Regional Blood Flow in Sea Turtles: Implications for Heat Exchange in an Aquatic Ectotherm

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ABSTRACT

Despite substantial knowledge on thermoregulation in reptiles, the mechanisms involved in heat exchange of sea turtles have not been investigated in detail. We studied blood flow in the front flippers of two green turtles, Chelonia mydas, and four loggerhead turtles, Caretta caretta, using Doppler ultrasound to assess the importance of regional blood flow in temperature regulation. Mean blood flow velocity and heart rate were determined for the water temperature at which the turtles were acclimated (19.3°C) and for several experimental water temperatures (17°C–32°C) to which the turtles were exposed for a short time. Flipper circulation increased with increasing water temperature, whereas during cooling, flipper circulation was greatly reduced. Heart rate was also positively correlated with water temperature; however, there were large variations between individual heart rate responses. Body temperatures, which were additionally determined for the two green turtles and six loggerhead turtles, increased faster during heating than during cooling. Heating rates were positively correlated with the difference between acclimation and experimental temperature and negatively correlated with body mass. Our data suggest that by varying circulation of the front flippers, turtles are capable of either transporting heat quickly into the body or retaining heat inside the body, depending on the prevailing thermal demands.

Introduction

Reptiles are generally defined as ectotherms. To achieve high body temperatures (Tb’s), they migrate between different microclimates and perform a variety of thermoregulatory behaviours. For example, effective absorption of solar radiation enables the lizard Liolaemus multiformis to become active at high altitudes even when ambient temperatures (Ta’s) are around zero (Pearson 1954). Early work on this subject is reviewed by Avery (1982); for more recent studies see, for example, Bauwens et al. (1996), Christian and Weavers (1996), and Seebacher et al. (1999). However, the utility of behavioural thermoregulation is limited for reptiles that live in or near water (Seymour 1982; but see Seebacher et al. 1999). This is due to the physical properties of water, particularly the high thermal conductivity and absorption of infrared radiation. For example, the Galápagos marine iguana, Amblyrhynchus cristatus, rapidly cools down to Ta while it forages in water at 25°C (Bartholomew 1966). Consequently, it has to warm up before and after foraging bouts. Sometimes an animal has to interrupt foraging to emerge and warm up. These thermal constraints mean that marine iguanas are obliged to spend more time on land basking in the sun than foraging in the sea (Bartholomew 1966; Trillmich and Trillmich 1986).

Few reptiles spend significant amounts of time in water. Some freshwater turtles that seldom leave the water thermoregulate by selecting water of particular temperatures rather than basking on land (Templeton 1970; Spotila et al. 1990). The absence of direct sunlight as a heat source particularly limits behavioural thermoregulation in fully marine reptiles like sea snakes and sea turtles, which usually leave the sea only to lay eggs. Moreover, the marine environment provides a relatively homogeneous thermal climate so that options for the selection of optimal temperatures are reduced. Although occasional basking at the water surface, or on beaches, has been observed in some sea turtle species (green turtles [Whittow and Balazs 1982] and loggerhead turtles [Sapsford and van der Riet 1979]), this behaviour does not occur frequently enough to represent a major source of incoming energy (turtles spent on average 35 min basking in a 20-d observation period [Whittow and Balazs 1982; see also Sato et al. 1995]). Despite these constraints, it has been suggested that leatherback turtles, Dermochelys coriacea, may maintain a large difference between Tb and Ta, even during prolonged periods of inactivity (Paladino et al. 1990). Davenport et al. (1990) reported that leatherback turtles are the only reptile with a peripheral layer of blubber similar to that of marine mammals. Moreover, other sea turtle species like loggerhead (Sakamoto et al. 1990; Sato et al. 1994, 1995) and green turtles (Standora et al. 1982; Sato et al. 1997) are also able to sustain their Tb’s above the water temperature.
These observations have raised the possibility that sea turtles are at least partially endothermic (Heath and McGinnis 1980; Standora et al. 1982; Spotila and Standora 1985; Goff and Stenson 1988; Davenport 1997). Whatever their status, the regulatory mechanisms of heat exchange in sea turtles are still poorly understood. There is, however, evidence that they heat up faster than they cool down, indicating the involvement of physiological control mechanisms (Heath and McGinnis 1980; Smith et al. 1986).

