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Body Size, Homeothermy and the Control of Heat Exchange in Mammal-like Reptiles

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Body Size and Endothermy among Mammal-like Reptiles

Dramatic changes in body size are a striking feature in the phylogeny of several lineages of mammal-like reptiles. Early Pennsylvanian pelycosaurs weighed less than 1 kg. By the early Permian, pelycosaurs such as the conservative *Ophiacodon* and the advanced genera *Dimetrodon* and *Edaphosaurus*, were as big as 250 kg (Romer and Price, 1940; Romer, 1966). Later Permian therapsids, such as dinocephalians, some gorgonopsians, and some dicynodonts, were even larger (Romer, 1966). In the Triassic, however, body size declined as the dominant therapsids of the Late Permian became extinct. Cynodonts such as *Thrinaxodon* and the *Tritylodonta*, were much smaller, less than 50 kg in body mass (Romer, 1966). Cynodont body size eventually declined to that of the diminutive mammals that shared the earth with the Archosauria during the Jurassic and Cretaceous periods (Romer, 1966; McNab, 1978).

Various authors have proposed that endothermy in mammals had its origin among the mammal-like reptiles (Bakker, 1971; McNab, 1978). McNab has suggested that the large changes in body size that occurred during the evolution of this group were crucial to the development of endothermy. His thesis is that large body size conferred homeothermy on the large mammal-like reptiles of the Permian. Later reductions in body size of the group were accompanied by rates of total metabolism that remained constant or slightly increased, and by simultaneous development of a lower thermal

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conductance through the origin of fur. This would have resulted in small animals that were essentially mammalian in their energetics, and presumably also in their thermoregulatory capabilities (McNab, 1978).

Crucial to this scenario is the contention that large body size necessarily renders an animal homeothermic. In general, this is true; when subjected to a change in environmental temperature, large reptiles change body temperature more slowly than do small reptiles. Consequently, the body temperatures of large ectotherms would be expected to exhibit less variation through the day than would those of small ectotherms—large reptiles would be “inertial homeotherms” (McNab, 1978; Spotila et al., 1973; Spotila, 1980).

Homeothermy is too widespread among living taxa to dispute its value, and there is little reason to believe that it did not occur among large mammal-like reptiles. High body temperature is also important (Heinrich, 1977); both extant classes of endothermic vertebrates have high, as well as constant, body temperatures. Many extant lizards regulate body temperatures at the highest level that energetic and ecological constraints will allow (Huey and Slatkin, 1976).

Yet homeothermy and high body temperature need not go together. For example, Galapagos land iguanas (*Conolophus pallidus*) regulate body temperatures in a way that makes the period of constant temperature during the day as long as possible, even though the animals are capable of attaining higher body temperatures. The actual body temperature regulated in these animals seems to be a secondary consideration (Christian, Tracy, and Porter, 1983).

If the large mammal-like reptiles of the Permian were inertial homeotherms, they probably were constrained to homeothermy at a relatively low body temperature (25°–30°C; Spotila et al., 1973; Tracy, Turner, and Huey, this volume). For mammal-like reptiles to become “mammalian” with respect to body temperature and energetics, they would have had to become homeothermic at a higher body temperature (35°–40°C).

Many extant reptiles have considerable control over rates of heat exchange with the environment. This control occurs through behavioral thermoregulation, which involves selection of favorable microclimates. It also can occur through physiology, most importantly through varying patterns of blood flow within the body (Templeton, 1970; Smith, 1979; Bartholomew, 1982;

Turner, 1982; Turner and Tracy, 1983). Utilizing these avenues of control, an animal can attain a high body temperature more quickly than its body mass might suggest. If it then could lose heat at a very slow rate, its body temperature would stay high for a long time. During this time, such an animal could spend time moving about, hunting prey and defending territories, with all the benefits a high body temperature might bring with it.

We might expect that control over heat exchange would be particularly useful to an animal with large thermal mass. It might enhance the inertial homeothermy presumed to exist among the large mammal-like reptiles, so that they were homeothermic at a high body temperature.

