

RESEARCH ARTICLE

Body temperature stability achieved by the large body mass of sea turtles

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ABSTRACT

To investigate the thermal characteristics of large reptiles living in water, temperature data were continuously recorded from 16 free-ranging loggerhead turtles, *Caretta caretta*, during interesting periods using data loggers. Core body temperatures were 0.7–1.7°C higher than ambient water temperatures and were kept relatively constant. Unsteady numerical simulations using a spherical thermodynamic model provided mechanistic explanations for these phenomena, and the body temperature responses to fluctuating water temperature can be simply explained by a large body mass with a constant thermal diffusivity and a heat production rate rather than physiological thermoregulation. By contrast, body temperatures increased 2.6–5.1°C in 107–152 min during their emergences to nest on land. The estimated heat production rates on land were 7.4–10.5 times the calculated values in the sea. The theoretical prediction that temperature difference between body and water temperatures would increase according to the body size was confirmed by empirical data recorded from several species of sea turtles. Comparing previously reported data, the interesting intervals of leatherback, green and loggerhead turtles were shorter when the body temperatures were higher. Sea turtles seem to benefit from a passive thermoregulatory strategy, which depends primarily on the physical attributes of their large body masses.

KEY WORDS: Data logger, Heat production rate, Thermal conductivity, Thermal diffusivity, Thermal inertia, Unsteady model

INTRODUCTION

Large reptiles, including giant dinosaurs, might have had relatively constant body temperatures (Colbert et al., 1946; Bakker, 1972; McNab and Auffenberg, 1976; Barrick and Showers, 1994). Theoretical simulation has raised the interesting idea that large reptiles might maintain a high body temperature as a result of large size alone (Spotila et al., 1973; Stevenson, 1985). Seebacher et al. (Seebacher et al., 1999) have previously used field data to demonstrate that high and stable body temperatures of land-living crocodiles are driven primarily by physical relationships between body temperature and environmental temperature. Water, in comparison with air, places much tighter constraints on thermoregulation in aquatic animals, owing to its high heat capacity and high thermal conductivity, which leads to a rapid transfer of heat from a warm animal to cold water. Thus, water strongly limits the warming effect of metabolism in aquatic living animals.

Sea turtles spend almost all their time under water, and their range of both vertical and horizontal movements are large. To substantiate their thermal characteristics under natural conditions, long and

continuous measurements in the sea were needed. Some aspects of body temperature of free-ranging turtles during the interesting period have been revealed previously using animal-borne recorders (Sakamoto et al., 1990; Sato et al., 1994; Sato et al., 1995; Southwood et al., 2005). Core body temperatures of loggerhead turtles (*Caretta caretta* Linnaeus 1758) are higher than the water temperatures throughout their interesting periods (Sakamoto et al., 1990; Sato et al., 1994), and the mean temperature differences between core body and water varies from 0.7 to 1.7°C (data from 15 turtles), with larger animals having a significantly higher mean difference (Sato et al., 1998). Despite this, body temperature followed long-term (>24 hours) fluctuations in water temperature with a lag of 2–3 hours, although body temperatures do not respond to sudden changes in ambient water temperature when they dive in the ocean (Sato et al., 1994). The development of a dynamic heat transfer model will be informative in order to understand the unsteady correlation between body and water temperatures.

Here, I investigate the non-equilibrium thermodynamics of body temperature in free-ranging adult loggerhead turtles (56–118 kg) by applying the continuous temperature measurements of body and water to a dynamic heat transfer model. In addition, I make allometric comparisons of the temperature difference between body and water with data from other species of sea turtle. Finally, the ecological implications of body temperature on the life history of the turtles are discussed.

RESULTS**Long-term relationship in the sea**

Fig. 1 shows a long-term relationship between the measured and calculated body temperature of a turtle (ID 9305) over an interesting period of 21.0 days. A radius of a spherical model for the turtle was calculated to be 0.25 m, and the thermal diffusivity and heat production rate were taken to be $4.5 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$ and $1.5 \times 10^2 \text{ J s}^{-1} \text{ m}^{-3}$, respectively. The calculated body temperature coincided well with measured body temperature (a coefficient of determination=0.94) and had a low mean residual (0.13°C). As shown in Table 1, the coefficients of determination between the measured and calculated body temperatures were high (0.79–0.98) and the mean residuals were low (0.12–0.33°C) in all turtles.

