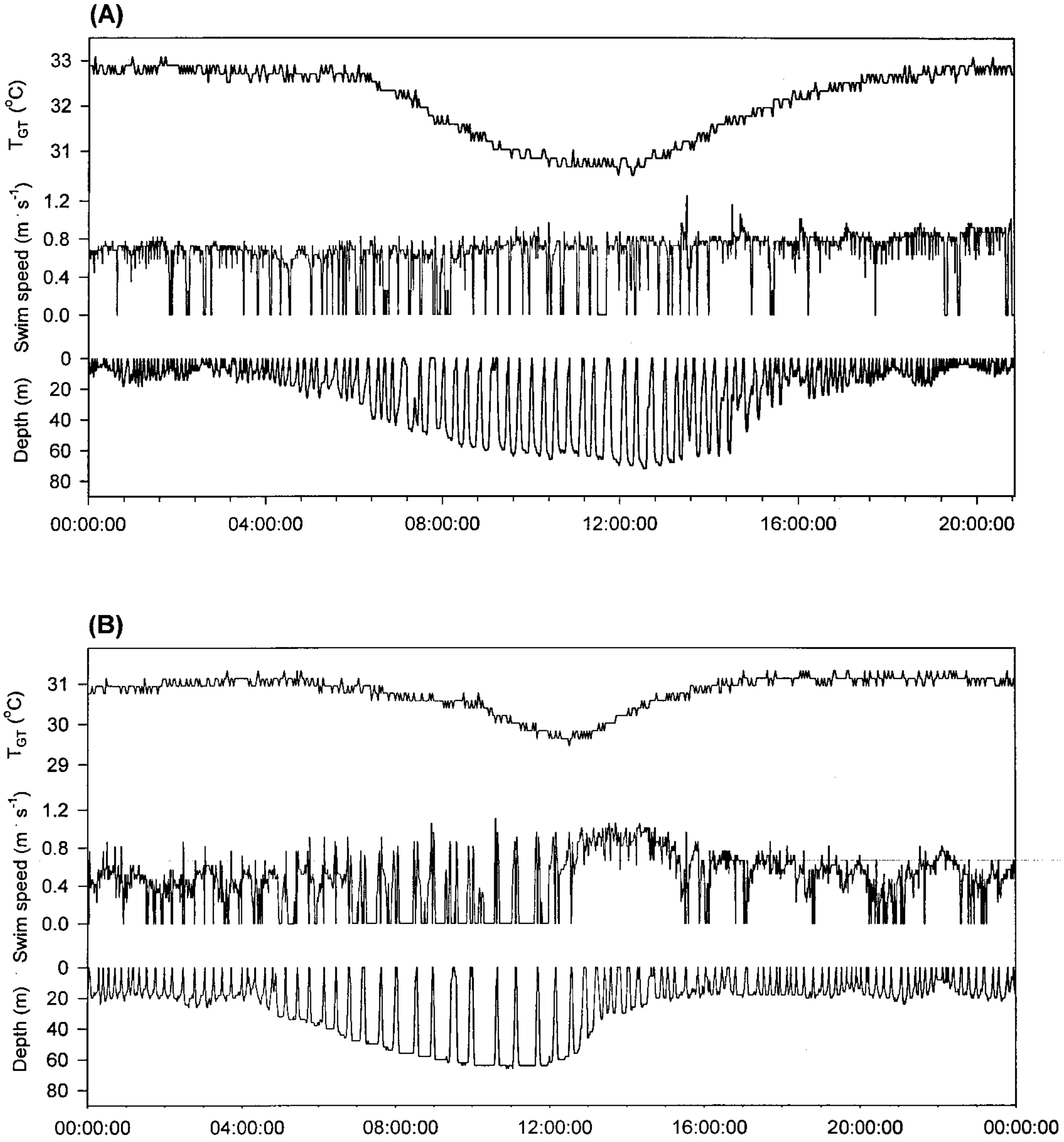

Figure 7. Gastrointestinal tract temperature (T_{GT}), swim speed, and dive depth for leatherback turtles 9861 (*A*) and 2373 (*B*), showing the effects of activity and diving patterns on turtle T_{GT}. Turtles swam continuously during V-shaped dives but often remained stationary at maximum depth during square-shaped dives. Regardless of whether dives were V shaped or square shaped, turtles generally did not swim at the surface during periods of deep diving. During periods of shallow diving, turtles swam both while diving and at the surface. Gastrointestinal tract temperature was higher during these periods of prolonged and continuous swimming at shallow depths compared with T_{GT} during periods of deep diving.

ever, given the unpredictable and variable nature of climatic conditions, it seems unlikely that leatherbacks could depend solely on basking to maintain high T_B. Sato et al. (1995) found that there was no correlation between light intensity and T_B in loggerhead turtles and concluded that loggerhead turtles did not depend on solar radiation to raise T_B above that of the environment.