Thus, there are two possible ways the large mammal-like reptiles of the Late Permian could have been homeothermic. If their large size was crucial to the evolution of endothermy, as McNab (1978) proposes, two possible scenarios for the origin of endothermy are suggested. If large therapsids were simply inertial homeotherms, their body temperatures would have been relatively low. In this case, it is likely that endothermy evolved first, with the attainment of a high body temperature appearing later in the evolution of mammals. If, on the other hand, large therapsids could exert control over heat exchange, they could have been homeothermic at high body temperatures. In this event, high body temperature would have appeared first, with endothermy being a later development to maintain high body temperature and whatever benefits accrue to it. To choose between these alternatives, we must know the extent to which large reptiles are able to control rates of heat exchange.

One of the important ways heat exchange can be controlled is through variations of blood flow within the body (Smith 1979; Bartholomew, 1982; Turner, 1982). In living reptiles, this is almost always manifest as higher rates of heating than of cooling. The appendages (limbs and tail) of small, “lizard-shaped” reptiles (those reptiles with limbs, a long tail, and a fusiform torso) are the most important sites for the control of heat exchange by blood flow (Turner and Tracy, 1983; Turner, 1982). The surface area of appendages can account for more than half of the total surface area available for heat exchange. The appendages are always better heat exchangers than the torso is, because of their larger surface-volume ratios and smaller convective boundary layers. Finally, conduction heat transfer between the torso and appendages is low. Thus, variation

in blood flow to appendages can exert considerable control over the flow of heat between the torso and appendages and hence the environment.

In the following section, we assess possible relationships between body size and the effectiveness of control of heat exchange at appendages. Then we consider the implications of these relationships for the physiological control of heat exchange among mammal-like reptiles.

A Model of Heat Transfer at Appendages

The transfer of heat between the core of the body and the environment, via an appendage, is opposed by an internal resistance to heat transfer (r_i ; K W^{-1}) and an external resistance to heat transfer (r_e ; K W^{-1}). The total resistance to heat transfer (r_{tot}) is simply the sum of the internal and external resistances (Appendix 1; Fig. 1).

We define control of heat exchange as the capability to effect large changes in total resistance to heat transfer. In our simple model, changes in total resistance can come about through changes in either internal or external resistances, or both. To assess an animal's capabilities to control heat exchange by blood flow, we need to ask: "Under what conditions will a change in internal resistance bring about a substantial change in total resistance?" A useful tool to address this question is the dimensionless Biot number (Tracy, 1972; Thomas, 1980) defined as:

$$Bi = r_i/r_e$$

A Biot number of 0.1 or less signifies that external resistance is at least ten times greater than internal resistance. In this circumstance, the resistance controlling heat transfer is that between the animal and its environment; a change in internal resistance (such as a change in blood flow) has essentially no effect on total resistance. Significant changes in total resistance can occur only through changes in external resistance, such as a change in wind speed, or in radiant heat load.

When Biot numbers are between 0.1 and 10, internal and external resistances are within an order of magnitude of each other, and neither predominates; changes in either resistance can cause notable changes in total resistance.

When Biot numbers are greater than 10, internal resistance is the limiting factor in heat transfer, and so the control of heat exchange resides with control of internal resistance (such as