Since the carapace is a good insulator (Standora et al. 1982), heat exchange with the surrounding water probably primarily takes place across other parts of the body. The front flippers, for example, possess both a large surface area over which heat can be exchanged and a relatively high resistance to blood flow since resistance increases with distance to the heart. If this resistance were regulated by vasoconstriction and vasodilation, then the circulatory system of the flippers would be an important thermoregulatory tool. The role of flippers and other appendages in thermoregulation has already been shown for a variety of marine mammals, the bodies of which are insulated by a thick fat layer (Scholander and Schevill 1955; Kvadsheim and Folkow 1997; Schmidt-Nielsen 1997; Noren et al. 1999).

We hypothesised that sea turtles are capable of altering the blood flow in the flippers to either transport heat into the body or restrict its loss. To test this hypothesis, we studied the blood flow in the front flippers of green turtles and loggerhead turtles at different water temperatures using a noninvasive Doppler ultrasound technique.

### Material and Methods

The present study consists of part 1 (blood flow) and part 2 (Tb), which were conducted in November and December 1999 and in December 2000 and January 2001, respectively. A total of 10 turtles (two juvenile green turtles, seven juvenile and one adult loggerhead turtle) were used (Table 1). The turtles were kept in separate tanks at the Aquarium of Naples (Stazione Zoologica Anton Dohrn, Naples, Italy) and were supplied with circulating seawater, which was pumped from the Gulf of Naples. Three different sizes of tanks were used. The smaller turtles were kept in 200-L tanks, the bigger turtles were kept in 400-L tanks, and the adult turtle (turtle 10) was kept in a 1,000-L tank. Both species were fed daily between 1000 and 1200 hours (except weekends) with anchovies, *Engraulis encrasicolus*.

### Doppler Ultrasound and Principles of Measurements

We measured blood flow using a handheld bidirectional Doppler ultrasound device (Multi Dopplex II, Huntleigh Diagnostics, Cardiff, U.K.). All measurements were made with a vascular probe connected to the control unit, which emitted ultrasound at a frequency of 5 MHz. However, for the two smallest loggerhead turtles (turtles 5 and 6; Table 1), a less powerful probe of 8 MHz was used. The emitted ultrasound (f0) was reflected by the moving blood cells, mainly the erythrocytes, at a different frequency (f). The resulting Doppler shift (f0 = f + f) gave information about direction, character, and velocity of the flow.

### Table 1: Body masses (BM), acclimation temperature (Tacr), experimental temperature (Tex), and average heating and cooling rates of individual turtles

<table>
<thead>
<tr>
<th>Individual</th>
<th>BM (kg)</th>
<th>Tacr (°C)</th>
<th>Tex (°C)</th>
<th>Heating (°C/min)</th>
<th>Cooling (°C/min)</th>
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<tbody>
<tr>
<td>1</td>
<td>17.3</td>
<td>21.0</td>
<td>16.9, 19.3, 24.8, 27.2, 31.0</td>
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<td>10.0</td>
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<td>16.0</td>
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<tr>
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<td>11.8</td>
<td>22.1</td>
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</tr>
<tr>
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<td>7.6</td>
<td>22.1</td>
<td>28.3</td>
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<tr>
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<td>3.35</td>
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<td>17.1, 24.0, 26.9, 29.5</td>
<td>7.1</td>
<td>17.0</td>
</tr>
<tr>
<td>6a</td>
<td>2.29</td>
<td>19.9</td>
<td>17.5, 24.0, 27.4, 30.0</td>
<td>6.7</td>
<td>23.5</td>
</tr>
<tr>
<td>6b</td>
<td>2.29</td>
<td>19.9</td>
<td>17.5, 24.0, 27.4, 30.0</td>
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<td>16.1</td>
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<td>59.3</td>
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</tbody>
</table>

