

## BODY SIZE AND THE CONTROL OF HEAT EXCHANGE IN ALLIGATORS

J. S. TURNER\* and C. R. TRACY

Department of Zoology and Entomology, Colorado State University, Fort Collins, CO 80523, U.S.A.

(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<sup>-1</sup>. 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 colon 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,  $-d(\ln \theta)/dt$ , where  $\theta =$  dimensionless temperature  $[(T_t - T_\infty)/(T_0 - T_\infty)]$ , with  $T_{0,t,\infty} =$  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 rates, we calculated ratios of heating rate/cooling rate ( $\phi \equiv E_h/E_c \equiv \tau_c/\tau_w$ ). The relationship between  $\phi$  and body mass was analysed using standard polynomial regression methods (Sokal 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:

$$\phi = 1.01 + 0.27 M - 0.028 M^2 \quad (1)$$

$$r^2 = 0.448.$$

For Smith's (1976) data alone:

$$\phi = 1.13 + 0.23 M - 0.026 M^2 \quad (2)$$

$$r^2 = 0.538.$$

For all data combined:

$$\phi = 1.08 + 0.24 M - 0.026 M^2 \quad (3)$$

$$r^2 = 0.516;$$

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

\*Present address: Department of Biology, Franklin and Marshall College, Lancaster, PA 17604, U.S.A.

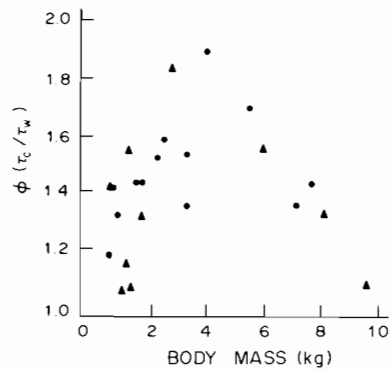


Fig. 1. Ratio of heating rate to cooling rate ( $\phi \equiv \tau_c/\tau_w$ ) for *Alligator mississippiensis*, from 600 g to 10 kg body mass. ●, Data from Smith (1976); ▲, data from this study.

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,  $r^2 = 0.0039$ . 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

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

	Calculated	Reported by Smith <i>et al.</i> (1984)
<i>Warming</i>		
$\tau$ (ks)	19.11	—
$T_x$ (°C)	36.31	35
<i>Cooling</i>		
$\tau$ (ks)	29.11	25.50
$T_x$ (°C)	14.25	15
<i>Warming/cooling</i>		
$\tau_c/\tau_w$	1.56	2

Data are taken from Smith *et al.* (1984) and analysed using a modification of the method of Bakken (1976).

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). It is possible, then, that rapid warming and slow cooling of the body arises in two ways. Among animals smaller than 10 kg body mass, differences in rates of warming and cooling hysteresis may occur mostly as a result of changes in blood flow. Among animals very much larger than this, hysteresis of heating and cooling rates may occur as a result of higher average levels of heat production by metabolism during warming.

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-

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

Range of body temperature (°C)	$\tau_w$ (ks)	$\tau_c$ (ks)	$\tau_c/\tau_w$
34–17	19.1	29.9	1.56
32–17	24.2	28.7	1.18
30–17	31.1	27.2	0.88

Data are from Smith *et al.* (1984) and analysed using a modification of the method of Bakken (1976).

tinuously 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 is 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

- Bakken G. S. (1976) An improved method for determining thermal conductance and equilibrium body temperature with cooling curve experiments. *J. therm. Biol.* **1**, 169–175.
- Bartholomew G. A. (1982) Physiological control of body temperature. In *Biology of the Reptilia*, Vol. 12 (Edited by Pough F. H. and Gans C.), pp. 167–211. Academic Press, London.
- Bell C. J. (1980) The scaling of the thermal inertia of lizards. *J. exp. Biol.* **86**, 79–85.
- Grigg G. C., Drane C. R. and Courtice G. P. (1979) Time constants of heating and cooling in the eastern water dragon, *Physignathus lesuerii* and some generalizations about heating and cooling in reptiles. *J. therm. Biol.* **4**, 354–360.
- Smith E. N. (1976) Heating and cooling rates of the American alligator, *Alligator mississippiensis*. *Physiol. Zool.* **49**, 37–48.
- Smith E. N., Standora E. A. and Robertson S. L. (1984) physiological thermoregulation of mature alligators. *Comp. Biochem. Physiol.* **77A**, 189–193.
- Sokal R. R. and F. J. Rohlf (1969) *Biometry. The Principles and Practice of Statistics in Biological Research*. Freeman, San Francisco, Calif.
- Tracy C. R. (1982) Biophysical modeling in reptilian physiology and ecology. In *Biology of the Reptilia*, Vol. 12 (Edited by Pough F. H. and Gans C.), pp. 275–321. Academic Press, London.
- Turner J. S. (1982) The relationship between heat exchange and blood flow in reptiles. Ph.D. Dissertation, Colorado State Univ., Ft. Collins, Colo.
- Turner J. S. and Tracy C. R. (1983) Blood flow to appendages and the control of heat exchange in the American alligator. *Physiol. Zool.* **56**, 195–200.
- Turner J. S. and C. R. Tracy (1985) Body size, homeothermy and the control of heat exchange in mammal-like reptiles. In *Ecology and Biology of the Mammal-like Reptiles* (Edited by Hotton N. J., Roth J. J., Roth E. C. and MacLean P. D.). Smithsonian Inst. Press, Washington, D.C.