Ingestion Events during the Internesting Interval

The rapid fluctuations in T_{GT} that we observed are indicative of ingestion of prey or water (Wilson et al. 1992; Sato et al. 1994). Sato et al. (1994) recorded similar fluctuations in stomach temperature of loggerhead sea turtles and concluded that the turtles were ingesting water to recover from dehydration during nesting. All of the ingestion events for leatherback turtles from this study took place within the first half of the internesting interval. However, since the STT was designed to pass through the digestive tract of the turtle instead of remaining in the stomach, we cannot be certain that ingestion events did not occur later on in the interval. If the STT had already moved into the intestines by midway through the interval, then it is unlikely that we would be able to detect ingestion events from that point on.

Turtle 3800a showed the most pronounced pattern of ingestion events. The other three turtles experienced three to 10 ingestion events during the first 3 d of the interval, while turtle 3800a had 27 ingestion events occur during this time. Video footage recorded from remote cameras (R. D. Reina and G. J. Marshall, personal communication) attached to leatherback females during the internesting interval show that jellyfish (the leatherback's main prey item) are present in the waters surrounding Playa Grande. Given the active diving pattern and cost of reproduction (egg production, nesting) during this time, it seems reasonable to assume that leatherbacks would consume jellyfish during the internesting interval.

A diel diving pattern was apparent during the second half of the internesting interval for three of the five turtles from which dive behavior was recorded. Dives were significantly shallower and shorter at night. Eckert et al. (1989) showed that this dive pattern was also apparent in leatherback turtles from the St. Croix nesting population and speculated that this pattern represented foraging by turtles on the deep scattering layer (DSL) as it moved from deep to shallow water in the evening. None of the turtles from this study showed the rapid fluctuations in T_{GT} that would suggest prey ingestion during the period when the diel diving pattern was apparent. However, as mentioned earlier, it is unlikely that the STT would detect ingestion events if it had already passed from the stomach into the intestines.

If leatherbacks survive in cold waters by maintaining T_B higher than T_W, consumption of cold prey and water could present a serious thermal challenge. Ingesting prey that is cooler than core temperature has the obvious effect of lowering core temperature (Fig. 4). Davenport (1998) addressed this problem and concluded that for a leatherback with a core T_B of 25°C in T_W of 8°C, much of the energy gained from eating medusae or pyrosomas would be expended solely in heating the prey to core temperature.

Comparison of Field Data and Mathematical Models

Paladino et al. (1990) proposed a mathematical model to describe the thermoregulatory abilities of leatherback turtles based on a "core-shell" cylinder design. In their model, the cylindrical turtle has a central core with radius r_C, within which T_B is homogenous. This inner core is surrounded by an outer shell, within which T_B may vary due to conduction between the core and surface. The total radius of the core and shell cylinders combined is r_T. The cylindrical turtle may increase the thermal gradient between core T_B and environmental temperature (T_E) either by increasing metabolic rate or by restricting blood flow to the peripheral tissues (i.e., the shell cylinder), thereby decreasing the ratio of r_C/r_T. In the latter scenario, the peripheral tissues effectively serve as insulation so that a large thermal gradient between core T_B and T_E can be established and maintained.

Retention of metabolically generated heat may be beneficial for leatherback turtles in temperate seas, but in tropical seas the opposite is probably true. According to the model, a leatherback turtle would need to perfuse peripheral tissues and raise r_C/r_T to near 1.0 in order to avoid overheating in warm tropical waters. If this is the case, we can reasonably assume that T_{SC} measurements would be similar to T_{GT} measurements for leatherback turtles in the tropics. Data from the one turtle for which we have both of these measurements (turtle 3800) support this assumption ($T_{SC} = 28.7° \pm 0.4°C$, $T_{GT} = 29.8° \pm 0.6°C$). Assuming an r_C/r_T of 0.95, the mathematical model predicts that a 400-kg leatherback turtle could maintain a temperature gradient of 1°–4°C with a metabolic rate of 0.2–0.8 W kg^{-1} (Paladino et al. 1990). The mean thermal gradient between T_{SC} and T_W for turtles in this study (mass = 297 ± 73 kg) is 3.2° ± 1.7°C, which corresponds well with the model's prediction for tropical conditions.

