Title:

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

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Short title:

Body temperature of sea turtles
Summary

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 internesting 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 showed 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. On the other hand, 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, internesting 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 physical attributes of their large body masses.
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 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 places much tighter constraints on thermoregulation in aquatic animals in comparison than air due 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 at the sea were needed. Some aspects of body temperature of free-ranging turtles during the internesting period have been revealed 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 were higher than water
temperatures throughout their internesting periods (Sakamoto et al., 1990; Sato et al., 1994) and mean temperature differences between core body and water varied from 0.7 to 1.7°C in 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 did not respond to sudden changes in ambient water temperature when they dove in the ocean (Sato et al., 1994). The development of a dynamic heat transfer model will be informative 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 made 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 their life history were discussed.

**Results**

**Long-term relationship in the sea**

Figure 1 shows a long-term relationship between measured and calculated body temperature of a turtle (ID 9305) over an internesting period of
21.0 days. A radius of a spherical model for the turtle was calculated to be 0.25 m and thermal diffusivity and heat production rate were taken to be $4.5 \times 10^{-7}$ m$^2$ s$^{-1}$ and $1.5 \times 10^2$ J s$^{-1}$ 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, coefficients of determination between measured and calculated body temperatures were high (range, 0.79-0.98) and mean residuals were low (range, 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, 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. Calculated core body temperature for a spherical model (69 kg, $r_R = 0.25$ m) fitted measured body temperature, which remained constant despite rapid changes in water temperature. Assuming smaller spheres, 10 kg ($r_R = 0.13$ m) and 1 kg ($r_R = 0.06$ m), with same thermal diffusivities and heat production rates, stability of their core body temperature was not maintained and calculated body temperature followed the rapid changes in water temperature (Fig. 2).
During nesting on land

Measured body temperatures of three turtles rose 2.6-5.1°C in 107-152 min during nesting behaviours on land (Fig. 3). The rate of change of body temperature was relatively higher during digging the chamber and covering the nest than 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 the same turtles’ values 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 thermodynamical analysis was applied to measured data obtained from adult loggerhead turtles under natural condition, 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 due to their large body masses.
The observed responses of body temperature to long-term fluctuation 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 internesting period, turtles repeat dives. The dives of loggerhead turtles were 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 swam during the descent and ascent phases but stayed at a certain depth without swimming during the gradual ascent phase. Turtles seemed 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 internesting period support the constant thermal diffusivity and heat production 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 internesting periods. This conclusion is conspicuous in
comparison with other aquatic animals.

Holland et al. (Holland et al., 1992) showed that swimming Bigeye
tunas actively regulated body temperature by a combination of physiological
and behavioural means, so that these fishes could raise the whole-body thermal
conductivity by two orders of magnitude to allow rapid warming when they
ascended from cold water into warmer surface waters, the reverse taking place
when they returned to the depths. Handrich et al. (Handrich et al., 1997)
reported that diving king penguins decreased abdominal temperature by more
than 10°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 or/and
a local metabolic depression. In both the cases of the fish and the bird, distinct
changes are needed in physiological condition to explain observed change in
body temperature. Although it has been reported that turtles could 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 was not needed 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

Body temperature of the three turtles rose 2.6-5.1°C during a series of nesting behaviours on land (Fig. 3). In 1980, Mrosovsky discussed 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 core temperatures of turtles nesting on land. The elevated heat production rates were likely to be due to the hard exercise during nesting behaviours, especially digging the chamber and covering the nest. Heat production rate was likely to be greatly affected by the behaviour of turtles and it appears that loggerhead turtles are similar to green turtles being able to raise their metabolism by a factor of 10 when they were 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 core and surface. If the equation 4 (in materials and methods section) was solved under the steady-state condition, \( \partial T_b / \partial t = 0 \), then,

\[
\Delta T_b = \frac{Q}{6K} r_R^2
\]

(1),

where \( \Delta T_b \) is difference between core and surface body temperatures, \( Q \) is rate of heat production (J s\(^{-1}\)m\(^{-3}\)), \( K \) is thermal conductivity (J s\(^{-1}\)m\(^{-1}\)°C\(^{-1}\)), and \( r_R \) is the radius (m) of the considered spherical model. Equation 1 suggests that larger turtles are expected to have larger temperature differences and then it has been confirmed by empirical data where temperature differences between body and water were positively correlated with body mass (Sato et al., 1998). According to equation 1, the difference depends upon the ratio of heat production rate \( Q \) to thermal conductance \( K \) (the degree of the thermal insulation). 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 temperature difference could be expected to correlate with body mass according to

\[
\Delta T_b \propto M^{5/12}
\]