Note. Individuals 1 and 2 = *Chelonia mydas*. Individuals 3–9 = *Caretta caretta*. x = still heating (or cooling, respectively) 30 min after retransfer; heating after 30 min in Tex.nh = not a experiment 1.

b Experiment 2.
Blood flow was audible in the loudspeaker of the Doppler. Arteries were distinguished from veins because they emitted a high-pitched pulsatile sound, while veins emitted a nonpulsatile sound similar to rushing wind. The Doppler unit was connected via an RS232 interface to a laptop personal computer (Toshiba Tecra 730CDT) running the Dopplex Reporter software programme (Huntleigh Diagnostics 1997). The audio signal was transformed and displayed as a waveform on the screen (Doppler shift frequency or flow velocity, respectively, vs. time). In this way, each measurement was recorded on-line, and data were stored for further waveform analysis. Because of the low heart rate (minimum 7–12 beats/min [bpm]), a measuring period of 20 s (i.e., the longest period permitted by the software) was chosen to facilitate the recording of at least two complete heart cycles.

Heart rate was calculated as the average number of cardiac cycles per minute using the reciprocal of the interbeat interval calculated from the complete cycles determined from the waveform. For this, and for all other calculations (see "Data Analysis"), we used a mean ± SD of 3.2 ± 1.8 heart cycles (range 1–8) depending on the length of the interbeat interval.

Since Doppler shift frequency is proportional to flow velocity, it was possible to calculate the blood flow velocity using the equation (Kremkau 1993)

$$F_b = f_r - f_s = \frac{2f_r \times \nu \times \cos \theta}{c},$$  \hspace{1cm} (1)

where $\nu$ is the reflector speed (= blood flow velocity), $\theta$ is the angle between the probe and the direction of the blood flow, and $c$ is the speed of ultrasound in the tissue. The calculation of the flow velocity therefore depends on the angle $\theta$. The optimum angle range for most vascular studies is recommended to be between 30° and 60°. In this study, the best signal was obtained when using an angle of 30°.

A useful method to characterise blood flow is to use defined parameters of the recorded waveform to calculate indices such as Pourcelot's resistance index (RI; Evans et al. 1989). To calculate this index, the maximum ($S$) and minimum ($D$) heights of the waveform during systole and diastole, respectively, must be known (Fig. 1). The RI gives a numerical value of the resistance opposed to the blood flow and is calculated as

$$RI = \frac{S}{D},$$  \hspace{1cm} (2)

where $0 < RI \leq 1$. The advantage of taking such a ratio is that both the numerator and denominator include the cosine of the angle between the Doppler probe and the blood vessel (see eq. [1]). The cosine term therefore cancels, and the index is independent of angle. We therefore used RI to control for the effect of probe angle on the measured blood flow velocities.

**Blood Flow Measurements on Sea Turtles**

Before the Doppler measurements, the water level in the tank was lowered so that the central part of the carapace and a small area on the neck and head were above the water surface. The turtles then remained in a relaxed state with their head submerged, and blood flow was measured without any disturbance due to movements. The Doppler probe was positioned on the ventral surface of the proximal front flipper, where the skin was thin enough for the ultrasound to penetrate. The large oval scale that is adjacent to the third large scale on the posterior
edge of the flipper was taken as an orientation point to ensure that the same area of approximately 1 cm² proximal of this scale was always examined. The flipper was taken as an anatomic plane to which the probe was oriented at a 30° angle. Presuming that the vessels under examination run parallel to the flipper surface, we took this 30° angle for all calculations of blood flow velocity. However, because the probe was handheld and values of calculated flow velocity from observed \( F_0 \) are only as accurate as the estimated Doppler angle \( \theta \), we allowed a deviation from this angle of ±5°. In this case, a deviation of 5° would result in an accuracy of ±5%. Preceding test runs during which both flippers were examined showed that there was no difference in blood flow between the two front flippers. Subsequently, only the left front flipper of each turtle was used. In addition, the blood flow in the neck of turtles 5 and 6 was measured on the left lateral side of the neck (relatively proximally to the carapace).