Short-term relationship in the sea

Vertical movements of turtles led to them being exposed to sudden changes in ambient water temperature; however, the measured body temperature did not follow such short-term (<90 min, maximum dive duration) fluctuations. One example of a turtle (ID 9305, 69 kg) is shown in Fig. 2. The calculated core body temperature for a spherical model (69 kg, $r_R=0.25 \text{ m}$) fitted with the measured body temperature, which remained constant despite rapid changes in water temperature. Assuming smaller spheres, 10 kg ($r_R=0.13 \text{ m}$) and 1 kg ($r_R=0.06 \text{ m}$), with the same thermal diffusivities and heat production rates, the stability of their core body temperature was not

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List of symbols and abbreviations

A	a constant in Eqn 3
BT	body temperature ($^{\circ}\text{C}$)
C_p	specific heat of the turtle body ($=3550 \text{ J kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$)
E	free energy (J mol^{-1})
ITV	interesting interval (days)
M	body mass (kg)
Q	rate of heat production ($\text{J s}^{-1} \text{ m}^{-3}$)
Q_{10}	temperature coefficient
R	gas constant ($=8.31451 \text{ J mol}^{-1} \text{ K}^{-1}$)
r_R	radius of the considered spherical model (m)
T	absolute temperature (K)
$T_b(r, t)$	body temperature ($^{\circ}\text{C}$) as a function of time t (s) and distance r (m) from the centre of the sphere
WT	water temperature ($^{\circ}\text{C}$)
ΔT_b	difference between core and surface body temperatures ($^{\circ}\text{C}$)
K	thermal conductivity ($\text{J s}^{-1} \text{ m}^{-1} \text{ }^{\circ}\text{C}^{-1}$)
χ	thermal diffusivity of the body ($\text{m}^2 \text{ s}^{-1}$)
ρ	density of the turtle body ($=1046.5 \text{ kg m}^{-3}$)

maintained, and the calculated body temperature followed the rapid changes in water temperature (Fig. 2).

During nesting on land

The measured body temperatures of three turtles rose 2.6–5.1 $^{\circ}\text{C}$ in 107–152 min during nesting behaviours on land (Fig. 3). The rate of change of body temperature was higher during digging the chamber and covering the nest than it was during landing and egg laying (Fig. 3A). The mean heat production rate that caused the rapid rise in body temperature was estimated for each turtle, assuming the same value of thermal diffusivity in the sea. The estimated heat production rates on land were 7.4–10.5 times the level of those for the same turtle in the sea (Table 1).

DISCUSSION**Dynamic mechanism to determine body temperature of turtles in water**

The body temperature stability of large reptiles, including dinosaurs, has already been described by several researchers as gigantothermy, thermal inertia or inertial homoiothermy (Frair et al., 1972; Spotila et al., 1973; Neill and Stevens, 1974; McNab and Auffenberg, 1976; Paladino et al., 1990). In the present study, the unsteady

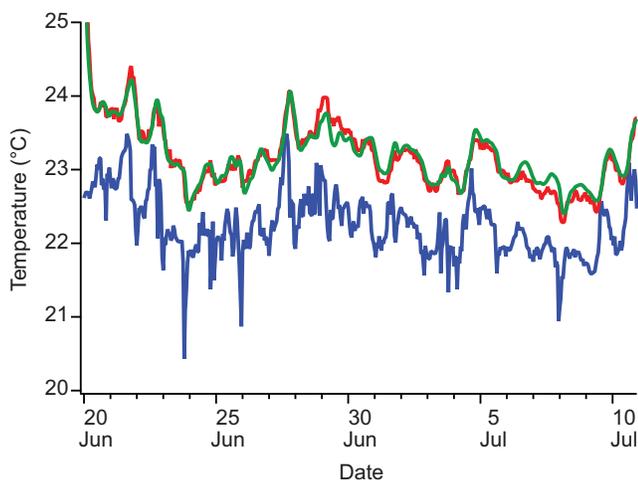


Fig. 1. Time series figure of a turtle (ID 9305) throughout an interesting period. Measured (red line) and calculated (green line) body temperatures, and ambient water temperature (blue line) were sampled every hour.

thermodynamic analysis was applied to measured data obtained from adult loggerhead turtles under natural conditions, and body temperature stability was not attained when assuming small body masses such as 10 and 1 kg (Fig. 2). This result leads me to conclude that adults could achieve their body temperature stabilities through their large body masses.

The observed responses of body temperature to long-term fluctuations in ambient water temperature were mostly explained by a hypothesis of a constant thermal diffusivity and a constant heat production rate (Fig. 1). The relationships between measured and calculated body temperatures had high coefficients of determination (0.79–0.98 in Table 1). Some individuals (ID 9101, 9102, 9103, 9201) had relatively lower coefficients of determination, which might be due to low sampling rate (Table 1). The others had high coefficients of determination (0.88–0.98), indicating that more than 88% of the variance in the body temperature was explained as dynamic heat transfer under constant thermal diffusivity and heat production.

During the interesting period, turtles repeat dives. The dives of loggerhead turtles have been classified into several types based on the time–depth profile, and some dominant types included three phases in each dive: (1) first descent, (2) gradual ascent, and (3) final ascent (Minamikawa et al., 1997). The turtles swim during the descent and ascent phases but stay at a certain depth without swimming during the gradual ascent phase. Turtles seem to be neutrally buoyant and rest for a large proportion of their dives in the middle of the water column (Minamikawa et al., 1997; Minamikawa et al., 2000). These inactive behavioural patterns of loggerhead turtles during the interesting period support the constant thermal diffusivity and heat production findings in the results of the present study. Thus, physiological thermoregulation does not appear to play an important role in determining the body temperature of adult female loggerhead turtles during their interesting periods. This conclusion is conspicuous in comparison with other aquatic animals.

