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The Cardiovascular Control of Heat Exchange: Consequences of Body Size[1]

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SYNOPSIS. For blood flow to be an effective agent for the control of heat exchange, it must occur in a region of the body where conduction resistance in the tissues is relatively high, and in an environment where external resistance to heat exchange is relatively low. If either of these conditions is not met, control of heat exchange by blood flow is not possible. Very small reptiles should not be able to control heat exchange by blood flow in any environment, unless they control blood flow specifically to appendages. Very large reptiles should be able to control heat exchange by blood flow only under certain conditions, such as in water, very high winds, or intense radiative heating. Otherwise, they should have little control. An optimum body size should exist for a reptile's ability to control heat exchange using blood flow. In air, this optimum body size for alligators appears to be about 5 kg. Theoretically, the optimum size should be substantially larger than 5 kg for reptiles heating and cooling in water.

INTRODUCTION

An important way that animals control heat exchange with the environment is to control blood flow to peripheral regions of the body. That many reptiles do this has been known for almost 30 years. In general, when a reptile is exposed to a step change in ambient temperature, it heats up faster than it cools. During warming, skin blood flow is higher, the heart beats faster and more blood flows through the systemic circulation than during cooling (Bartholomew, 1982). Some reptiles cool faster than they warm, but whether this is the direct result of variations in blood flow still is an open question, in my view. Still largely unknown is how the amount and distribution of blood flow is controlled during temperature changes and the extent to which physiological control of heat exchange is important to a reptile in nature.

I do not intend to provide a detailed summary of the work done over the past 30 years that supports these generalizations. Two excellent reviews on this subject have appeared in the last few years (Smith, 1979; Bartholomew, 1982), and I will not try to duplicate those efforts. Rather, I will explore a very basic question: how does a change in blood flow translate into a change in the exchanges of heat between an animal and its environment?

This may be putting the question on *too* basic a level, but I think not. As we shall see, the connection between blood flow and heat exchange is not straightforward, something that has not always been appreciated. For example, a change in blood flow usually is thought to always carry with it a change in the transport of heat. This often is true, but is not always true. To see when the assumption is true and when it is not, it may be useful to take a step back and examine the problem at its most basic level.

It also is my opinion that the ecological significance of the control of heating and cooling rates is not well understood. At present, the hysteresis of heating and cooling in reptiles is an interesting laboratory phenomenon, but little more. Whether it will remain so, or whether it can tell us something about how reptiles live in a complex thermal environment also calls for approaching the question at its most fundamental level.

In this article, I outline a simple heat exchange model that explicitly considers the effects of changing blood flow. The model helps to identify the constraints on using blood flow as an agent in the control of heat exchange, and shows in a general way how these constraints are affected by

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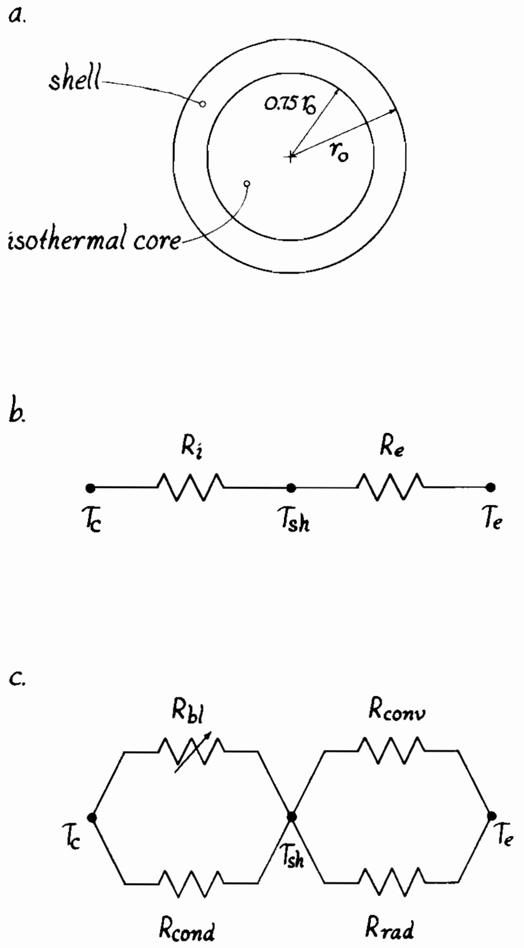

FIG. 1. Model of the exchanges of heat between a cylindrical "animal" and the environment. (a) Core-shell model of heat exchange. (b) Equivalent circuit diagram of heat exchange between core and environment. (c) Internal and external resistances resolved into component resistances.

body size. Using the model, I will examine two specific questions: (1) Can very small reptiles control heating and cooling rates using blood flow and if so, how? (2) How does body size, especially large body size, affect a reptile's ability to control heating and cooling rates using blood flow?

CONTROL OF HEAT EXCHANGE BY BLOOD FLOW: GENERAL PRINCIPLES

The control of heat exchange as it applies to heating and cooling rates of reptiles is a transient-state problem; that is, the storage rate of thermal energy within the body is not zero. Transient-state analysis of body temperature can be complex, but I will simplify the analysis greatly.