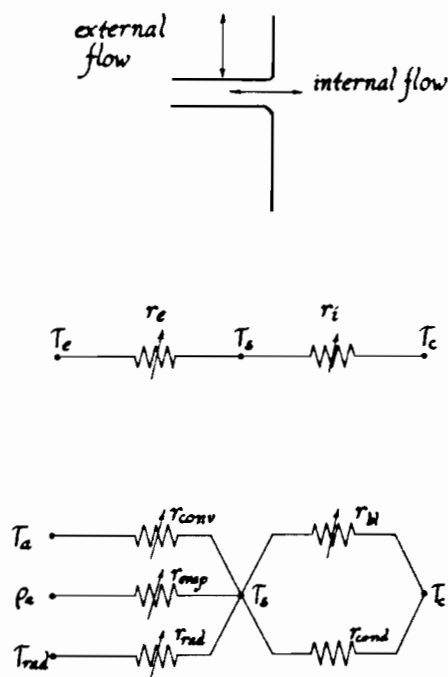


Figure 1. The interaction of internal and external resistance to heat transfer. Top drawing: schematic depiction of the flow of heat from the body core through an appendage (horizontal arrow), and to the environment (vertical arrow). Middle drawing: equivalent circuit diagram of the flow of heat in the upper diagram, with internal (r_i) and external (r_e) resistances to heat transfer in series. Core temperature, T_c ; surface temperature of torso, T_s ; environmental temperature, T_e . Bottom drawing: a more detailed equivalent circuit, with external resistance resolved into parallel resistances arising from evaporation (r_{evap}), radiation (r_{rad}), and convection (r_{conv}), and internal resistance resolved into two parallel resistors arising from conduction (r_{cond}) and blood flow (r_{b1}). T_e resolved into ambient air temperature, T_a ; ambient vapor density, ρ_a ; and radiant temperature of environment, T_{rad} .

control of blood flow). Total resistance is relatively insensitive to changes in external resistance.

Calculations of heat transfer resistance require information on such bodily dimensions as length of torso and diameter, length, volume, and surface area of the appendages. We constructed allometric equations for the relationships of these parameters (fore and hind limbs) to torso length up to 0.3 m in American alligators (see Appendix 1). There are no such data available for therapsids, but Romer and Price (1940) present data on both the body and limb lengths of pelycosaurs, which are similar to American alligators in these dimensions (Fig. 2). If this similarity in linear dimensions reflects similarities in body stature and size and location of muscles, then the alligator provides a satisfac-

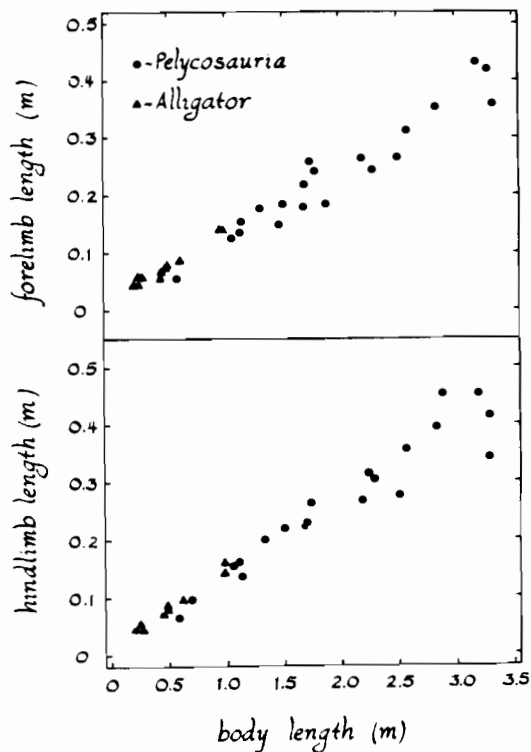


Figure 2. Relationship between limb and body lengths for pelycosaurs (circles) and the American alligator (triangles). Body length does not include the length of the head. Forelimb lengths were defined as the sum of the humerus and radius lengths. Hind-limb lengths were defined as the sum of the femur and tibia lengths. Data for pelycosaurs were taken from Romer and Price (1940). Data for alligators were taken from living specimens.

tory template for describing limb dimensions as they relate to body size in the Pelycosauria.

Details of the calculation of both external and internal resistances may be found in Appendix 1. Many possible permutations of both external and internal resistance could be explored, but we have limited ourselves to a few that we consider important. Temperature differentials between the animal and its environment was set at 5°C for all simulations. Wind speeds normal to the long axis of the appendages were varied from 0.0 to 1.0 m s^{-1} in our simulations. Finally, blood flow through the appendage was assumed to be the "normal" rate for reptilian white muscle ($9.67 \cdot 10^{-4}\text{ cm}^3\text{ s}^{-1}\text{ g tissue}^{-1}$; Berger and Heisler 1977).