Holland et al. (Holland et al., 1992) show that swimming Bigeye tunas actively regulate body temperature through a combination of physiological and behavioural means; therefore, these fish can raise the whole-body thermal conductivity by two orders of magnitude to allow rapid warming when they ascend from cold water into warmer surface waters, the reverse taking place when they return to the depths. Handrich et al. (Handrich et al., 1997) have also reported that diving king penguins decrease their abdominal temperature by more than 10 $^{\circ}\text{C}$, which would lead to a metabolic depression and might help to explain the long dive duration of these endotherms. The decline in body temperature in king penguin may be the result of an increase in heat loss and/or a local metabolic depression. In both the cases of the fish and the bird, distinct changes are needed in the physiological condition to explain the observed changes in body temperature. Although it has been reported that turtles can change their physiological condition according to environmental and behavioural characteristics (Weathers and White, 1971; Heath and McGinnis, 1980; Butler et al., 1984; Smith et al., 1986), a substantial change in thermal diffusivity or heat production rate is unnecessary to explain the body temperature response of loggerhead turtles to fluctuations in water temperature (Figs 1, 2).

Elevated heat production rate during nesting behaviour on land

The body temperature of the three turtles rose 2.6–5.1 $^{\circ}\text{C}$ during a series of nesting behaviours on land (Fig. 3). In 1980, Mrosovsky

Table 1. Individual data and results of numerical simulation

Turtle ID	Body mass (kg)	Length of data (days)	Thermal diffusivity $\times 10^{-7}$ ($\text{m}^2 \text{s}^{-1}$)	Coefficient of determination	Mean residual ($^{\circ}\text{C}$)	Heat production rate		
						In the sea $\times 10^2$ ($\text{J s}^{-1} \text{m}^{-3}$)	On land $\times 10^2$ ($\text{J s}^{-1} \text{m}^{-3}$)	Ratio land:sea
8901	68.9	4.1	5.0	0.88	0.23	2.1		
9101	80.8	11.0*	5.8	0.79	0.25	2.9		
9102	72.2	16.0*	5.4	0.81	0.33	2.3		
9103	88.2	15.8*	4.0	0.86	0.24	2.1		
9201	69.4	7.2**	3.2	0.81	0.25	8.0		
9303	107.0	21.0	6.0	0.88	0.19	2.2		
9304	71.5	20.8	5.8	0.94	0.13	1.4		
9305	69.0	21.0	4.5	0.94	0.13	1.5	15	10
9305-2***	71.0	1.9	6.4	0.98	0.20	2.1		
9307	56.0	21.0	5.2	0.94	0.12	1.5		
9401	92.5	15.9	6.8	0.98	0.19	2.1		
9402	94.0	15.8	6.8	0.96	0.20	2.7	20	7.4
9402-2***	96.0	4.9	7.7	0.92	0.30	2.9	20	10.5
9405	118.0	14.9	6.6	0.98	0.17	1.9		
9405-2***	117.0	6.3	6.9	0.96	0.29	2.0		
9406	107.0	17.8	6.6	0.98	0.22	3.1		

*Sampling rate was 10 min; **sampling rate was 5 min for water temperature and 1 min for body temperature; ***data were obtained for subsequent interesting period; however, data recording was stopped in the middle of the interesting period because of less memory capacity.

discussed the body temperature of nesting turtles using the available data at that time and predicted that metabolic heat production may warm up nesting turtles less than 2°C (Mrosovsky, 1980). My data support the prediction qualitatively, but the scope of body temperature change was higher than the prediction. According to the numerical simulation, higher heat production rates are needed to explain the rapid rises in body temperature during nesting behaviour on land. Actual heat production rates on land are likely to be even higher than the estimations because I assumed that there was no evaporative water loss and that surface body temperatures were equal to air temperatures. Despite this, an increase in heat production of at least 7.4–10.5 fold above that in water would be needed to explain the rapid rises in the core temperatures of turtles nesting on land. The elevated heat production rates are probably due to the hard exercise during nesting behaviours, especially digging the chamber and covering the nest. The heat production rate is likely to be greatly affected by the behaviour of turtles, and it appears that loggerhead turtles are similar to green turtles in that they are able to raise their metabolism by a factor of 10 when they are active (Prange and Jackson, 1976; Jackson and Prange, 1979).