In all the measurements, the probe was held so that it pointed toward the body core. The time between the first placement of the Doppler probe and the first recorded blood flow varied according to the strength of the blood flow signal. Generally, in relatively warm water, the blood flow signal was strong enough that an artery was found in <30 s. However, in relatively cold water, there were only weak blood flow signals, which made it difficult to find an artery. In these situations, it took up to a maximum of 5 min to complete the first recorded measurement. Once a clear signal was received from an artery, recordings of blood flow were taken almost continuously; the only interruptions were due to the closing of the recording window after 20 s and the opening of a new recording window of the Reporter software programme. A Doppler session was terminated when an average of at least seven waveforms was recorded. The time until this was achieved varied due to interruptions of the measurements caused by movements of the turtle. In the latter, the measurements could only be continued when the turtles rested again. However, the average duration of one Doppler session seldom exceeded 15 min; in a few cases, the maximum duration was 30 min.

In November, 2000, we took turtle 5 to Vincenzo Monaldi Hospital, Naples, to examine the flipper vessels using Colour Doppler Echography (Acuson Sequoia). With the help of this sophisticated ultrasound machine, it was possible to visualise the local arrangement of arteries and veins in a cross section of 16 mm². The investigation was undertaken with a 7.5-MHz probe on the unanesthetised turtle while it was lying on its carapace.

Transfer Trials: Part 1
Turtles were exposed to a sudden temperature change by transferring them from their home tank into an adjacent tank of different water temperature \( (T_w) \). The temperature in the transfer tank was manipulated in such a way that differences to the acclimation temperature \( (T_{ac}) \) of ca. 3°, 6°, and 9°C were established. Since the turtles were subject to natural variation in seawater temperature, \( T_w \) and, hence, experimental temperature \( (T_{ex}) \) were slightly different for each turtle. All corresponding temperatures are listed in Table 1.

Two of the turtles were also transferred into a tank that contained water of the same temperature as the home tank. Blood flow measurements conducted on these control animals were taken to evaluate the handling effect on the turtles.

The six turtles used in this experimental part were divided into three groups (group 1: turtles 3 and 4; group 2: turtles 1 and 2; group 3: turtles 5 and 6) that were examined in consecutive experimental periods (duration each: 4–5 d). Each turtle was exposed only once per day to a \( T_{ex} \). Blood flow was measured as soon as the turtle rested calmly in one corner of the tank. Usually the first measurement after a transfer was initiated immediately after the turtle had been placed into the transfer tank. In some cases, however, especially when transferred into colder water, the turtles moved around for 1–2 min before they calmed down and the measurements could be undertaken. The turtles raised their heads to breathe once or twice during such a session. The mean length of apnoic intervals was 17.4 min for loggerhead turtles in 20°C (F. Bentivegna, S. Hochscheid, and C. Minucci, unpublished data). Similar apnoic interval lengths were observed for the green turtles. Since blood flow measurements during breathing were normally affected by the respiratory movements of the turtle (e.g., the lifting of the head above the water line), only blood flow data during apnoea were used in this present analysis except where stated otherwise.

Transfer Trials: Part 2
A second set of transfer trials was conducted to determine the effect of a 30-min transfer experiment (as described in “Transfer Trials: Part 1”) on \( T_b \) (see Table 1). Turtles 1, 8, 9, and 10 were fed miniature temperature loggers (DS1921 Thermocron 1-Wire iButton, Dallas Semiconductor, Dallas) that recorded \( T_b \) in 1-min intervals (resolution: 0.5°C; accuracy: ±1°C).