In response to a step change in environmental temperature, the transient body temperature of an ectotherm at any time t (T_t, K) is readily approximated as:

$$T_t \cong (T_0 - T_\infty)e^{(-t/\tau)} + T_\infty \qquad (1)$$

where T_0 is temperature at the beginning of the transient (t = 0), T_∞ is temperature at equilibrium ($t \rightarrow \infty$), and τ is the time constant (s).

The time constant is itself the product of the body's total resistance to heat exchange, R_{tot} ($K\ W^{-1}$), and its capacitance, C ($J\ K^{-1}$):

$$\tau = R_{tot}C \qquad (2)$$

For comparing the heating and cooling rates of an individual, we may formulate a dimensionless number, ϕ, which is the ratio of the time constants for cooling and warming, and which is equivalent to the ratio of the rates of temperature change for heating and cooling:

$$\phi = \tau_c/\tau_w = R_{tot,c}C_c/R_{tot,w}C_w \qquad (3)$$

For an individual, capacitance is not likely to change between warming and cooling, and in this case, Eq. 3 simplifies to:

$$\phi = \tau_c/\tau_w = R_{tot,c}/R_{tot,w} \qquad (4)$$

Thus, a transient state analysis that could be very complex is reduced to one involving only resistances. This simplification is valid as long as heating and cooling rates are considered without dimension (*i.e.*, using ϕ only).

From Eq. 4, it is easy to see that hysteresis of heating and cooling (*i.e.*, a value of ϕ that is not unity) must arise from some difference between warming and cooling in R_{tot}. To see where changes of blood flow fit into this, R_{tot} can be dissected into its component resistances. To do this, let us make some assumptions about the nature of the "animal" (Fig. 1a). Let us assume that an animal can be treated as a cylinder with outer radius r_o, comprised of a core of radius $0.75r_o$ (Tracy *et al.*, 1985), and surrounded by a "shell," comprised of a layer of muscle and skin.

This, of course, is the "core-shell" model that is commonplace in biophysical analysis of body temperature. The core-shell model has been used with success by others (*e.g.*, Porter and Gates, 1969; Porter *et al.*, 1973; Spotila *et al.*, 1973; Spotila, 1980) to predict the body temperatures of reptiles under both steady and transient conditions. These models, along with others that use a variation on the core-shell model (*e.g.*, Grigg *et al.*, 1979) have not explicitly considered the effects of changing blood flow, however. Some recent biophysical models do consider changing blood flow (Tracy *et al.*, 1980; Tracy, 1982; Tracy *et al.*, 1986; Turner and Tracy, 1986) and the model presented here is a "stripped-down" version of these, eliminating capacitance (Eq. 4). Because of this, the model presented here has the deficiency of not being able to predict the actual temperatures of a particular animal in transient. This deficiency hopefully will be offset by making it easier to identify when blood flow will and will not be important for heat exchange.

Eliminating capacitance from the model (Eqs. 2–4) allows us to treat the flows of heat with an equivalent circuit of resistances only. The resistance to heat exchange (R_{tot}) between the core and environment is a composite resistance, which can be broken down into at least two component resistances in series: an internal resistance through the shell (R_i) and an external resistance (R_e) between the surface of the shell and the environment. Because R_i and R_e are in series (Fig. 1b):

$$R_{tot} = R_i + R_e \qquad (5)$$

Any change in R_{tot} that arises from a change of blood flow must arise then from a change in R_i.

The internal resistance itself is a composite resistance, comprised of at least two component resistances in parallel. Heat can move through the shell either by conduction through the tissues or by transport in blood. We designate a resistance for each (R_{cond} and R_{bl}, respectively; Fig. 1c), and because they are parallel resistances:

$$1/R_i = 1/R_{cond} + 1/R_{bl} \qquad (6)$$

External resistance also is a composite resistance, arising from multiple parallel modes of heat transfer, and may include convection, radiation, evaporation and conduction to a substrate. Let us assume for the present that radiation and convection are the most important modes for heat exchange, with resistances R_{rad} and R_{conv} (Fig. 1c), respectively. Therefore, external resistance is:

$$1/R_e = 1/R_{rad} + 1/R_{conv} \qquad (7)$$

When will a change of blood flow cause a significant change in R_{tot}? This will only happen if R_{bl} cannot be ignored as part of the circuit that describes R_{tot} (Fig. 1c). There are two "rules of thumb" that help us decide when this condition is met. For the internal and external resistances in series (Fig. 1b; Eq. 5), the rule (hereafter, Rule 1) is—*internal resistance may not be less than one-tenth the external resistance.* For the two parallel resistances that comprise internal resistance (Fig. 1c; Eq. 6), the rule (hereafter, Rule 2) is—*the blood flow resistance may not be more than ten times the conduction resistance.*