Effect of body size on temperature gradient

Thermoregulatory capabilities of animals can be expressed as a temperature difference between the core and surface. If Eqn 4 (Materials and methods) was solved under the steady-state condition, $\partial T_b(r, t)/\partial t = 0$, then,

$$\Delta T_b = \frac{Q}{6K} r_R^2, \quad (1)$$

where ΔT_b is the difference between the core and surface body temperatures, Q is rate of heat production ($\text{J s}^{-1} \text{m}^{-3}$), K is the thermal conductivity ($\text{J s}^{-1} \text{m}^{-1} \text{ }^{\circ}\text{C}^{-1}$) and r_R is the radius (m) of the considered spherical model. Eqn 1 suggests that larger turtles are expected to have larger temperature differences, and this has been confirmed previously by empirical data where temperature differences between body and water were positively correlated with body mass (Sato et al., 1998). According to Eqn 1, the difference depends upon the ratio of the heat production rate Q to the thermal conductance K (the degree of the thermal insulation). The mass-specific heat production rate is generally proportional to the body mass to the power $-1/4$ (Kleiber, 1975). Assuming that thermal conductivity K does not change with body size, the

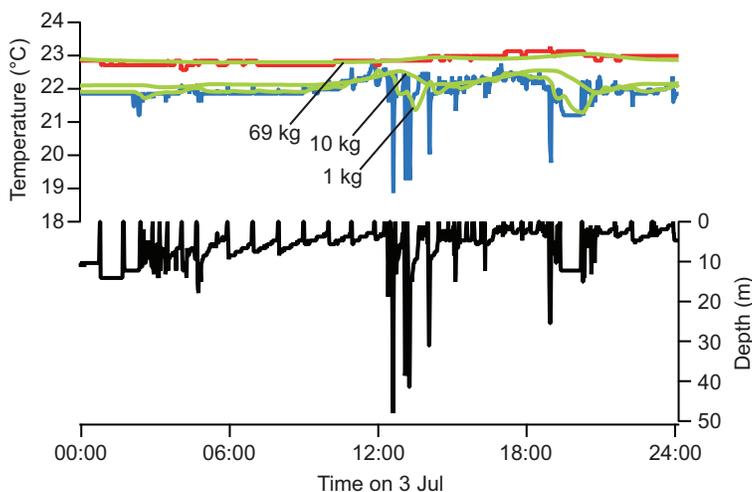


Fig. 2. Time series figure of a turtle (ID 9305) for 24 hours. Upper panel shows the measured body (red line) and ambient water (blue line) temperatures of a 69 kg turtle (ID 9305). The calculated body temperature for actual body mass (69 kg) and other calculated body temperatures assuming smaller body masses (10 kg and 1 kg) are indicated by green lines. The lower panel shows the diving profile of this individual.

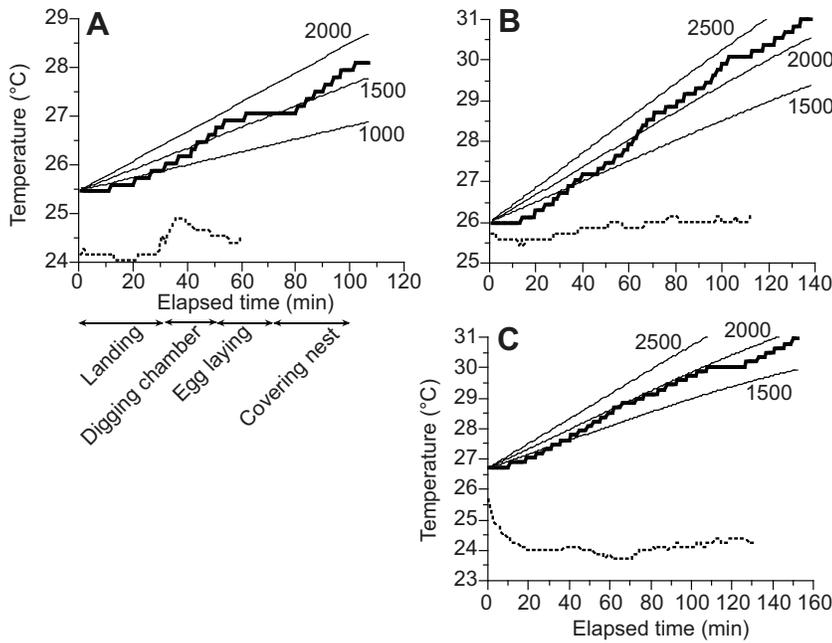


Fig. 3. Body temperatures of nesting turtles. The measured (thick line) and calculated (thin line) body temperatures, and ambient air temperature (dotted line) of three turtles during nesting behaviour on land (A, ID 9305; B, ID 9402; C, ID 9405). Values besides the lines are the heat production rates ($J s^{-1} m^{-3}$) used in the numerical simulations. All three turtles succeeded in egg laying. Data loggers were retrieved after the nest was covered. Observed behaviours are also shown in A.