\( T_b \) of the other turtles was taken in the cloaca using a digital thermometer (accuracy: ±0.3°C; Checktemp, Hanna Instruments, Leighton Buzzard, United Kingdom), which was also used to measure \( T_w \). Cloacal \( T_b \) of each of these turtles was measured three times: (1) before the transfer, (2) after a period of 30 min during which the turtle remained in the transfer tank, and (3) 30 min after the turtle was returned to the home tank. The corresponding heating \( (k_h) \) and cooling \( (k_c) \) rates (listed in Table 1) during a 30-min period were calculated using the equation

\[
k_h = \frac{\ln (T_{ex} - T_{ac}) - \ln (T_{ex} - T_{bas})}{t}
\]

(3)
The control experiment \( \left( T_{cs} \right) \) revealed no changes in results from regression analysis (Minitab 11). Temperature after 30 min in the experimental temperature, and a covariate. We analysed the changes in Tt, arteries (diameter ca. 0.3–0.5 mm), but there was also one smaller veins (diameter ca. 0.15 mm) surrounding larger veins. We verified that veins are located in the vicinity of arteries. We found smaller veins (diameter ca. 0.3–0.5 mm), but there was also one major vein running along a major artery (both ca. 0.3 mm in diameter).

The decrease in \( T_w \) due to seasonal change in seawater temperature also resulted in different blood flow patterns in the individual turtles. It was possible to obtain a clear Doppler signal from turtles 1–4 in their home tank \( (T_w = 21^\circ–22^\circ \text{C}) \). However, blood flow in turtles 5 and 6 was heard only as very low pulses during breathing periods in water of their \( T_w \) (20°C). The signal was too weak to be recorded by computer and, moreover, was likely to be affected by movements of the turtles. During apnoea, circulation in their flippers was below the Doppler detection threshold \( (<0.1 \text{ cm/s}) \).

There was no blood flowing in the flipper arteries at \( T_w \) at the end of the diastolic phase \( (D = 0; \text{ top graph, Fig. 2a, 2b) } \). \( M \) was between 0.4 and 0.5 cm/s and considered to be 0 in those cases where blood flow could not be recorded (e.g., turtles 5 and 6). Maximum recorded blood flow velocities at systolic peak \( (S) \) were between 2.5 and 2.8 cm/s. Transfer into warmer water resulted in an elevated blood flow velocity (bottom graph, Fig. 2a, 2b). Some of the measurements of the elevated blood flow were obtained within 30 s after the turtle had been exposed to the warmer \( T_w \). A series of good waveforms was recorded for one turtle during a warm water exposure at a time of 0.5, 2, 5, and 20 min after transfer. All waveforms were similar, with similar mean blood flow velocities, so that no change in blood flow over exposure time was detected.

The maximum recorded \( S \) was 13.5 cm/s in water of 30°C, and \( M \) was between 3.1 and 11.1 cm/s at temperatures between 30°C and 32°C. When the turtles were transferred into colder water, the blood flow was greatly reduced, and in three turtles, it virtually ceased \( (<0.1 \text{ cm/s}) \). In water of 17°C, \( M \) was 0.1 cm/s, and \( S \) was between 1.4 and 1.9 cm/s in those turtles for which blood flow data at this low temperature could be obtained.

Overall, blood flow velocity in the front flippers of both species increased significantly with \( T_w \) (GLM after log transformation of the data: \( F = 134.99; \text{ df} = 26; P<0.001; \text{ Fig. 3} \)). The response of the blood flow to \( T_w \) was not significantly different between the individuals \( (F = 1.19; P>0.05) \) or between the two species \( (F = 1.28; P>0.05) \).