Scaling of Heat Exchange at the Fore Limb

In both still (Fig. 3; curve a) and moving air (Fig. 3; curves b and c), the Biot number for the fore limb declines as body size increases. The same

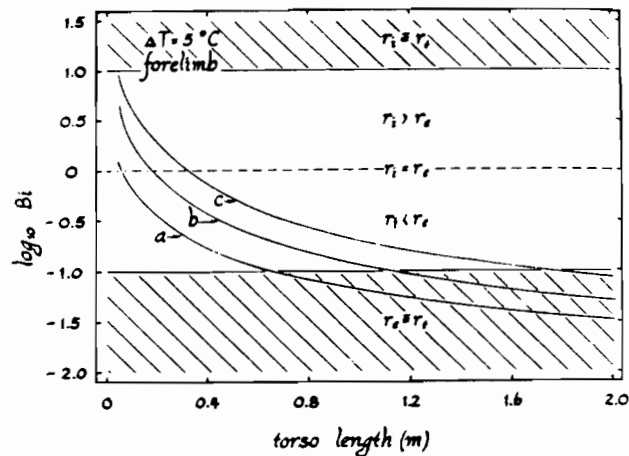


Figure 3. The relationship between the Biot number and the torso length for the fore-limb of pelycosaurs. Curve a, Biot numbers in still air; curve b, Biot numbers at a wind speed of 0.2 m/s ; curve c, Biot numbers at a wind speed of 1.0 m/s . Wind speeds are normal to the long axis of the appendage. Temperature differential in all cases is 5°C .

general pattern is evident for the hind limb (not shown). Thus, as body size increases, external resistance to heat transfer comes more and more to dominate total resistance. From this, we may infer that any increase in size within a lineage of mammal-like reptiles would reduce capacity to control heat exchange by blood flow.

This point is quantified by calculating the change in blood flow to an appendage required to bring about a given change in total resistance. The percent change in blood flow required to produce either a ten-percent increase or decrease in total resistance to heat transfer is plotted against torso length (Fig. 4). As body size increases, the change in blood flow required to bring about a ten-percent change in total resistance increases (Fig. 4), reflective of the greater importance of external resistance at larger and larger body sizes. Consequently, large body size may have rendered the mammal-like reptiles of the Late Permian unable to control heat exchange by blood flow. If these animals were homeothermic, they probably did not maintain the high body temperatures of modern mammals.

Thermal Biology of Mammal-like Reptiles

Our model suggests that large body size among mammal-like reptiles favored homeothermy at low body temperatures. This prediction is very explicit, but it applies only to limited circumstances of body morphology and environmental conditions. By exploring the departures of mam-

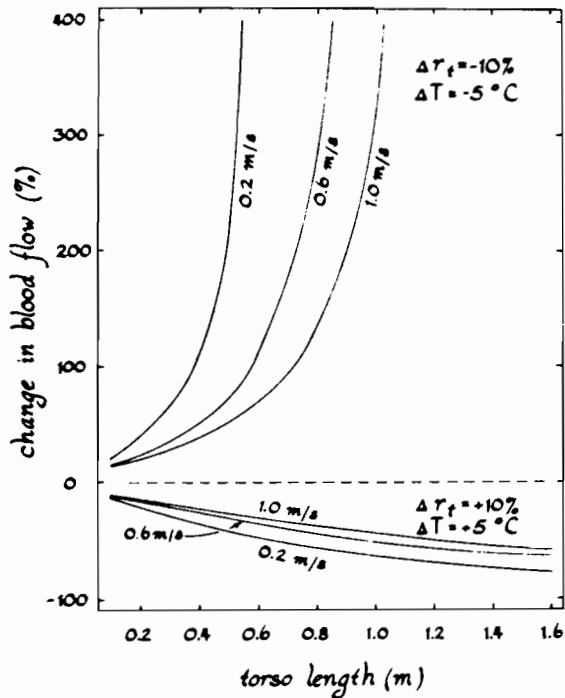


Figure 4. Percent change in mass = specific blood flow required for a $\pm 10\%$ change in total resistance to heat transfer. Three conditions of wind speed are shown: 0.2 m/s, 0.6 m/s, and 1.0 m/s.