temperature difference could be expected to correlate with body mass according to

$$\Delta T_b \propto M^{5/12}, \quad (2)$$

where M is body mass (kg). The data from loggerheads indicated that a 100 kg turtle had a temperature difference of ca. 1.5°C. The expected temperature difference of an animal, which has the same body shape and physiological characteristics as a loggerhead turtle, can be calculated from body mass using Eqn 2. If this analysis is performed on other species, I can see that empirical data from leatherback, green, loggerhead and olive ridley turtles around breeding sites are generally in close accord with the expected

values (Table 2). It indicates that there is no apparent difference in the ratio of heat production rate Q to thermal insulation K in Eqn 1 among different species of sea turtle. A major exception, however, is a 417 kg leatherback turtle that had a body temperature of 25.5°C when it was lifted from 7.5°C subarctic water (Frair et al., 1972). The measured temperature difference is 6.7 times larger than the expected value (Table 2). In order for the turtle to continuously maintain this 18°C temperature difference in subarctic water, some corrective mechanism, such as a high rate of heat production Q (6.7 times larger) or more effective insulation K ($0.15 = 1/6.7$ times less), is needed. Although there are some reports that leatherback turtles have higher metabolic rates on land

Table 2. Summary of thermal difference (ΔT) between body and water temperatures of turtles

Species	Body mass (kg)	ΔT (°C)		Notes about measurement	References
		Expected	Measured		
Leatherback (matured)	374	2.6	2.75	Egg temperature on beach	(Mrosovsky and Prichard, 1971)
Leatherback	417	2.7	18	Body cavity temperature on a wooden shipdeck	(Frair et al., 1972)
Leatherback (matured)			5.3-6.25	Cloacal temperature on beach	(Sapsford and Hughes, 1978)
Leatherback (matured)			3.5	Egg temperature on beach	(Mrosovsky, 1980)
Leatherback (matured)	354	2.5	2.5-5.1	Core body temperature on beach	(Paladino et al., 1996)
Leatherback (matured)	244-381	2.2-2.6	1.2-4.3	Subcarapace temperature during internesting period	(Southwood et al., 2005)
Leatherback (matured)	391-589	2.6-3.1	10.0-12.2	Gastrointestinal tract temperature during foraging period	(Casey et al., 2014)
Green (matured)	175	1.9	2.0	Egg temperature on beach	(Mrosovsky and Prichard, 1971)
Green	2-60	0.3-1.2	1-2.5	Stomach temperature in a lagoon	(Heath and McGinnis, 1980)
Green (matured)	110,121	1.6, 1.6	1-2	Body cavity temperature in the sea	(Standora et al., 1982)
Green (matured)	134,140	1.7, 1.7	1.4, 1.8	Stomach temperature during internesting period	(Sato et al., 1998)
Green	11, 52	0.6, 1.1	0.4, 0.7	Stomach temperature in a tank	(Fujiwara et al., 2007)
Loggerhead (matured)			1.9-3.22	Cloacal temperature on beach	(Sapsford and Hughes, 1978)
Loggerhead	42	1.0	0*, 3.75**	Body temperature at 5 cm depth of the plastron in the tank	(Sapsford and van der Riet, 1979)
Loggerhead (matured)	56-118	1.2-1.6	0.7-1.7	Stomach temperature during internesting period	(Sato et al., 1998)
Loggerhead	39, 85	1.0, 1.4	0.7, 0.8	Stomach temperature in a tank	(Fujiwara et al., 2007)
Olive ridley	35	1.0	0.75	Egg temperature on beach	(Mrosovsky and Prichard, 1971)

Expected ΔT was calculated from body mass using Eqn 2 assuming surface body temperature was identical to water temperature (see Materials and methods).

*Value on a rainy and overcast day; **value on a hot sunny day.

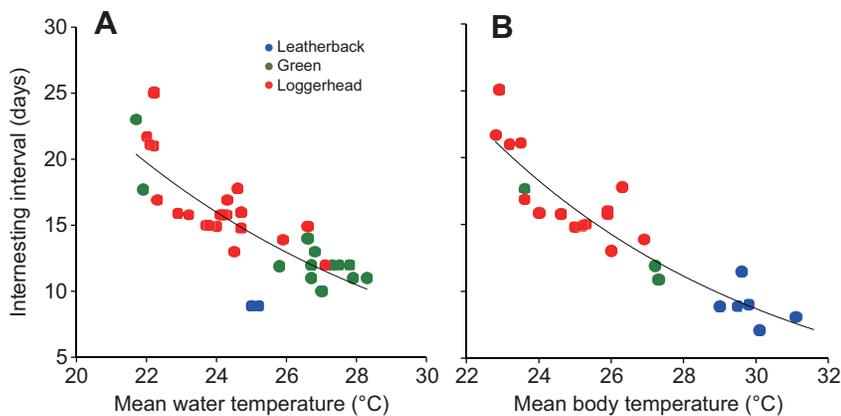


Fig. 4. Relationship between interesting interval and mean water temperature or mean body temperature for three species. The relationship between the interesting interval (ITV) and (A) mean water temperature (WT) or (B) mean body temperature (BT) is shown. Curves indicate the interesting interval (days) estimated from temperatures (K) using Eqn 3 [WT, $ITV=3.09 \times 10^{-13} \exp(9383/T)$; BT, $ITV=1.03 \times 10^{-15} \exp(11118/T)$].