CONTROL OF HEAT EXCHANGE IN SMALL REPTILES

Very small reptiles (<20 g body mass) are generally agreed to not have significant control over their rates of heating and cooling (Smith, 1976; Smith and Adams, 1978; Grigg *et al.*, 1979; Bartholomew, 1982; Fraser and Grigg, 1984). This is readily predicted using my simple model; for expected values of the thermal conductivity of muscle (Bowman *et al.*, 1975) and for blood flow during steady conditions (Smith *et al.*, 1978), it is readily shown that R_{bl} is more than an order of magnitude larger than R_{cond} when torso radius is smaller than 1–2 cm. This violates Rule 2, and so reptiles with a torso radius smaller than 1–2 cm should not be able to control heat exchange by blood flow. Nevertheless, some lizards smaller than this heat faster than they cool (McKenna and Packard, 1975; Claussen and Art, 1981), in defiance of the supposed physical limitation. How do they do it?

It has been suggested that hysteresis of body temperature in very small lizards is

TABLE 1. *Heating and cooling rates of a small, limbless reptile,* Thamnophis elegans.

	Mean	SEM	n
τ_W	670	50.3	7
τ_C	716	79.2	6
ϕ (τ_C/τ_W)	1.07	0.07	6*

* Not significantly different from 1, at $P = 0.05$.

an artifact, caused by uncontrolled hystereses of temperature in the experimental chambers (Fraser and Grigg, 1984). Given the difficulties of controlling external conditions for heat exchange (Fraser and Grigg, 1984), some skepticism of hystereses of body temperature in very small reptiles certainly is warranted. However, it may be rash to attribute all such results to artifact. A very slight change in the assumptions about the shape of the model "animal" suggests a possible way for even the tiniest reptiles to control heat exchange by blood flow.

Consider that, for a so-called "lizard-shaped reptile," heat can move between the core and environment not only through the torso "shell," but through the appendages as well. It is readily shown that conduction resistance along an appendage is large when its diameter is small (Turner and Tracy, 1986). Thus, the conduction resistance along an appendage is large in those very animals where conduction resistance in the torso is small. Rule 2 for the appendages is therefore met, and C. R. Tracy and I have shown elsewhere (Turner and Tracy, 1986) that Rule 1 for the appendages is satisfied also. Thus, locomotory appendages (limbs and tail) are expected to be most effective in the smallest animals for the control of heat exchange by blood flow. There is some empirical support for these claims.

For example, could small snakes control their heating and cooling rates? Snakes obviously have no appendages, and if the theory just outlined is correct, the answer to the question should be "no." For small garter snakes, no larger than 2–3 cm torso diameter, heating and cooling rates indeed are virtually identical (Table 1). On the other hand, larger snakes, in which Rule 2 probably is fulfilled (see below), appear to control their rates of heating and cooling (Dmi'el and Borut, 1972).

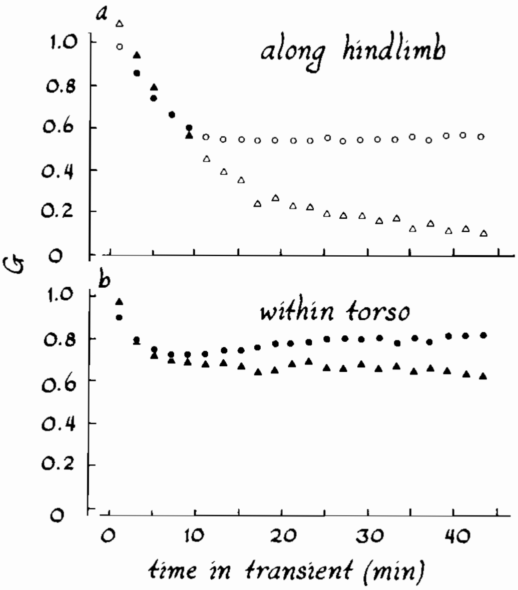

FIG. 2. Dimensionless temperature gradients (G) in the bodies of six hatchling alligators during warming (circles) and cooling (triangles) in wind of 2 m s^{-1}. For two temperatures in the body, T_1 and T_2, $G = T_1 - T_\infty/T_2 - T_\infty$. A value of G that is unity signifies the smallest temperature gradient that can exist at any time in the transient. A value of G that is zero signifies the largest temperature gradient that can exist at that point in the transient. (a) Values of G for the gradient between the proximal hindlimb and the distal hindlimb. G is small during cooling and large during warming, signifying large rates of heat flow along the length of the limb during warming and lower rates during cooling. (b) Values of G for the gradient between the colon and the surface of the abdominal torso surface. G is large during both warming and cooling, and does not differ significantly between warming and cooling.