mammal-like reptiles from these conditions, we can infer other possible patterns of thermoregulation in the group. Mammal-like reptiles departed from the postulated conditions by reducing external resistance to heat transfer, thus making internal resistance more important (that is, Biot numbers for the appendages increased). They may have done so either by physiological or behavioral means, or by evolutionary modification of body form. We will consider each of these possibilities in turn, to see how they may explain observed features in the evolution of the mammal-like reptiles, particularly in the transition from Pelycosauria to Therapsida.

External Resistance to Heat Transfer

External resistance to heat transfer can be resolved into three major components (Fig. 1); convection, radiation and evaporation (conduction is considered relatively unimportant for an appendage). Anything that reduces resistance in any of these modes will make internal resistance a more important component of total resistance. This leaves us with the curious result that animals may actually sacrifice conservation of heat, reducing external resistance to achieve greater internal control over total resistance.

The effect of altering convection heat transfer is explicitly considered in Fig. 3. Increased wind speed will increase heat exchange through convection; as a result, Biot numbers for the appendage increase for all body sizes (Fig. 3). If air flow past the appendage is turbulent, heat exchange through convection is enhanced even more. Thus, large mammal-like reptiles may have sought turbulent or windy areas as a behavioral adjunct to the control of heat exchange.

Perhaps a more effective way to accomplish this would be to live in a different fluid—water as opposed to air. This is the behavior of many of the largest extant reptiles, such as crocodilians and marine turtles. Convection resistance in water is considerably less than in air, and a large animal in water can effect considerably more control over heat exchange by blood flow than it can in air.

Large, active predators, such as the sphenacodonts (Romer, 1966) were presumably faced with two opposed, but simultaneous, alternatives. Probability of success in finding and subduing prey was probably enhanced by high body temperature, as it is for modern reptiles (Werner 1972; Greenwald 1974; Huey 1982). At the same time, capture of prey can be a vigorous business, and in a large animal it can impose a substantial burden of metabolic heat production, with consequent increase in body temperature. If body temperature is already high to maximize success in predation, dangerous overheating can result unless there is a way to quickly dump large amounts of heat.

We argue that the amphibious lifestyles of modern crocodilians are a compromise solution to just this dilemma. Warming can occur quickly on land, in a setting of intense solar radiation. Activity in these situations is minimal, and precise and rapid variation in heat exchange may not be necessary. Control of heat exchange is important when the animals are active, however, and extended activity occurs almost solely in the water, where control of heat exchange will be most effective. This may explain why many of the fossils of the advanced pelycosaurs are found in deposits indicating a formerly copious water supply (see Olson, this volume), suggesting that these animals had a relatively amphibious lifestyle.

External resistance can also be modified by changes in the radiative properties of the animal's surface. The emissivity of reptile skin is probably not amenable to control, being constant at 0.9–1.0 (Campbell, 1977), and our simulations

suggest that the small changes in temperature that an animal would exhibit likewise does not affect emission of radiation much. Thus, mammal-like reptiles may not have had much control over heat loss by radiation.