The analysis of the angle-independent RI gave a similar significant relationship (GLM after arcsine transformation: \( F = 79.19; \text{ df} = 26; P<0.001 \)), thus supporting the accuracy of the velocity data. The only difference was that RI, as expected, decreased with increasing \( T_w \). Differences between the individual responses were not significant (slopes not significantly different: \( F = 1.43; P<0.05 \)) and the intercepts of the responses also did not differ significantly between individuals \( (F = 2.71; P>0.05) \). In a few exceptional cases, it was possible to hold the Doppler probe in place while the turtle was breathing so that blood flow could be recorded. \( M \) and heart rates during breathing and apnoea are presented in Table 2.
Figure 2. Arterial blood flow in the left front flipper of a loggerhead turtle (a) and a green turtle (b) at different temperatures; dashed line indicates mean blood flow velocity.
Apnoea only recorded during warming in water of 27°C. warming transfer into 17°C of waveforms for each of the following situations: a cooling restricted to the systolic period (Fig. 4). Figure 4 shows a couple measured in the flippers because blood flow was generally re¬tracted to the necks. The waveforms looked different from those that were measured on turtles 5 and 6, which did not retract their neck blood flow routinely, but we were able to obtain some measurements on these turtles at 20°C (4.7-fold as compared to eightfold in the flipper). In contrast to the absent circulation in the flippers of loggerhead and green turtles at varying water temperatures. Different symbols mark individual turtles as shown in the key above. Figure 3. Mean blood flow velocity in the front flipper arteries of turtles 5 and 6, which did not retract their necks since the turtles retracted their heads once the probe came in contact with the skin. Consequently, we did not measure blood flow in the neck of turtle 7 (around 5.5 s). However, seven of these eight arrhythmic heart sodes, heart rate was 1.5- to 2.5-fold the heart rate during submergence in the home tank after heating, they all cooled down again but at a significantly lower rate than that at which they had heated up (paired t-test: t = 8.25; N = 8; P < 0.001; Table 1).

**Blood Flow in the Neck**

It was generally more difficult to measure blood flow in the neck since the turtles retracted their head once the probe came in contact with the skin. Consequently, we did not measure neck blood flow routinely, but we were able to obtain some measurements on turtles 5 and 6, which did not retract their necks. The waveforms looked different from those that were measured in the flippers because blood flow was generally re¬stricted to the systolic period (Fig. 4). Figure 4 shows a couple of waveforms for each of the following situations: a cooling transfer into 17°C, in the home tank of T<sub>ac</sub> = 20°C, and a warming transfer into 27°C. M increased only moderately between 17°C and 27°C (4.7-fold as compared to eightfold in the flipper). In contrast to the absent circulation in the flippers of these turtles at T<sub>ac</sub> of 20°C (see above), it was still possible to obtain blood flow recordings from their neck arteries. The same was true for the coldest T<sub>ac</sub>. Flow in the diastolic period was only recorded during warming in water of 27°C.

**Heart Rate**

Mean heart rates of all turtles during submergence in the home tanks were between 8.5 and 15.8 bpm. During breathing episodes, heart rate was 1.5- to 2.5-fold the heart rate during apnoea. Occasionally (eight out of 40 sessions), there was a marked arrhythmia in heart rate consisting of "double beats" with one short cycle (around 2.5 s) followed by one long cycle (around 5.5 s). However, seven of these eight arrhythmic heart beats occurred in the same turtle, and the blood flow data in all eight cases were not considered for further analysis. In the transfer experiments, heart rate increased significantly with increasing T<sub>ac</sub> (GLM: F = 17.48; df = 26; P < 0.01; Fig. 5), although the individuals showed different responses (different slopes: F = 3.83; P < 0.05; Fig. 5).

**Body Temperature**

T<sub>ac</sub>'s (range: 16°–23.9°C) of all turtles varied linearly in correspondence with variations in T<sub>b</sub> (range: 16°–23.5°C) during the study period (regression equation: T<sub>b</sub> = 1.07 × T<sub>ac</sub> − 0.8; r<sup>2</sup> = 0.9792; ANOVA: F = 282.32; df = 7; P < 0.001). None of the individuals showed different responses (different slopes: F = 3.83; P < 0.05; Fig. 5).