(2),

where \( M \) is body mass (kg). Data of 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 same body shape and physiological characteristics as a loggerhead turtle, can be calculated from body mass using equation 2. If this is done on other species, I can see that empirical data from leatherback, green, loggerhead and olive ridley turtles around breeding sites generally accord closely 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 equation 1 among species of sea turtle. A major exception, however, is a 417-kg leatherback turtle which 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 expected value (Table 2). In order for the turtle to maintain this 18°C temperature difference continuously 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 (Lutcavege 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 gives a good insight into the endothermic capacities of leatherback turtles. Southwood et al. (Southwood et al., 2005) measured subcarapace temperature of three leatherback turtles during internesting periods and reported
that their body temperatures were maintained higher than ambient water temperature. The range of differences between body and water temperatures of leatherback turtles (1.2-4.3°C) was similar to the model’s prediction (Table 2). Bradshaw et al. (Bradshaw et al., 2007) estimated diving metabolic rate from dive duration and depth data 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 internesting period 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 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 values calculated from their body masses using equation 2. Thus, leatherback turtles swimming at high-latitudes cold water (13.6-15.9°C) seemed to have different physiological condition from turtles around nesting grounds.

*Ecological implication of elevated body temperature*
Sato et al. (1998) described the significant influence of water (body) temperature on the length of the internesting interval in loggerhead and green turtles, there being a negative relationship between temperature and internesting interval. This relationship was common across several populations (Hays et al., 2002). Leatherback turtles generally have relatively short internesting 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 internesting 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 internesting interval and mean temperature are compared (Fig. 4). The reciprocal of the internesting 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.

\[ \frac{1}{ITV} = A^{-1}\exp \left( \frac{E}{RT} \right) \]

(3),

where \( ITV \) is the internesting 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 internesting 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 equation 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 internesting interval to a change in mean temperatures. Considering that a correlation coefficient between body temperature and internesting interval was significantly higher than a correlation coefficient between water temperature and internesting interval ($Z=2.164$, $P<0.05$) (Zar, 2010), it is evident that body temperature rather than water temperature explains length of internesting interval of sea turtles.

As discussed in a previous paper (Schofield et al., 2009), shorter internesting interval might have some advantages for female adult loggerhead turtles to begin nesting earlier in the year and make 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) seemed to search for small patches of warm water to make their body temperature higher (Schofield et al., 2009). My study sites (33.8°N, 134.7°E;
33.8°N, 135.3°E) are situated at the middle of Japanese nesting grounds of this species and available nesting season may not constrain their reproductive output. However, shorter internesting interval might have another advantage because reducing the total time required to lay all clutches per season will contribute turtles to minimize the time that they spend away from their foraging areas. Although adult loggerhead turtles are known to have some endothermic capacities during internesting periods (Sato et al. 1995), there is no evidence that they have higher rates of metabolism than the values for reptiles of similar mass. Indeed, it would be less advantageous to have higher metabolic heat production rate to elevate body temperature because these animals apparently do not feed actively during internesting periods (Tanaka et al., 1995) and energy reserves might constrain their reproductive output. Thus, adult loggerhead turtles during internesting periods would seem to benefit from a passive thermoregulatory strategy, which depends primarily on 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 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 through 1994. We attached data loggers on the carapaces of turtles to record water temperature, depth, and light intensity during their internesting 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 which body temperature was also measured during nesting behaviour on land (Table 1). 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 the 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, 0.68 (n=66), of tagged turtles without data loggers. It is unlikely that attachment of data loggers led turtles to avoid the nesting beach or cease next nesting. All experimental procedure was approved by a board of education in Minabe town, Wakayama Prefecture, Japan.

Unsteady thermodynamical analysis

The first purpose of the analysis is to quantify the effect of large body mass of 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 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 (°C) as a function of time \( t \) (s) and distance \( r \) (m) from the center of the sphere, \( \chi \) is thermal diffusivity (m² s⁻¹) of the body, \( Q \) is rate of heat production (J s⁻¹ m⁻³), and \( C_p \) is the specific heat (= 3550 J kg⁻¹°C⁻¹) which was measured using a dead 2.0 kg loggerhead turtle (Sato unpublished data). The second question in the mathematical analysis is whether turtles regulate their body temperatures by physiological means or not. To examine this, the values of thermal diffusivity \( \chi \) and heat production rate \( Q \) were assumed to be constant in time.