Finally, internal control of heat transfer could be enhanced by making evaporation heat exchange more important. Among extant reptiles, such as the alligator, all avenues of evaporation account for less than two percent of the animal's steady-state energy balance (Terpin, Spotila, and Foley, 1979; Tracy, 1982). Evaporative conductance of reptilian skin is very low, and modern reptiles do not sweat (Campbell, 1977; Spotila and Berman, 1976; Davis, Spotila, and Schaefer, 1980; Tracy, 1982). However, evaporative heat exchange varies in response to shedding cycles (Zucker and Maderson, 1980) and changes in the lipid content of the skin (Roberts and Lillywhite, 1980), and by control of respiration and oxygen consumption (Duvdevani and Borut, 1974), by control of evaporation from the surfaces of the eyes (Mautz, 1980), and by control of blood flow through the skin (Cohen, 1975). Evaporation can be important to the animal for local control of brain temperature while gaping (Spotila, Terpin, and Dodson, 1977) or panting (Templeton, 1971; Pough and McFarland, 1976; Crawford, Palomeque, and Barber, 1977) or for cooling the appendages during thermal crises, such as when the animal urinates or defecates on its hind limbs (Riedesel, Cloudsley-Thompson, and Cloudsley-Thompson, 1971; Cloudsley-Thompson, 1974; Sturbaum and Riedesel, 1974). By far the most significant control of evaporative heat exchange originates with behavioral selection of hydric microclimates (Davis, Spotila, and Schaefer, 1980; Thorpe and Kontoginnis, 1977; Spotila and Berman, 1976; Mautz, 1980; Cohen, 1975). Some mammal-like reptiles had skin with numerous and conspicuous glandlike structures (Chudinov, 1968), which suggests that some of these animals may have had the capacity to sweat.

Adjustments in Body Shape

The simulations reported here assume that the dimensions of the appendages, on which all the resistances to heat transfer depend, are in scale with body size in much the same way as those of an alligator. Among the Pelycosauria, for example (Fig. 2), this is probably a good assumption; the relationship between the dimensions of the locomotory appendages and body remained rela-

tively constant throughout their evolutionary history.

However, there are two ways to subvert this limitation: develop ancillary appendages, separate from the locomotory appendages, designed mostly for the control of heat exchange; or modify the shape and structure of the locomotory appendages, to make control of heat exchange at them more effective.

The larger and more advanced pelycosaurs, such as *Dimetrodon* and *Edaphosaurus*, may have pursued the first strategy during their evolution, developing an ancillary heat exchanger in the form of a dorsal sail. The thermal consequences of possession of a sail are substantial, allowing the members of these genera to heat quickly and cool slowly and so remain homeothermic at a high body temperature, despite large body size (Tracy, Turner, and Huey, this volume).

The sphenacodonts that eventually gave rise to the therapsids did not include animals with sails. In the predecessors of the therapsids, we see little evidence of the morphological features that may have enabled *Dimetrodon* to be ectothermic and yet to have a high, relatively constant body temperature. These transitional animals, if ectothermic, would have been homeothermic at a relatively low body temperature (Tracy, Turner, and Huey, this volume).

Restructuring of the locomotory appendages for better control of heat exchange probably did not occur in the Pelycosauria (Fig. 2). However, the limbs underwent considerable change during the evolution of the Therapsids. They rotated ventrally so that therapsids stood more erect than their "sprawling" predecessors, in a more nearly "mammalian" posture (Bakker, 1971). This allowed a more mammalian locomotion, with the limbs moving in a parasagittal plane during walking and running. Accompanying these shifts was relocation of the appendicular muscles closer to the limb girdles. Simultaneously, the caudo-femoralis musculature of the tail was greatly reduced, because of the reduction of lateral vertebral flexion (Sues, this volume). The result was that the limbs became more slender, and the tail became greatly reduced in mass.

These changes principally reflect the development of a new mode of locomotion. However, a change in the heat exchange properties of the appendages would have accompanied these locomotory alterations. Reducing the diameter of the

appendages increases the Biot number, enhancing the importance of internal resistance in heat transfer (Fig. 3). Further, the relocation of the appendicular muscles into the body would have enabled these muscles to be nourished by blood flow without the blood having to flow out into the appendages, where it could exchange its heat readily with the environment. This also increases the Biot numbers of the appendages. In both cases, the capabilities for physiological control of heat exchange at the appendages are enhanced. The thermoregulatory significance of these changes is unknown but can be surmised: the more slender limbs of the Gorgonopsia, the Therocephalia, and perhaps the Dicynodontia could well have been exploited as controlled heat-loss fins if the animals were highly active and maintained high body temperatures.