(Lutcavage and Lutz, 1986; Paladino et al., 1990; Lutcavage et al., 1992), the sustained metabolic rates of swimming leatherbacks are not known. Long and continuous measurement of body temperature provides substantial insights into the endothermic capacities of leatherback turtles.

Southwood et al. (Southwood et al., 2005) have measured the subcarapace temperature of three leatherback turtles during interesting periods and reported that their body temperatures were maintained higher than ambient water temperature. The range of differences between the body and water temperatures of leatherback turtles (1.2–4.3°C) was similar to the prediction using the model (Table 2). Bradshaw et al. (Bradshaw et al., 2007) have previously estimated the diving metabolic rate from dive duration and depth data that was collected for nine free-ranging leatherback turtles over long periods (181–431 days). The behaviourally derived diving metabolic rates were close to the predicted field metabolic rate for a reptile of equivalent size and were nearly an order magnitude lower than the field metabolic rate predicted for a mammal of equivalent size (Bradshaw et al., 2007). Considering these previous studies and the present study, the relatively higher temperature gradient of leatherback turtles during interesting periods can be attributed mainly to their larger body sizes. A recent published paper reported interesting records from leatherback turtles foraging in the Northwest Atlantic Ocean (Casey et al., 2014). The mean body temperature of leatherback turtles (391–589 kg) ranged from 25.4 to 27.2°C, and the mean temperature gradient between body and water ranged from 10.0 to 12.2°C (Table 2). These values are 3.6–4.6 times larger than the values calculated from their body masses using Eqn 2. Thus, leatherback turtles swimming in high-latitude cold water (13.6–15.9°C) seemed to have different physiological conditions from turtles around nesting grounds.

Ecological implication of elevated body temperature

Sato et al. (Sato et al., 1998) described the significant influence of water (body) temperature on the length of the interesting interval in loggerhead and green turtles, there being a negative relationship between temperature and interesting interval. This relationship was common across several populations (Hays et al., 2002). Leatherback turtles generally have relatively short interesting intervals (7.1–11.5 days) in comparison with other species (Southwood et al., 2005). When each turtle experiences the same water temperature, larger temperature differences might contribute to reduce interesting interval. Combining the previously published information on loggerhead, green and leatherback turtles (Sato et al., 1998; Hays et al., 2002; Southwood et al., 2005), relationships between interesting interval and mean temperature are compared

(Fig. 4). The reciprocal of the interesting interval was considered to be the development rate per day. Arrhenius' equation was used to describe the influence of temperature on development rate (Sato et al., 1998). The following equation, which is a modification of Arrhenius' equation, was fitted to the data.

$$ITV = A^{-1} \exp\left(\frac{E}{RT}\right), \quad (3)$$

where ITV is the interesting interval (days), A is a constant, R ($=8.31451 \text{ J mol}^{-1} \text{ K}^{-1}$) is the gas constant, T (K) is the absolute temperature and E (J mol^{-1}) is the free energy. To transform the equation into a simple linear regression equation, the interesting interval was transformed into the natural logarithm, the mean absolute water (or body) temperature (K) was transformed into the reciprocal. The simple linear regression equations were calculated for water (WT) and body (BT) temperatures, respectively, using the method of least square regression (WT: $r^2=0.64$, $F=63.1$, $N=37$, $P<0.0001$; BT: $r^2=0.88$, $F=156.1$, $N=24$, $P<0.0001$). Then, E values (78015 for water temperature, 92441 for body temperature) in Eqn 3 were used to calculate Q_{10} values between 20 and 30°C (2.9 for water temperature, 3.5 for body temperature), which describes the sensitivity of the response of the interesting interval to a change in mean temperatures. Considering that a correlation coefficient between body temperature and interesting interval was significantly higher than a correlation coefficient between water temperature and interesting interval ($Z=2.164$, a two-tailed hypothesis that both correlation coefficients were the same was rejected, $P<0.05$) (Zar, 2010), it is evident that body temperature, rather than water temperature explains the length of interesting interval of sea turtles.

As discussed in a previous paper (Schofield et al., 2009), shorter interesting intervals might have some advantages for female adult loggerhead turtles – they can begin nesting earlier in the year and generate more clutches to be incubated when sand conditions are optimal during the summer. Loggerhead turtles breeding at their northern margin (Greek island of Zakynthos: 37.7°N, 20.9°E) seem to search for small patches of warm water in order to make raise their body temperature (Schofield et al., 2009). My study sites (33.8°N, 134.7°E; 33.8°N, 135.3°E) are situated in the middle of Japanese nesting grounds of this species, and the available nesting season may not constrain their reproductive output. However, shorter interesting intervals might have another advantage because reducing the total time required to lay all clutches per season will contribute to turtles minimizing the time that they spend away from their foraging areas. Although adult loggerhead turtles are known to have some endothermic capacities during interesting periods (Sato et al., 1995), there is no evidence that they have higher rates of

metabolism than that for reptiles of similar mass. Indeed, it would be less advantageous to have a higher metabolic heat production rate in order to elevate body temperature because these animals apparently do not feed actively during interesting periods (Tanaka et al., 1995), and energy reserves might constrain their reproductive output. Thus, adult loggerhead turtles during interesting periods seem to benefit from a passive thermoregulatory strategy, which depends primarily on the physical attributes of their large body masses, rather than physiological mechanisms.