Small reptiles *with* appendages, however, may rely heavily on them for the control of heat exchange. Among hatchling alligators, for example, blood flow to appendages is high during warming and low during cooling (Turner and Tracy, 1983), and these variations in blood flow are accompanied by large differences between warming and cooling in both the temperature distribution along the appendages and in the amounts of heat exchanged at the appendage surfaces (Figs. 2, 3). In contrast, there is little difference between heating and cooling in the temperature distribu-

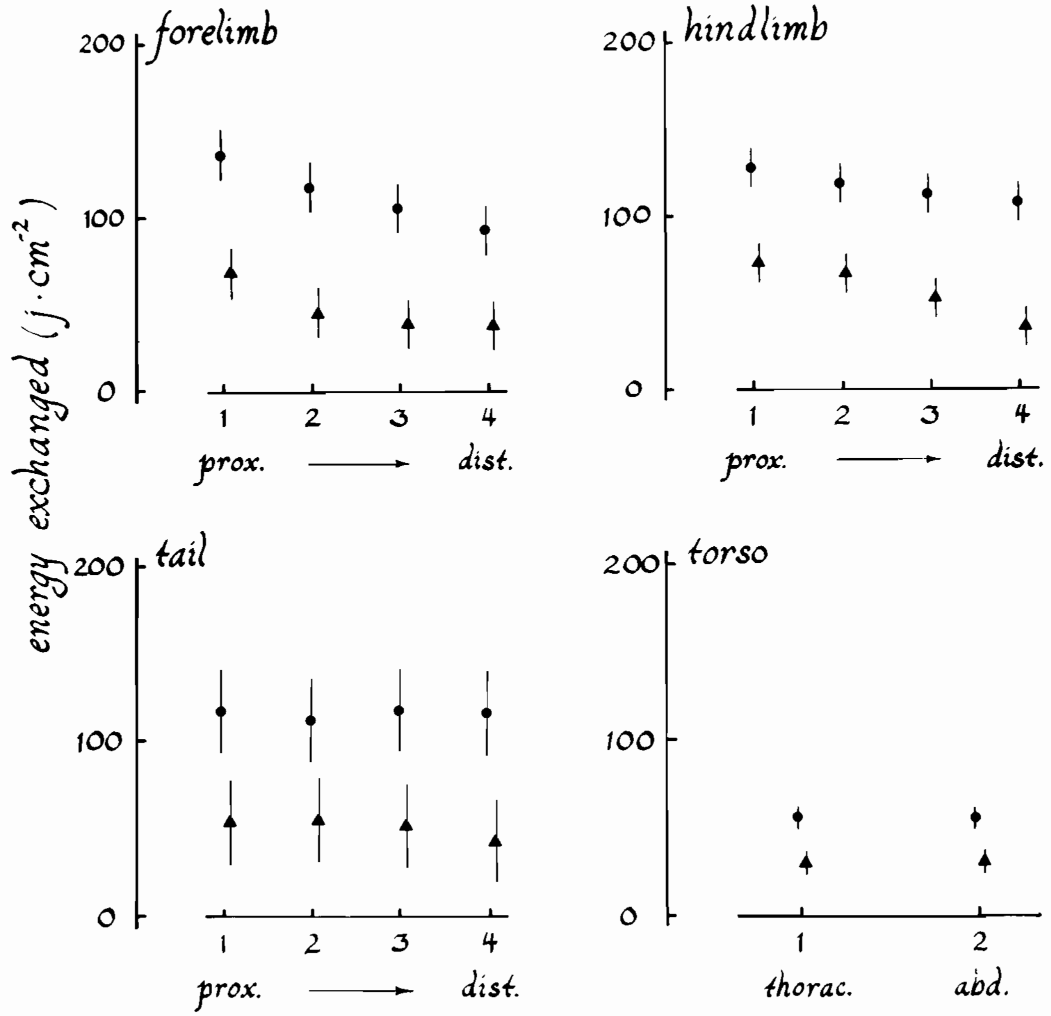

FIG. 3. Measured exchanges of heat from various surfaces of the bodies of six hatchling alligators during warming (circles) and cooling (triangles) in a wind of 2 m s^{-1}, during a 45 min transient. Data are shown for four surfaces on each appendage, from most proximal to the body (1) to most distal from the body (4), and at two torso surfaces, the lateral thoracic torso surface and the lateral abdominal torso surface. The differences in heat exchanged between warming and cooling are large at the appendages, and very small at the torso surfaces.

tions or exchanges of heat at the torso (Figs. 2, 3). Heating rates of hatchling alligators can be manipulated at will by occlusion of blood flow to the appendages (Turner and Tracy, 1983). Indeed, the entire difference in heating and cooling rates in these small alligators is attributable to changes in blood flow to the appendages (Turner and Tracy, 1983).