Acknowledgments

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Appendix 1. Model of thermal resistance of appendage

Circuits for Resistance to Heat Transfer

Circuits for the transfer of heat are analagous to circuits for the transfer of electrical energy (Fig. 1). For thermal circuits, we may use an analogy of Ohm's Law to express the relations between heat flow, temperature difference and resistance to heat transfer:

$$\dot{q} = dT/r \quad (1)$$

where \dot{q} = heat flow (W; J s⁻¹), dT = temperature difference (°C), and r = resistance to heat transfer (°C/W).

Calculating resistances in thermal circuits is done the same way that resistance is calculated in an electrical circuit. For the circuit in Figure 1, external and internal resistances to heat transfer are arranged in series. Therefore,

$$r_{tot} = r_i + r_e \quad (2)$$

where r_{tot} , i.e = total, internal and external resistances, respectively. Both internal and external resistances can be further resolved into different modes of heat exchange, each of which is arranged in parallel with the other resistances in its circuit. Thus, internal resistance can be resolved into parallel resistances arising from conduction heat transfer (r_{cond}) and arising from heat transfer by blood flow (r_{bl});

$$1/r_i = 1/r_{cond} + 1/r_{bl} \quad (3)$$

Resistance arising from blood flow is variable. Likewise, external resistance can be resolved into the parallel resistances associated with convection (r_{conv}), evaporation (r_{evap}) and radiation (r_{rad}):

$$1/r_e = 1/r_{conv} + 1/r_{evap} + 1/r_{rad} \quad (4)$$

Total resistance can be calculated from the component resistances associated with the simultaneous process of internal conduction, blood flow, evaporation, convection and radiation.

Calculation of Internal Resistances

Conduction

The appendage was considered to be a single homogeneous node. Conduction heat transfer within a cylindrical fin is:

$$\dot{q}_{cond} = l k_{app} dT \quad (5)$$

where l = characteristic length (m; V_{app}/A_{app}), and k_{app} = thermal conductivity of the composite material (W m⁻¹ °C⁻¹, assumed to be 0.5). Conduction resistance is therefore;

$$r_{cond} = 1/l k_{app} \quad (6)$$

Blood Flow

Heat transfer arising from blood flow is calculated by:

$$\dot{q}_{bl} = \dot{m} c_{bl} dt \quad (7)$$

where \dot{m} = mass flow rate of blood (g s⁻¹), and c_{bl} = specific heat of blood (J g⁻¹ °C⁻¹). Resistance arising from blood flow is, therefore:

$$r_{bl} = 1/\dot{m} c_{bl} \quad (8)$$

Calculation of External Resistance

Evaporation

Evaporation was considered to be a negligible source of heat exchange at appendages.

Radiation

Heat transfer arising from radiation is calculated as:

$$q_{\text{rad}} = A_{\text{app}} \epsilon \sigma (T_s^4 - T_j^4) \quad (9)$$

where A_{app} = surface area of the appendage (m^2), σ Stefan-Boltzmann constant ($5.67 \cdot 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$), ϵ emissivity (assumed to be 0.95), and $T_{s,j}$ = absolute temperature of surfaces s and j , respectively. Because radiation is proportional to the fourth power of the absolute temperature, resistance to heat transfer will depend partly upon temperature differences between the surfaces exchanging radiation. Resistance for radiation heat transfer is calculated as:

$$r_{\text{rad}} = 1/[A_{\text{app}} \epsilon \sigma (T_s + T_j) (T_s^2 + T_j^2)] \quad (10)$$