For temperate conditions, the model predicts that turtles could maintain a thermal gradient of 5°–18°C for the same range of metabolic rates (0.2–0.8 W kg^{-1}) and an r_C/r_T of 0.7. Frair et al. (1972) recorded deep body temperatures from a single leatherback turtle that had been entangled in a fishnet off the coast of Nova Scotia in late July and found that the turtle's T_B was up to 18°C higher than T_W. However, this turtle had been in captivity for 2 d, first tethered in a tidal pool and then held in a small tank, before the temperature was recorded. During the holding period, the turtle "swam vigorously for long periods" (Frair et al. 1972, p. 791) and had a high respiratory rate (2–3 breaths min^{-1}). It is likely that increased metabolic heat production during the holding period contributed to the large gradient between T_B and T_W observed for this animal. Standora et al. (1984) measured deep body temperatures from a subadult leatherback turtle that had been captured in a fish pound net off the coast of Rhode Island in August. Body temperatures for this animal were up to 8.3°C higher than air temperature, but T_W was not measured. These studies clearly demonstrate that leatherback turtles are capable of achieving an impressive thermal gradient between T_B and ambient temperatures, and results from these studies match the mathematical model predictions. However, field data on T_B and T_W for leatherbacks freely diving in temperate seas are still needed to confirm whether or not these animals maintain such large thermal gradients at high latitudes. Leatherbacks forage on gelatinous prey while in temperate waters, and, as mentioned previously, the ingestion of cold prey and water has the effect of lowering core T_B. One of the assumptions of the mathematical model is that T_B within the core remains homogenous due to blood flow, an assumption that is violated if turtles are foraging or drinking seawater. This may result in an overestimation of the thermal gradient if other factors, such as metabolic rate, remain the same.

While a great deal of attention has been given to the ability of leatherback turtles to create large thermal gradients between T_B and ambient temperatures, other aspects of the thermal biology of this species have been ignored. For instance, there is a paucity of data on the physiological and biochemical adjustments to cold exposure in leatherback turtles. Penick et al. (1998) demonstrated that metabolism of isolated leatherback pectoralis muscle tissue was independent of changes in temperature over the range of 5°–38°C ($Q_{10} = 1$). If other tissues and overall metabolic rate also have a low thermal dependence, then the argument could be made that there is no need for leatherback turtles to invest energy in maintaining elevated T_B in cold climates. Another alternative is that leatherback turtles are capable of some degree of thermal acclimation, such that metabolic processes and physiological function are maintained over the wide range of temperatures experienced during migrations. Seasonal metabolic compensation has been observed in numerous species of reptiles (Bennett and Dawson 1976), and recent studies have shown that compensation of anaerobic enzyme function occurs with prolonged exposure to cold temperatures in green sea turtles (Southwood et al. 2003*a*). Compensation of biochemical and physiological processes in response to changing environmental temperatures may be a more energetically efficient thermal strategy than the maintenance of high T_B in cold climates. Unfortunately, virtually nothing is known of the metabolic and thermal compensatory mechanisms in leatherback turtles. In addition to recordings of T_B, activity, and dive patterns of leatherback turtles in the far northern and southern extents of their range, detailed studies of the cellular and molecular adaptations of leatherbacks to life in tropical to temperate seas are necessary in order to understand how this reptile adapts to varying thermal conditions experienced during long-distance migrations.

Acknowledgments

The authors would like to thank the Costa Rican Ministry of Environment (MINAE) for granting permission to conduct this study. Molly Lutcavage, Nigel West, Bob George, Mark Swingle, Pam Plotkin, Pat Butler, Richard Reina, Philippe Mayor, Vivienne Jones, Tara Law, David Penick, Drexel University undergraduate students, and Earthwatch staff and volunteers offered invaluable assistance in the field. This study was funded by Natural Sciences and Engineering Research Council (NSERC) Research and Equipment Grants and an NSERC Collaborative Grant.

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