Therefore, hystereses of body temperature in small reptiles may be artifact, but a hysteresis also can be the result of controlling blood flow specifically to appendages. Whether many small reptiles actually do this still is an open question, but there are reasons to suggest that it probably is not widespread. Time constants for very small reptiles are so short that even a considerable capacity for control of heat exchange (indicated by a large value of ϕ) will result in a difference in time constants between warming and cooling of only sec-

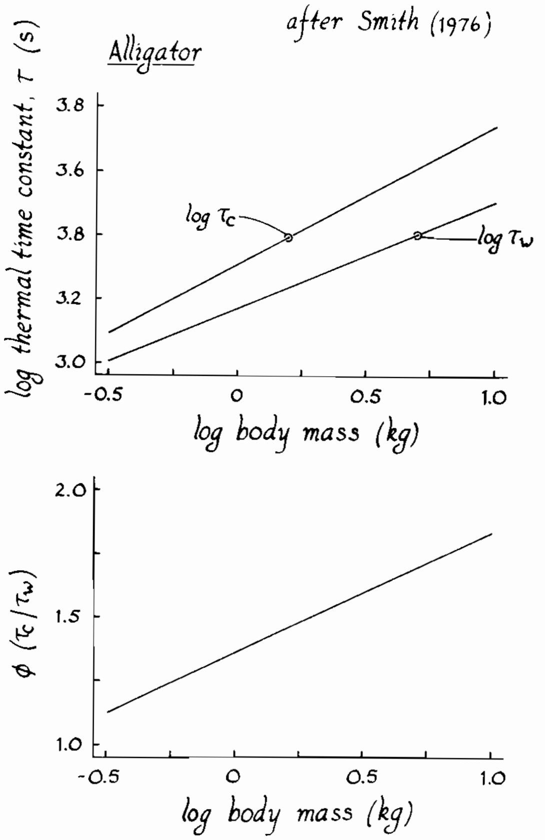

Fig. 4. Summary of the results of Smith (1976), describing rates of heating and cooling of alligators and their variation with respect to body size. (upper) Time constants for warming (τ_w) and cooling (τ_c) as functions of body mass. (lower) Ratios of heating and cooling rates ($\phi = \tau_c/\tau_w$) as a function of body mass.

onds. Whether such a small difference will confer significant ecological benefits is doubtful (Bartholomew, 1982), although it still is an open question. The answer depends on a better understanding of the possible ecological benefits accruing to an animal that controls its rates of temperature change.

CONTROL OF HEAT EXCHANGE IN LARGER REPTILES

How body size affects the heating and cooling rates of reptiles has attracted much attention (Smith, 1976; Johnson *et al.*, 1978; Grigg *et al.*, 1979; Bell, 1980; Claussen and Art, 1981; Fraser and Grigg, 1984; Smith *et al.*, 1984). Many of these treatments are compilations of data from several species—for the present discussion, the results of Smith (1976) on alligators are a useful summary of the general areas of agreement (Fig. 4).

Both τ_w and τ_c increase exponentially with body mass (Fig. 4a), as expected from Eq. 2. Additionally, the time constants for warming and cooling diverge with increasing body mass (Fig. 4a). Consequently, their ratio, ϕ, increases monotonically with respect to body mass (Fig. 4b). Some suggest this signifies that larger reptiles have greater capabilities for the control of heat exchange than do smaller reptiles (Smith, 1976). This interpretation has been questioned (Grigg *et al.*, 1979)—nevertheless, there is general agreement that ϕ increases monotonically with increasing body mass. The results summarized in Figure 4 happen to be for warming and cooling in air. Similar trends are evident for reptiles warming and cooling in water, with the obvious exception that time constants in water are much shorter than in air.

I suggest that the relation of ϕ and body mass is more complex than this, and most of the rest of this article is devoted to justifying this statement. I do so by considering how total resistance and its component resistances should scale with body size, and then considering how this affects the hysteresis of heating and cooling.

Scaling of composite resistances with body size

It is a common assumption that resistance to heat exchange scales exponentially to body size; the literature is replete with statistical estimates of the exponential relation between conductance (the inverse of R_{tot}) and body mass (Peters, 1983). For the component resistances that comprise either R_i or R_e, this is a reasonable assumption. But when the component resistances combine, will the resulting composite resistance also scale exponentially with body size? A simple hand calculation can show the answer to be "yes" if the scaling exponents of all the component resistances are identical, or at least very similar. But if the scaling exponents of the component resistances are not identical, the answer clearly