### Discussion

Among the present marine reptiles, sea turtles are the most widely distributed. Although they are mainly tropically and subtropically distributed, they can also experience colder water temperatures (e.g., green turtles encounter cooler oceanic water when migrating between Brazil and Ascension Island; Mortimer and Portier 1989; Luschi et al. 1998). Apart from these long-distance migrations, sea turtles also encounter vertical temperature differences while diving (Sakamoto et al. 1990). Since sea turtles are mainly confronted with varying T<sub>b</sub> when they are actively swimming, the question arises as to whether their T<sub>b</sub> has to stay within a certain range for them to sustain their

<table>
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<th>Breath</th>
<th>Apnoea</th>
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<tr>
<td>Turtle</td>
<td>M (cm/s)</td>
</tr>
<tr>
<td>1</td>
<td>0.9</td>
</tr>
<tr>
<td>1</td>
<td>1.4</td>
</tr>
<tr>
<td>1</td>
<td>2.8</td>
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<td>1.6</td>
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<tr>
<td>3</td>
<td>0.8</td>
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</tbody>
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Note. T<sub>b</sub> = acclimation temperature.
activity. If this is the case, they should possess adaptations to regulate heat flow.

In this study, we found that when $T_w$ increased above $T_{ac}$, blood circulation in the front flippers increased. This was achieved by a faster blood flow velocity and by a lower resistance opposed to the flow (e.g., widening of the vessels). In contrast, blood flow came virtually to a halt when $T_w$ dropped below $T_{ac}$. This may reduce heat exchange, helping to retain heat inside the body.

Such a state could not be sustained indefinitely because the tissues would be deprived of oxygen. This problem was probably avoided by the circulatory response to breathing. For a short period during and after the turtle surfaced to breathe, heart rate as well as blood flow velocity increased, presumably facilitating replenishment of oxygen and removal of toxic metabolites. It might be argued that normally most of the heat is exchanged during these breathing-induced increases in circulation. However, these periods accounted only for about 5% of the time (e.g., 3 min in 1 h), which is representative of that observed in free-living sea turtles (Renaud and Carpenter 1994; van Dam and Diez 1996). Although obtaining accurate measurements during breathing was difficult, heart rate was, if at all, only elevated 1.9–2.3 times during these short periods, and blood velocity was elevated three- to ninefold. Heat flow will depend on a number of characteristics in addition to blood flow velocity, but assuming these other unmeasured parameters remain unaffected, heat exchange during breathing might be expected to account for around 20% of the total heat exchange (average five times greater flow for 5% of the time).

Circulation to the head never ceased, even at the lowest $T_w$, suggesting that the brain was continuously supplied with oxygen. This may be part of the phenomenon that has been described as the "dive response" (Butler and Jones 1997; Elsner 1999); most aquatic air-breathing animals have reduced circulation while they are diving, providing only the most im-

Figure 4. Arterial blood flow in the neck of a loggerhead turtle (turtle 5). Vertical lines indicate onset of a measurement in water of different temperature; dashed lines are mean blood flow velocities.

Figure 5. Heart rate of turtles 1–6 at various experimental water temperatures. Symbols as in Figure 3. Dashed lines indicate exemplary differences between individuals.
important organs (e.g., brain) with oxygen. The mechanism serves primarily to reduce total oxygen consumption and thus to maximise the time spent underwater (Handrich et al. 1997). In addition to this function, the reduced peripheral circulation may also assist in keeping heat inside the body core. However, when the animal warms up during periods of high activity, it may need to dissipate heat via increased blood flow to the periphery. The different blood flow responses in neck and flippers to changing environmental temperatures support our hypothesis that the flippers play a role in heat exchange.

The vascular net of the flippers is organised similarly to that found in the limbs of humans (M. Scherillo, personal communication). Even though Mrosovsky (1980) reported that no well-developed countercurrent heat exchangers were found in the flippers of a loggerhead hatchling, it is possible that there is some heat exchange between adjacent arteries and veins. Because of this and the large surface to volume ratio, the flippers are more suitable for modulating the heat exchange than is, for example, the carapace with its much lower thermal conductivity (Heath and McGinnis 1980).