The increment of body temperature per unit time (the left term in equation 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 equation 4).
thermal diffusivity $\chi$ ($m^2 s^{-1}$) is an expression for the case with which a
temperature changes in a given material and is defined as follows:

$$\chi = \frac{K}{\rho C_p}$$

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

Solar radiation is an important parameter for analyzing the body
temperature of reptiles on land but adult loggerhead turtles in water did 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 the equation 4).

Equation 4 was substituted into the differential equation for each layer
with $\Delta r = 1$ cm and $\Delta t = 20$ 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 ($r = 0 \sim r_R \cdot \Delta r$). 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 (Sato unpublished data). Initially ($t = \Delta t$), $T_b(r_R \cdot \Delta r, \Delta t)$ was
calculated from the differential equation, then, $T_b(r_R \cdot 2\Delta r, \Delta t)$ was calculated with
decreasing value of $r$ until reaching 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**

Figure 5BC shows the general relationship between fluctuating surface temperature $T_b(r, t)$ 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 was described 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 heat
production rate makes core body temperature lower or higher but does not affect
the time lag between core and surface body temperatures (Fig. 5C). Heat
production rate was assumed to be appropriate for the turtle when the mean
residual between measured and calculated temperatures was smallest. Both
values, $\chi$ 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 $\chi$ values used for the
turtles varied between $3.2 \times 10^{-7}$ and $7.7 \times 10^{-7}$ m$^2$ s$^{-1}$ (Table 1), which can be
transformed to the thermal conductivities $K$ of $1.2$-$2.9$ J s$^{-1}$m$^{-1}$°C$^{-1}$ using
equation 5. These values are greater than the expected level for turtle tissue by
one order of magnitude, e.g. human muscle $0.46$ J s$^{-1}$m$^{-1}$°C$^{-1}$ and adipose tissue
$0.21$ J s$^{-1}$m$^{-1}$°C$^{-1}$ (Schmidt-Nielsen, 1990). The thermal diffusivity $\chi$ 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 larger
surface area in comparison with a sphere.
List of symbols and abbreviations

A: a constant in equation 3.

$BT$: body temperature ($^\circ$C).

$C_p$: the specific heat of the turtle body ($= 3550 \text{ J kg}^{-1}\text{C}^{-1}$).

$E$: the free energy ($\text{J mol}^{-1}$).

$ITV$: internesting interval (days).

$M$: body mass (kg).

$Q$: rate of heat production ($\text{J s}^{-1}\text{m}^{-3}$).

$Q_{10}$: temperature coefficient.

$R$: the gas constant ($=8.31451 \text{ J mol}^{-1}\text{ K}^{-1}$).

$r_R$: the radius of the considered spherical model (m).

$T$: absolute temperature (K).

$T_b(r, t)$: body temperature ($^\circ$C) as a function of time $t$ (s) and distance $r$ (m) from the center of the sphere.

$WT$: water temperature ($^\circ$C).

$\Delta T_b$: difference between core and surface body temperatures ($^\circ$C).

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

$\chi$: thermal diffusivity of the body ($\text{m}^2\text{s}^{-1}$).

$\rho$: density of the turtle body ($= 1046.5 \text{ kg m}^{-3}$).

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References


**Figure legends**

**Fig. 1** Time series figure of a turtle (ID 9305) throughout an internesting period. Measured (red line) and calculated (green line) body temperatures and ambient water temperature (blue line) were re-sampled every 1 hour to draw lines.

**Fig. 2** Time series figure of a turtle (ID 9305) for 24 hours. Upper panel shows 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. Lower panel shows diving profile of this individual.
**Fig. 3** **Body temperatures of nesting turtles.** 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 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 (A).

**Fig. 4** **Relationship between internesting interval and mean water temperature** (A) or mean body temperature (B) for three species. Curves indicate internesting interval (day) estimated from temperatures (K) using equation 3 ($WT$: $ITV = 3.09 \times 10^{-13} \exp(9383/T)$, $BT$: $ITV = 1.03 \times 10^{-15} \exp(11118/T)$).