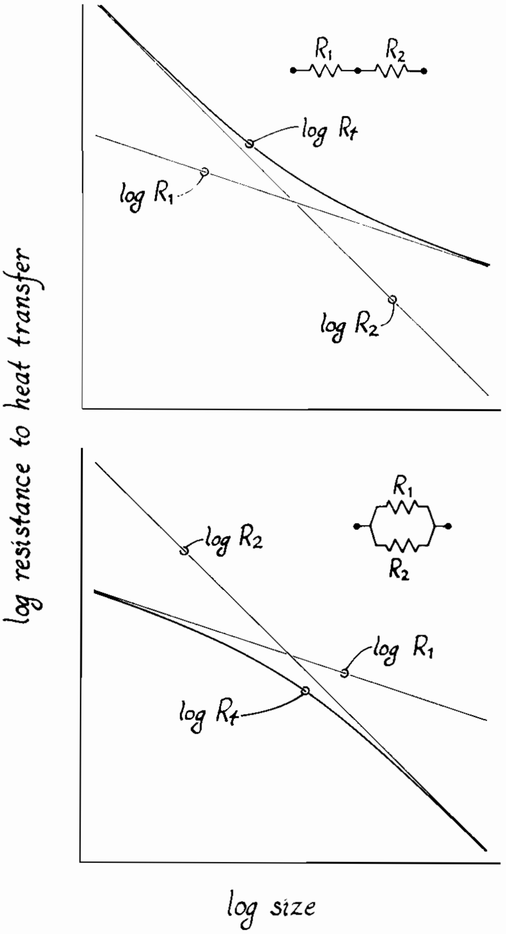

FIG. 5. Relation between the log of a hypothetical composite resistance (R_t) with log size. R_t is comprised of the component resistances R_1 and R_2, both of which scale exponentially with size of the object. (upper) R_1 and R_2 are arranged in series; (lower) R_1 and R_2 are arranged in parallel.

is "no." For two component resistances combining either in series or parallel, the relationship of log R_{tot} *vs.* log mass no longer is linear, but hyperbolic (Fig. 5).

Some interesting generalizations for body size and the control of heating and cooling rates follow from this unusual type of scaling. I illustrate by simplifying even further the morphology of the model "animal," assuming that it can be treated as a sphere. This may render my quantitative predictions suspect. However, the qualitative aspects of these predictions are the most interesting, in my view. It is fortunate, therefore, that the qualitative predictions derived hold for any body shape, as long as the major transfers of heat are radial.

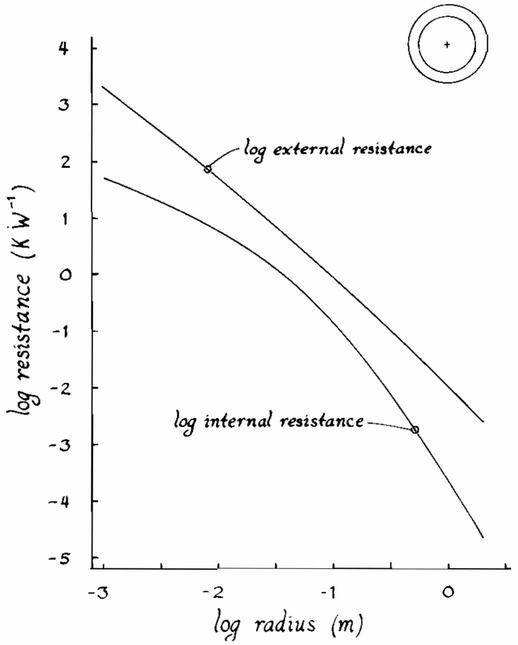

FIG. 6. Expected scaling of logs R_i and R_e *vs.* log diameter for spheres of various sizes. Convection from the surface is assumed to be free, with a temperature difference between the surface and environment of 5°C. The surface of the sphere is assumed to have an emissivity of 0.95.

For expected values of R_e and R_i for spherical "animals," the hyperbolic relationship between log R and log body mass is evident for both (Fig. 6). At very small sizes, R_e approaches R_{conv} asymptotically, indicating that external resistance is dominated by convection. At very large sizes, R_e approaches R_{rad} asymptotically, indicating that external resistance is dominated by radiation. This is in agreement with the work of several others (Porter and Gates, 1969; Spotila *et al.*, 1973; Spotila, 1980). Because R_{conv} and R_{rad} scale with slightly different exponents (Turner, 1985), the relation of log R_e *vs.* log size is almost linear, but still hyperbolic. With respect to internal resistance, R_i approaches R_{cond} asymptotically for small spheres, in conformity with my earlier statement that conduction dominates internal heat transfer

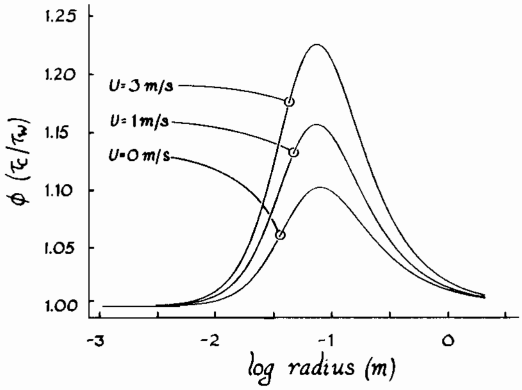

FIG. 7. Estimated ratios of heating rates and cooling rates (ϕ) for the spheres described in Figure 6. $R_{tot,w}$ and $R_{tot,c}$ are calculated with the values of blood flow measured for alligators during warming and cooling by Smith *et al.* (1978). Values of ϕ were calculated assuming three different conditions for convection: free convection ($U = 0$ m s^{-1}) and forced convection at two different wind speeds ($U = 1$ m s^{-1} and $U = 3$ m s^{-1}). Air flow is assumed in all cases to be laminar. Transition to turbulent conditions boosts the value of ϕ to higher values than shown.

in small bodies. For very large spheres, R_i approaches R_{bl} asymptotically. Because the expected scaling exponents of R_{cond} and R_{bl} are very different (Turner, unpublished), the relation of log R_i and log size is a very eccentric hyperbola (Fig. 6).