The method used in this study did not allow us to record changes in blood flow continuously. Although it appeared as if elevated blood flow during warm water exposure remained basically on the same level, this could not be established quantitatively. However, since none of the turtles reached a new stable T<sub>b</sub> during the transfer experiment, it can be inferred that blood flow remains elevated at least until a new T<sub>b</sub> is stabilised.

A great deal of our knowledge of reptilian thermal biology has been obtained from heating and cooling experiments. In such trials, the study animal is placed in experimentally manipulated T<sub>r</sub>. Under these controlled conditions, it is possible to monitor physiological data such as heart rate, T<sub>b</sub>, oxygen consumption, blood flow, and so forth. One important feature of these experiments is that a relatively rapid change in temperature is forced on the animal, which does not have the opportunity to acclimatise to the given temperature(s) or to move to another place of more favourable temperature. Because ectotherms, in contrast to endotherms, lack significant amounts of external insulation, they are more immediately affected by external temperature changes, and hence their T<sub>b</sub> drops or rises accordingly. However, heating and cooling experiments on Galápagos marine iguanas, *Amblyrhynchus cristatus* (Bartholomew and Lasiewski 1965), American alligators, *Alligator mississippiensis* (Smith 1976 cited in Smith 1979), aquatic turtles, *Pseudemys floridana* and *Chelydra serpentina* (Weathers and White 1971), green turtles, *Chelonia mydas* (Heath and McGinnis 1980; Smith et al. 1986; this study), and loggerhead turtles (this study) revealed that all these animals warm up faster than they cool down. This implicates the involvement of a physiological regulatory control mechanism. Morgareidge and White (1969) inferred that vasomotor control of cutaneous blood flow enables the Galápagos marine iguana to retain thermal stability under extreme environmental conditions (e.g., when moving from hot lava substrate into cold water to forage). Other factors, such as thermal variation in blood viscosity, may play a role of as yet unknown importance. Sea turtles live in a comparatively more stable environment, yet Smith et al. (1986) claimed that they are efficient at regulating their heating and cooling rates. This interpretation is supported by the circulatory changes presented in this article. A 10°C difference in T<sub>a</sub> caused a greater than 100-fold increase in blood flow velocity from 0.1 cm/s to 11.1 cm/s.

In many heating and cooling experiments, heart rate is considered to be an important, variable factor that accompanies different heating and cooling rates. Heart rate is typically faster during heating than during cooling (lizards: reviewed by Bartholomew 1982; green turtles: Smith et al. 1986). Although we also observed an average increase, we observed significant individual variation in the response of heart rate to increasing T<sub>a</sub>. Our data suggest that heart rate does not necessarily reflect regional heat-exchange regulation. Whereas the turtle in Figure 2a almost doubled its heart rate in 10° warmer water, the turtle in Figure 2b had almost the same heart rate during heating as it had at T<sub>a</sub>. Despite this, there was a dramatic increase in flipper blood flow in both turtles. These data do not support Smith et al.’s (1986) statement that changes in peripheral blood flow alter heart rate because heart rate was independent of T<sub>a</sub> in some turtles, yet in other animals we determined parallel alterations in peripheral blood flow with T<sub>a</sub> (see also Morgareidge and White 1969; Baker et al. 1972).

In summary, using a simple, noninvasive method, we have...

Figure 6. Increase in body temperature (T<sub>b</sub>) of turtle 1 during heating after a transfer from 16.1°C water into 28.8°C water and decrease of T<sub>b</sub> during cooling after the retransfer into 16.1°C water (transfer was initiated 30 min after transfer).
shown that externally induced heating rates are accompanied by faster blood flow velocities in the front flippers of both loggerhead and green turtles. This response was more pronounced at higher experimental temperatures. In contrast, cooling resulted in drastically reduced blood flow. This leads us to the conclusion that the front flippers play a previously undescribed role in the heat exchange between sea turtles and their environment.

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