**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 $\chi$ (B), and variable heat production rates $Q(C)$.
Table 1. Individual data and results of numerical simulation

<table>
<thead>
<tr>
<th>Turtle ID</th>
<th>Body mass (kg)</th>
<th>Length of data (days)</th>
<th>Thermal diffusivity ( \times 10^{-7} ) (m(^2)s(^{-1}))</th>
<th>Coefficient of determination</th>
<th>Mean residual (°C)</th>
<th>Heat production rate in the sea ( \times 10^2 ) (J s(^{-1})m(^{-3}))</th>
<th>Heat production rate on land ( \times 10^2 ) (J s(^{-1})m(^{-3}))</th>
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<td>4.5</td>
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<td>3.1</td>
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</table>

* Sampling rate was 10 min.

** Sampling rate was 5 min for water temperature and 1 min for body temperature.
Table 2. Summary of thermal difference (ΔT) between body and water temperatures of turtles. Expected ΔT was calculated from body mass using equation 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Body mass (kg)</th>
<th>∆T (°C) expected</th>
<th>∆T (°C) measured</th>
<th>Notes about measurement</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>leatherback (matured)</td>
<td>374</td>
<td>2.6</td>
<td>2.75</td>
<td>egg temperature on beach</td>
<td>(Mrosovsky and Prichard, 1971)</td>
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<td>leatherback</td>
<td>417</td>
<td>2.7</td>
<td>18</td>
<td>body cavity temperature on a wooden shipdeck</td>
<td>(Frair et al., 1972)</td>
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<td>leatherback (matured)</td>
<td>354</td>
<td>2.5</td>
<td>2.5-5.1</td>
<td>cloacal temperature on beach</td>
<td>(Sapsford and Hughes, 1978)</td>
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<td>244-381</td>
<td>2.2-2.6</td>
<td>1.2-4.3</td>
<td>core body temperature on beach</td>
<td>(Paladino et al., 1996)</td>
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<td>leatherback (matured)</td>
<td>391-589</td>
<td>2.6-3.1</td>
<td>10.0-12.2</td>
<td>gastrointestinal tract temperature</td>
<td>(Southwood et al., 2005)</td>
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<td>green (matured)</td>
<td>175</td>
<td>1.9</td>
<td>2.0</td>
<td>egg temperature on beach</td>
<td>(Mrosovsky and Prichard, 1971)</td>
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<td>green</td>
<td>2-60</td>
<td>0.3-1.2</td>
<td>1-2.5</td>
<td>stomach temperature in a lagoon</td>
<td>(Heath and McGinnis, 1980)</td>
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<td>110,121</td>
<td>1.6, 1.6</td>
<td>1-2</td>
<td>body cavity temperature in the sea</td>
<td>(Standora et al., 1982)</td>
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<td>134,140</td>
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<td>1.4, 1.8</td>
<td>stomach temperature during internesting period</td>
<td>(Sato et al., 1998)</td>
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<td>green</td>
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<td>0.6, 1.1</td>
<td>0.4, 0.7</td>
<td>stomach temperature in a tank</td>
<td>(Fujiwara et al., 2007)</td>
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<td>42</td>
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<td>1.9-3.22</td>
<td>cloacal temperature on beach</td>
<td>(Sapsford and Hughes, 1978)</td>
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<td>56-118</td>
<td>1.2-1.6</td>
<td>0.7-1.7</td>
<td>stomach temperature at 5cm depth of the plastron in the tank</td>
<td>(Sapsford and van der Riet, 1979)</td>
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<td>0.7-1.7</td>
<td>stomach temperature during internesting period</td>
<td>(Sato et al., 1998)</td>
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<td>Value</td>
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<tr>
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<td>39, 85</td>
<td>1.0, 1.4</td>
<td>0.7, 0.8</td>
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<td>stomach temperature in a tank</td>
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<td>olive ridley</td>
<td>35</td>
<td>1.0</td>
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<td></td>
<td>egg temperature on beach</td>
</tr>
</tbody>
</table>

* Value on a rainy and overcast day. ** Value on a hot sunny day.
Fig. 1 Sato

Temperature (°C)

Date

June

July

20

25

30

35

40
Fig. 2  Sato
Fig. 3 Sato

(A) 2000 J s\(^{-1}\) m\(^{-3}\)

(B) 2500 J s\(^{-1}\) m\(^{-3}\)

(C) 2500 J s\(^{-1}\) m\(^{-3}\)
Fig. 4  Sato
Fig. 5  Sato