Control of heating and cooling rates in air

The pronounced eccentricity of log R_i *vs.* log size results in a size at which R_i most closely approaches R_e. By Eq. 5, a given change in R_i at this size will have the greatest effect on R_{tot}. One can show this explicitly by calculating values of R_{tot} for warming and cooling, using published values for subcutaneous blood flow in alligators while warming and cooling (Smith *et al.*, 1978). It is then possible to calculate values of ϕ at all sizes of sphere (Fig. 7). Clearly, there is a size at which ϕ should be maximized for a given change of blood flow. Animals much smaller than this optimum size cannot control heat exchange because conduction dominates internal heat transfer, and because external resistance dominates total resistance (neither Rule 1 nor Rule 2 are fulfilled). Animals much larger than this optimum size also cannot control heat exchange, but for a different reason—even though blood flow dominates internal heat exchange (Rule 2 fulfilled), external resistance dominates total resistance (Rule 1 not fulfilled).

This logic is readily extended to include forced convection. Increasing wind speed simply results in a downward and approximately parallel shift of the curve of R_e shown in Figure 6. This, of course, places R_i closer to R_e over all body sizes. Consequently, higher wind speeds result in larger values of ϕ over all body sizes, excepting of course very small animals where blood flow is insignificant for internal heat exchange (Fig. 7).

The existence of an optimum body size for ϕ (Fig. 7) stands in marked contrast to the monotonically increasing values of ϕ with body size that are accepted by most authors (Fig. 4). Yet, the monotonic relation of ϕ *vs.* mass shown in Figure 4 is an empirical relationship (Smith, 1976). If the data are sound, then the prediction I have just developed must be dismissed as manifestly false. Yet, the physics behind the prediction also is basically sound. How do we resolve this quandary?

When values of ϕ are measured for alligators, ranging from about 700 g body mass to nearly 10 kg body mass (Fig. 8; Turner and Tracy, 1985), the result supports the prediction and contradicts the empirical relationship of Figure 4; ϕ does not appear to increase monotonically with respect to mass. Rather, a maximum in ϕ exists at about 5 kg body mass (Turner and Tracy, 1985). Alligators approaching 10 kg body mass have values of ϕ that approach unity. Note also that the data plotted in Figure 8 include Smith's (1976) data; even they show a maximum in ϕ at about 5 kg body mass, not continually increasing values of ϕ, as Smith (1976), and several others (Grigg *et al.*, 1979; Bell, 1980; Claussen and Art, 1981) have thought.

Control of heat exchange and body size: General analysis

In most laboratory measurements of heating and cooling rates in air, convection is the dominating mode of external heat

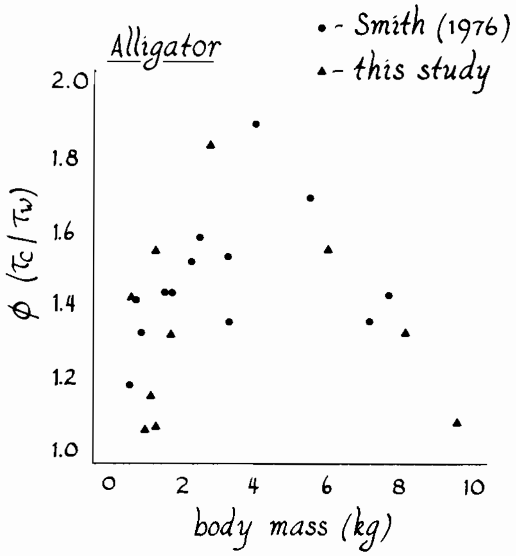

FIG. 8. Values of ϕ measured for American alligators, ranging in body mass from 700 g to nearly 10 kg. Data are from two independent experiments. Circles are data from Turner and Tracy (1985); triangles are data from Smith (1976). Reprinted from Turner and Tracy (1985), with permission from Pergamon Press Ltd.

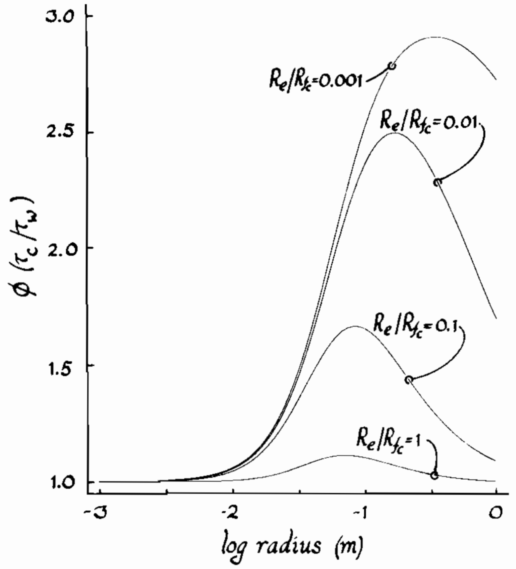

FIG. 9. Generalized treatment of expected values of ϕ for various values of external resistance. See text for explanation.

transfer. We already have seen how increasing wind speed should boost values of ϕ that result from a given alteration of blood flow (Fig. 7). However, even large variations of wind speed (0–5 m s^{-1}) do not change external resistance very much, generally less than an order of magnitude. Because convection is less important for heat exchange at larger body sizes, the possible variation in total resistance that can result from changing wind speed will be still less for very large animals.