Convection

Heat transfer arising from convection is described by;

$$\dot{q}_{\text{conv}} = A_{\text{app}} h_c dT \quad (11)$$

where h_c = convection coefficient ($\text{W m}^{-2} \text{ }^\circ\text{C}^{-1}$). Therefore, resistance to heat transfer by convection is:

$$r_{\text{conv}} = 1/A_{\text{app}} h_c \quad (12)$$

The calculation of the convection coefficient partly depends upon the speed of air moving past the appendage, which will determine whether the air is still, or is moving past the appendage in laminar or turbulent flow. The choice of equations for still air is trivial. The choice between the equations for laminar or turbulent flow depends upon the Reynolds number, Re (dimensionless);

$$Re = u l / \nu \quad (13)$$

where u = wind speed normal to the long axis of the appendage (m s^{-1}), l = diameter (m), and ν = kinematic viscosity of the air ($\text{m}^2 \text{ s}^{-1}$). Generally is $Re > 10^5$, air flow past the appendage will be turbulent. If $Re < 10^5$, air flow past the appendage will be laminar.

If $Re < 10^5$, the convection coefficient is calculated by;

$$h_c = [(0.04 Re^{1.2} + 0.06 Re^{2.3}) (\mu_\infty / \mu_0) / Pr^{0.4} k_{\text{air}}] \quad (14)$$

where Pr = Prandtl number (dimensionless; $Pr = \nu / (c_p k_{\text{air}})$), where c_p = specific heat of the air [$\text{J m}^{-3} \text{ K}$], and $\mu_{0,\infty}$ = dynamic viscosity of the air in the region of fully developed flow (∞) and at the surface of the limb (0).

If $Re > 10^5$, the convection coefficient can be estimated by;

$$h_c = (430 + 0.005 Re + 0.025 \cdot 10^{-9} Re - 3.1 \cdot 10^{-17} Re) k_{\text{air}} l \quad (15)$$

In still air, the convection coefficient is estimated by;

$$h_c = [0.54 (Gr Pr)^{1/4}] k_{\text{air}} l \quad (16)$$

where Gr = Grashof number (dimensionless; $Gr = g \beta l^3 (T_s - T_f) / \mu_0$, where g = gravitational acceleration (9.8 m s^{-2}), β = volume coefficient of expansion for air ($^\circ\text{C}^{-1}$), l = diameter (m), and $T_{s,f}$ = temperatures of the surface and fluid, respectively ($^\circ\text{C}$).

A fairly complete discussion of the principles of heat transfer outlined here may be found in Thomas (1980). Many of the quantitative properties of air required for these calculations were calculated from subroutines provided in Tracy et al. (1978).

Calculation of Appendage Dimensions

Allometric equations for limb diameter, volume, and surface area, as functions of torso length, were formulated using the alligator as a model. For the forelimb:

$$\log d_f = -0.960 + 1.010 \log L_{\text{torso}} \quad (17)$$

$$\log V_f = -2.379 + 2.994 \log L_{\text{torso}} \quad (18)$$

$$\log A_f = -0.817 + 4.984 \log L_{\text{torso}} \quad (19)$$

where d = diameter (m), V = volume (m^3), and A = surface area (m^2) of the appendage, and L_{torso} = torso length (m).

For the hind limb:

$$\log d_h = -0.781 + 1.066 \log L_{\text{torso}} \quad (20)$$

$$\log V_h = -1.873 + 3.239 \log L_{\text{torso}} \quad (21)$$

$$\log A_h = -0.490 + 2.173 \log L_{\text{torso}} \quad (22)$$

Calculation of Appendage Blood Flow

Blood flow in the appendage was calculated as a function of the volume of the appendage and the mass specific perfusion rate for reptilian muscle (Berger and Heisler 1977):

$$Q_{\text{app}} = V_{\text{app}} \rho_{\text{app}} Q_{\text{muscle}} \quad (23)$$

where V_{app} = volume of appendage (m^3), ρ = density of the appendage (g m^{-3}), and Q = mass specific volume flow rate for reptilian muscle ($9.67 \cdot 10^{-4} \text{ cm}^3 \text{ g}^{-1}$).

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