BODY SIZE AND THE CONTROL OF HEAT EXCHANGE IN ALLIGATORS

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(Received 16 November 1983; accepted in revised form 20 July 1984)

Abstract—1. The ratio of rates of heating and cooling in American alligators is maximum at a body mass of about 5 kg.
2. There may be an optimum body size for the control of heat exchange by blood flow in American alligators.

Key Word Index—Thermoregulation; heating; cooling; heat exchange; alligator; reptile; body size; body temperature; Alligator mississippiensis.

INTRODUCTION
An important way that reptiles control body temperature is by adjustments of blood flow within the body (Bartholomew, 1982; Turner, 1982). For example, the body usually warms somewhat faster than it cools. The difference in rates of temperature change is accompanied by marked differences in the transport of heat within the body by blood flow (Bartholomew, 1982; Tracy, 1982; Turner, 1982).

Several authors (Smith, 1976; Grigg et al., 1979; Bell, 1980) have suggested that large body size confers upon a reptile greater capacity for the control of heat exchange by blood flow. The theoretical and empirical justification for this claim is substantial. However, plausible arguments also can be made that support the opposite conclusion, i.e. that large body size diminishes reptiles’ abilities to control heat exchange in this way (Turner and Tracy, 1985). Recent work in our laboratory suggests that neither of these viewpoints can adequately describe the consequences of body size for the control of heat exchange.

MATERIALS AND METHODS
Twelve American alligators (Alligator mississippiensis), ranging in body mass from 656 g to 9.58 kg were heated and cooled from 20–35–20°C in a temperature-controlled wind-tunnel. In the wind-tunnel, the animals were exposed to a constant wind speed of 1.5 m s⁻¹. The alligators were restrained on a Plexiglas platform, which held them facing into the wind, and which placed them in the centre of the wind-tunnel’s test section. The limbs were allowed to dangle freely. While the animals were warming or cooling, temperatures of the air and color were monitored continuously and recorded at 1-min intervals onto magnetic tape for subsequent analysis by computer. We were careful to ensure that the alligator was at thermal equilibrium at the start of the transient.

From data on temperatures during cooling and warming, we calculated equilibration rates (E). E is the rate of change of dimensionless temperature with respect to time, \(-\frac{d}{dt}(\ln \Theta)\), where \(\Theta = \frac{T - T_a}{T - T_{w}}\), with \(T_{w}\) temperature at times 0 (beginning of transient), \(t\) and \(\infty\) (equilibrium temperature, respectively). Thus, \(E\) is independent of direction of temperature change, and the magnitude of the temperature excursion during a transient. It is the inverse of the time constant, \(\tau\). From the equilibration rate, we calculated ratios of heating rate/cooling rate (\(\phi = E_h/E_c = \tau_h/\tau_c\)). The relationship between \(\phi\) and body mass was analysed using standard polynomial regression methods (So
dal and Rohlf, 1969).

Re-analysis of the data on heating and cooling rates of American alligators gathered by Smith (1976) is very important to our conclusions, and so we have included these data with the data gathered in this study. We present results for our data alone, a re-analysis of Smith’s data alone and results for data from the two studies combined.

RESULTS
The relationship between \(\phi\) and body mass (Fig. 1) describes an obvious parabolic relationship. For our data alone:
\[
\phi = 1.01 + 0.27 M - 0.028 M^2
\]
\(r^2 = 0.448\)

For Smith’s (1976) data alone:
\[
\phi = 1.13 + 0.23 M - 0.026 M^2
\]
\(r^2 = 0.538\)

For all data combined:
\[
\phi = 1.08 + 0.24 M - 0.026 M^2
\]
\(r^2 = 0.516\)

where \(M\) = body mass (kg). In each case, a quadratic

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polynomial equation describes the data better than does a linear equation. For fits of linear equations to Smith’s data alone, $r^2 = 0.0796$, and to our data alone, $r^2 = 0.0639$. We point out that the explained variance reported by Smith (1976) for the linear relationship of $\phi$ vs log $M$ was 0.587. The difference from the value reported above appears for two reasons: we did not logarithmically transform body masses; we did not exclude data from the two largest animals from our analysis. The reasons and consequences of these changes are discussed below.

For all data analysed together, the maximum capability for the control of heat exchange (i.e. where $d\phi/dM = 0$) occurs at a body mass of about 4.6 kg. At body masses above and below this, capability for control of heat exchange is apparently diminished (Fig. 1).

**DISCUSSION**

Several investigators have reported that the time constants, $\tau$, for heating and cooling of “lizard-shaped” reptiles relate to body mass in such a way that the ratio of heating and cooling rates ($\phi \equiv \tau_c/\tau_w$) increases continuously with increasing body mass (Smith, 1976; Grigg et al., 1979; Bell, 1980). This has been taken to mean that large reptiles have greater capabilities for the physiological adjustment of heat exchange than do small reptiles (Smith, 1976), although this has been questioned (Grigg et al., 1979).