MATERIALS AND METHODS

Field study

Loggerhead turtles make several serial nests on the same beach at 13–25 day intervals on the Japanese nesting grounds (Sato et al., 1998). This regular pattern of reproduction is ideal for the deployment and retrieval of data loggers on turtles. Field studies for this work were conducted at nesting beaches in the Japanese archipelago in 1989 and from 1991 to 1994. We attached data loggers onto the carapaces of turtles to record water temperature, depth and light intensity during their interesting periods, and induced animals to swallow units to record core body temperature (Sato et al., 1995; Sato et al., 1998). Body and water temperatures were simultaneously recorded from a total of 16 turtles, in three of these body temperature was also measured during nesting behaviour on land (Table 1). The sampling interval was 1 min, except for four individuals where intervals were 5 or 10 min. Data were recorded for between 1.9 and 21.0 days (Table 1). The body mass of turtles was measured for each individual on the beach using a hanging scale and a net, and these data were used in the mathematical analysis in this paper.

The recapture ratio for turtles with data loggers was 0.69 ($N=35$), which is almost same as the ratio of tagged turtles without data loggers, 0.68 ($N=66$). It is unlikely that the attachment of data loggers led turtles to avoid the nesting beach or cease the next nesting. All experimental procedures were approved by a board of education in Minabe town, Wakayama Prefecture, Japan.

Unsteady thermodynamic analysis

The first purpose of the analysis was to quantify the effect of the large body mass of the animal on the core body temperature. To do this, the model animal was regarded to be a sphere, this being the simplest three-dimensional shape. The diagrammatic representation of the model is shown in Fig. 5A. The radius (r_R) of the considered spherical model was calculated

from the known body mass of each animal with a density taken to be $\rho=1046.5 \text{ kg m}^{-3}$. The density was measured in an aquarium using two green turtles, weighing 42.7 kg and 71.5 kg, and loggerhead turtles were assumed to have equivalent densities.

The basic equation for heat diffusion within a sphere was used in the numerical simulation.

$$\frac{\partial T_b(r, t)}{\partial t} = \chi \left\{ \frac{2}{r} \frac{\partial T_b(r, t)}{\partial r} + \frac{\partial^2 T_b(r, t)}{\partial r^2} \right\} + \frac{Q}{\rho C_p}, \quad (4)$$

where $T_b(r, t)$ is body temperature ($^{\circ}\text{C}$) as a function of time t (s) and distance r (m) from the centre of the sphere, χ is thermal diffusivity ($\text{m}^2 \text{s}^{-1}$) of the body, Q is rate of heat production ($\text{J s}^{-1} \text{m}^{-3}$) and C_p is the specific heat ($=3550 \text{ J kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$), which was measured using a dead 2.0 kg loggerhead turtle (K.S., unpublished data). The second question in the mathematical analysis is whether turtles regulate their body temperatures using physiological means or not. To examine this, the values of thermal diffusivity χ and heat production rate Q were assumed to be constant in time.

The increment of body temperature per unit of time (the left term in Eqn 4) is influenced by the effect of heat flow from the warmer inside to the colder surface (the first term of the right hand side of the Eqn 4). The thermal diffusivity χ ($\text{m}^2 \text{s}^{-1}$) is an expression for the case with which a temperature changes in a given material and is defined as follows:

$$\chi = \frac{K}{\rho C_p}, \quad (5)$$

where K is thermal conductivity ($\text{J s}^{-1} \text{m}^{-1} \text{ }^{\circ}\text{C}^{-1}$).

Solar radiation is an important parameter for analyzing the body temperature of reptiles on land, but adult loggerhead turtles in water do not benefit from solar radiation as an external heat source (Sato et al., 1995). Thus, only metabolic heat production is considered as a heat source in the model (the second term of the right hand side of Eqn 4).