Animals in the wild likely experience larger changes in external resistance than this. For example, an animal in water may experience an external resistance that is two or more orders of magnitude smaller than for air (Turner, unpublished). A similar argument can be made for an animal that is exposed to intense solar radiation.

The analysis is readily extended to include these situations simply by estimating an external resistance that is some fraction of the highest external resistance an animal is likely to encounter. For a reptile, the highest external resistance likely will be for free convection in air (R_{fc}). I have done this in Figure 9, for external resistances that are identical to free convection in air ($R_e/R_{fc} = 1$), and one ($R_e/R_{fc} = 0.1$), two ($R_e/R_{fc} = 0.01$) and three ($R_e/R_{fc} = 0.001$) orders of magnitude less than for free convection in air.

The results are generally those seen for heating and cooling in air (Fig. 7). Values of ϕ are higher over all body sizes as the external resistance is lowered. An optimum body size is evident for all conditions. However, the body size at which the optimum occurs increases with decreasing external resistance (Fig. 9).

CONCLUSIONS

The conclusions that can be drawn from a theoretical exploration such as this are necessarily tentative. Some things are worthy of note, however.

The first concerns the interpretation of data on body size and rates of temperature change. I have mentioned the general agreement that ratio of heating and cooling rates increases with increasing body size (Fig. 4; Grigg *et al.*, 1979; Smith, 1976; Bell, 1980; Claussen and Art, 1981). I also have shown theoretically that this should not be so—there always should be some optimum size for the control of heating and cooling rates (Figs. 7, 9). For heating and cooling in air, this seems reasonably well supported empirically (Fig. 8; Turner and Tracy, 1985)—the optimum body size of alligators for control of heating and cooling in air appears to be about 5 kg body mass. However, I cannot make this claim for heating and cooling in water. The data for heating and cooling in water are more strongly supportive of a continually increasing value of ϕ with body size (Johnson *et al.*, 1978; Grigg *et al.*, 1979; Bell, 1980).

This may not negate the conclusions of my model, however. While the model predicts some optimum size for the control of heat exchange for any external conditions, the body size at which the optimum occurs is itself dependent upon external conditions—lower values of R_e correspond to a larger optimum body size (Fig. 9). It is possible that the largest animals tested in water are smaller than the optimum size for this condition, while the largest animals tested in air have exceeded the optimum. This is a question that only more data will clarify.

The second set of conclusions concerns mechanism, for this model tells us how and under what circumstances blood flow should significantly affect heat exchange. For example, very small animals should have little control over heat exchange at the torso, although they could control it at the appendages. As body size increases, the appendages become less effective for this (Turner and Tracy, 1986). Could then the control of heat exchange shift from the appendages to the torso surface at larger and larger body sizes? If so, this raises some interesting physiological questions. For example, what about an animal whose body size changes a great deal during its lifetime, such as a crocodilian, large lizard or a marine turtle? Do changes occur in the distribution of blood flow during heating and cooling, principally involving the appendages in small animals, and principally involving the torso in larger ones? This question has not been explored.

We have seen that control of heat exchange at the torso should become ineffective once body size exceeds some optimum (Fig. 9). For animals larger than this, how could control over heat exchange be accomplished? A very large ectotherm may regain control over heat exchange by developing an ancillary heat exchange appendage, such as a sail or crest. This option has been discussed in some detail elsewhere (Tracy *et al.*, 1986; Turner and Tracy, 1986). However, the absence of an ancillary heat exchange appendage does not indicate that a large reptile has no control over its rates of heating and cooling. Control of heat exchange for a large reptile may be impossible under some conditions (*e.g.*, still air; Fig. 9), but for the very same animal, it may be quite effective under other conditions (*e.g.*, water, high wind or intense sunlight; Fig. 9). Along the same lines, a body size that is the optimum for the control of heat exchange in one environment may not be the optimum in another (Fig. 9).

Finally, it really is not possible to speak of "the" physiological capabilities or "the" optimum body size for controlling heat exchange—both should depend strongly upon the environmental context in which the heat exchange occurs. This raises the interesting possibility that animals may select environments that maximize their control over heating and cooling rates. Thus, very large reptiles, such as crocodilians or marine turtles typically are found in water, or very intense sunlight, environments which not only boost rates of temperature change, but which also might render heat exchange more susceptible to control by blood flow. Animals smaller than this, however, might find optimum control in environments that have higher resistances, such as in air. These are possibilities that also have not been explored.

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