Yet, our data, and even all the original data of Smith (1976) do not conform to this pattern. Rather, the relationship between $\phi$ and body mass is best described by a parabolic equation, increasing up to a body mass of about 5 kg, and declining toward unity at a body mass of approx. 10 kg. Can this generalization be extended to very large alligators? We might anticipate two possible outcomes from the data in Fig. 1: (i) $\phi$ may asymptotically approach unity as body mass increases or (ii) $\phi$ may fall below unity at larger body masses. However, ratios of heating and cooling rates may actually increase again at very large body masses. For example, Smith et al. (1984) report that a 67.1 kg alligator “heated twice as fast as it cooled”.

In alligators as large as this, production of metabolic heat can comprise a significant portion of the animal’s energy budget in the transient state. This production of heat can introduce distortions in the curves that normally are used to calculate thermal time constants, because temperature of the animal at equilibrium can no longer be considered equivalent to air temperature (Bakken, 1976); this is especially important during warming of the body. Using Smith et al.’s (1984) data, we calculated time constants for warming and cooling, using a method that determines both equilibrium temperature and time constant simultaneously [modified from Bakken (1976)]. It is noteworthy that the actual value of $\phi$ is 1.56 (Table 1)—a value considerably less than two. It also is considerably greater than unity and warrants an explanation.

Differences in rates of warming and cooling need not arise only through changes of blood flow within the body. Especially for very large animals, it also may arise from the higher average production of metabolic heat that occurs during warming. A value of $\phi$ greater than unity at very large body masses may be a reflection of the important role that metabolic heat production plays in the energetics of the transient state of large animals. Smith et al.’s (1984) data support this hypothesis: the ratio of heating to cooling rates is greater at higher ranges of body temperature (Table 2).

When trying to explain the unusual pattern seen in Fig. 1, it is tempting to posit an artefact which precludes the control of heat exchange that potentially might exist in the larger alligators. Smith (1976) came to the conclusion that $\phi$ must increase con-

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**Table 1.** Time constants ($\tau$) and equilibrium temperatures ($T_e$) of a 67.1 kg alligator

<table>
<thead>
<tr>
<th>Warming</th>
<th>Calculated</th>
<th>Reported by Smith et al. (1984)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\tau_w$ (s)</td>
<td>19.11</td>
<td>—</td>
</tr>
<tr>
<td>$T_e$ (C)</td>
<td>36.31</td>
<td>35</td>
</tr>
<tr>
<td>Cooling</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\tau_c$ (s)</td>
<td>14.25</td>
<td>15</td>
</tr>
<tr>
<td>$T_e$ (C)</td>
<td>25.50</td>
<td></td>
</tr>
</tbody>
</table>

$\phi \equiv \tau_c/\tau_w$

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**Table 2.** Time constants ($\tau$) of a 67.1 kg alligator for warming and cooling over various temperature ranges

<table>
<thead>
<tr>
<th>Range of body temperature</th>
<th>$\tau_w$ (s)</th>
<th>$\tau_c$ (s)</th>
<th>$\phi$</th>
</tr>
</thead>
<tbody>
<tr>
<td>34–17</td>
<td>19.1</td>
<td>29.9</td>
<td>1.56</td>
</tr>
<tr>
<td>32–17</td>
<td>24.2</td>
<td>28.7</td>
<td>1.18</td>
</tr>
<tr>
<td>30–17</td>
<td>31.1</td>
<td>27.2</td>
<td>0.88</td>
</tr>
</tbody>
</table>

Data are from Smith et al. (1984) and analysed using a modification of the method of Bakken (1976).
continuous at greater and greater body masses because he took the prudent step of ignoring data from his two largest animals, fearing that their vigorous struggling would invalidate the data. The large animals in our study did not struggle appreciably during the experiments. Yet, the correspondence between the data from our experiment and the data from Smith's (1976) is, to our eyes, striking (Fig. 1). This leads us to question whether any of Smith's data should have been considered artefactual and excluded from his original analysis. This doubt becomes especially important when Smith's original analysis (which excluded data from his largest animals) has comprised an important element of subsequent studies (Grigg et al., 1979; Bell, 1980).

The relation between $\phi$ and body mass at body masses less than 5 kg has impressive theoretical justification from simple biophysical models (Grigg et al., 1979; Bell, 1980). Yet, the decline in $\phi$ at body masses larger than 5 kg also has some theoretical support from simple biophysical models (Turner and Tracy, 1985). The difference between the two predictions resides primarily in assumptions on how morphology of the body interacts with the flow of heat within the body. The models of Grigg et al. (1979) and of Bell (1980) assume a reptile is adequately described as a simple cylinder or flat slab, in which the principal component of heat transfer as radial (i.e. from the centre of a cylinder to its surface). The model of Turner and Tracy (1985) incorporates the fact that small lizard-shaped reptiles use the appendages as important sites for the control of heat exchange (Turner and Tracy, 1983). They assume, therefore, that the principal component of heat transfer is along the longitudinal axis of an appendage “fin”.

Both these models begin with equally valid a priori assumptions, and so are equally legitimate approaches to their problem. One appraises the “correctness” of competing models such as these by comparing their predictions with the real phenomenon—in this case, control of heating and cooling rates. We argue here that both models can predict only a portion of the phenomenon they purport to describe. The interaction of body size with the physiological control of heat exchange appears to be more complex than previously imagined.

Acknowledgements—This work was supported in part by a Biomedical Research Support Grant to C. R. Tracy and J. S. Turner.

REFERENCES