Eqn 4 was substituted into the differential equation for each layer with $\Delta r=1 \text{ cm}$ and $\Delta t=20 \text{ s}$ being used as finite difference. At the beginning of a calculation ($t=0$), a uniform temperature= $T_b(0,0)$, initial core body temperature, was assigned throughout the body ($r=0 \sim r_R$). The measured water temperature was assigned as surface body temperature $T_b(r_R, t)$ because surface body temperatures were nearly identical to water temperature in an experiment using captive turtles (K.S., unpublished data). Initially ($t=\Delta t$), $T_b(r_R-\Delta r, \Delta t)$ was calculated from the differential equation, then, $T_b(r_R-2\Delta r, \Delta t)$ was calculated with decreasing value of r until reaching

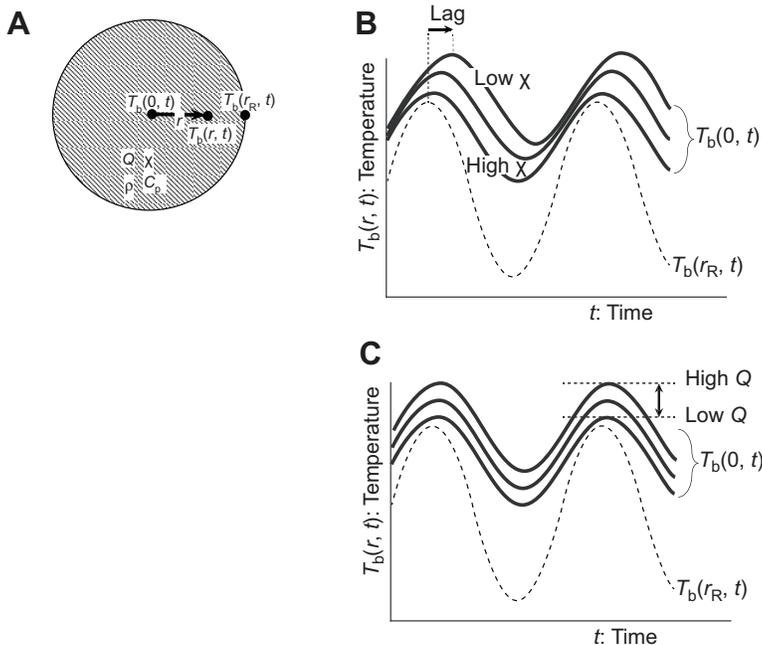


Fig. 5. Unsteady numerical simulation. Structure of the spherical dynamic heat transfer model (A), and idealized relationships between core body temperature $T_b(0, t)$ and surface body temperature $T_b(r_R, t)$ under conditions of variable thermal diffusivities χ (B), and variable heat production rates Q (C).

core body temperature $T_b(0, \Delta t)$. The simulation was then run to the next time period ($t=2\Delta t$). After computation over extended periods, the calculated core body temperature was compared with the measured body temperature of turtles.

Procedure of the model simulation

Fig. 5B,C shows the general relationship between fluctuating surface temperature $T_b(r_R, t)$ and calculated core body temperature $T_b(0, t)$ of a febrifacient sphere. The core body temperature is higher than surface temperature and lags behind the surface temperature fluctuation. In addition, the range of fluctuation of core temperature is less than that of the surface temperature. These phenomena qualitatively coincide with that described previously in free-ranging loggerhead turtles (Sato et al., 1994). Where core body temperatures were calculated with high value for thermal diffusivity, the lag between surface temperature and core body temperature became smaller (Fig. 5B).

The model simulation was run several times using several values for thermal diffusivity, and the calculated core body temperatures were compared with the measured body temperature of a turtle. The thermal diffusivity, under which the smallest coefficient of determination between measured and calculated core body temperatures was calculated, was assumed to be the most appropriate value for the turtle.

Thereafter body temperatures were calculated using an appropriate thermal diffusivity and several heat production rates. Differences in the heat production rate made the core body temperature lower or higher but did not affect the time lag between core and surface body temperatures (Fig. 5C). The heat production rate was assumed to be appropriate for the turtle when the mean residual between the measured and calculated temperatures was smallest. Both values, χ and Q , were determined for each turtle using the same procedure (Table 1).

Evaluation of the thermal diffusivity

Although my simple model enabled me to answer some biological questions, it is important to appreciate that the thermal diffusivities assumed to be appropriate for each turtle contain an effect of transformation of actual body shape to a sphere in the model. The thermal diffusivity χ values used for the turtles varied between 3.2×10^{-7} and $7.7 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$ (Table 1), which can be transformed to the thermal conductivities K of $1.2\text{--}2.9 \text{ J s}^{-1} \text{ m}^{-1} \text{ }^\circ\text{C}^{-1}$ using Eqn 5. These values are greater than the expected level for turtle tissue by one order of magnitude, e.g. human muscle $0.46 \text{ J s}^{-1} \text{ m}^{-1} \text{ }^\circ\text{C}^{-1}$ and adipose tissue $0.21 \text{ J s}^{-1} \text{ m}^{-1} \text{ }^\circ\text{C}^{-1}$ (Schmidt-Nielsen, 1990). The thermal diffusivity χ and thermal conductivity K used in this paper represent the degree of the thermal insulation, including the effect of the actual body shape of animals, which has a larger surface area in comparison with a sphere.

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Competing interests

The author declares no competing financial interests.

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