Newtonian Cooling and Reptilian Thermal Ecology

by

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my mother

and Bob

Abstract

The effects of experimental variables (wind speed, fluid type, animal restraint, etc.) on the thermal time constant are analyzed. Results suggest that insufficient attention paid to these variables has resulted in equivocal results. A model is proposed that could normalize some of these variables and provide a better basis for the theoretical interpretation of reptile thermal ecology. Modelled literature data indicate that: 1) very small reptiles (20 g or less) are able to control their rates of heat exchange; 2) aquatic reptiles probably have the same ability to thermoregulate as terrestrial reptiles; 3) variations in the reported thermal time constants of turtles might reflect changes in surface area; 4) changes in humidity (without condensation) will not affect Tau; 5) constant or variable metabolic rates cannot account for differences between heating and cooling thermal time constants; 6) constant or variable metabolic rates are not likely to lead to the evolution of homeothermy.

Keywords

TAU, 'THERMAL TIME CONSTANTS, REPTILES, THERMOREGULATION, HEAT TRANSFER, NEWTON'S LAW OF COOLING, METABOLIC RATE, CARDIOVASCULAR ADJUSTMENTS, MODEL.

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Résumé

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Les effets de certaines variables expérimentales (la vitesse du vent, la nature du fluide, les contraintes animales etc.) sur la constante thermale Tau sont analysés. Les résultats équivoques qui proviennent d'études antérieures sont dûs à un manque de soin apporté aux traitement de telles variables. Un modèle qui normalise ces variables est donc proposé. Ce modèle pourra servir de base pour une interprétation théorique de l'écologie thermale des reptiles. Le modèle montre que 1) les petits reptiles (20g ou moins) contrôlent leur taux d'échange de chaleur, 2) les reptiles aquatique ont probablement les mêmes capacités de thermorégulation que les reptiles terrestres; et 3) les variations observées de la constante thermale des tortues pourraient être causées par de différences de surface; 4) les variations d'humidité (sans condensation) n'affectent pas la constante thermale, Tau; 5) un métabolisme constant ou variable ne explique pas les différentes entre les constantes thermales obtenues par chauffage et refroidissement; et 6) les reptiles avec un métabolisme constant ou variable ne sont pas susceptibles d'évolution de homéothermie.

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Preface

This thesis contains the following original contributions to the knowledge of the thermal ecology of reptiles:

- 1. errors made by Strunk in his generalized model for the heat transfer from reptiles were corrected,
- 2. a general relationship between the physical dimensions and the mass of reptiles was developed,
- 3. the effect of the retraction and extension of turtle limbs have on the thermal time constant was estimated,
- 4. the data for thermal time constants presented in the literature were normalized to constant environmental conditions to eliminate any influence that experimental conditions might have on the results,

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A significant contribution was made by R. Garner in deriving the generalized mathematical model for the heat transfer from reptiles and in explaining heat transfer theory.

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Part 1. Newtonian Cooling and Reptilian Thermal Ecology

Introduction

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While a reptile may warm or cool itself for a limited time, overall it must remain in an energy balance with its environment. Failure to maintain a viable temperature can impair or kill an animal since excessive temperatures irreversibly denature muscles while excessive cold deactivates muscles and enzymes (Aleksiuk, 1971; Whitman, 1988). To avoid these consequences of thermal imbalance, most reptiles utilize heterogeneities in their environments to gain or lose heat as required. As a result, reptiles are constrained to specific thermal microclimates. If reptiles could reduce the time required for heating and increase the time required for cooling, they could maintain a functional body temperature while extending their activity times and ability to exploit their environment.

Many reptiles have been reported able to manipulate their heating and cooling rates (Weathers, 1970; Smith, 1976; Muth, 1977). However, existing data provide a poor base for any generalizations about reptile thermal ecology because they reflect the uncontrolled influences of factors such as absorption properties, air velocity, humidity, evaporation, and changes in thermal conductance. The effect of methodological factors, such as the use of physical restraints and the site of measuring body temperature, cannot be easily assessed but also influence data generated. Insufficient attention to these factors has resulted in lack of generality and data that are valid only for specific experimental conditions.

To arrive at a more general theory of reptile thermal relations, I will discuss the effects of contingent factors on heating and cooling in reptiles. I will present a model that normalizes many of these factors, allows more accurate comparisons of experimental data and provides a better basis for the theoretical interpretation of reptile thermal ecology.

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Finally, I intend to present a general method that facilitates direct comparisons of data from different species under different conditions.

Basic Concepts of Thermodynamics

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ating.

Whenever a temperature gradient exists within a system, or when two systems at different temperatures are brought into contact, energy is transferred (Kreith, 1969). Three distinct modes of heat transfer are recognized: conduction, radiation and convection. Conduction is a process whereby heat flows from a region of higher temperature to a region of lower temperature either within a medium or between different mediums in direct physical contact. Radiation occurs when heat flows from a high temperature body to a lower temperature body separated in space. Unlike conduction and radiation, which depend solely upon temperature differences, convection is a process that combines the action of heat conduction, energy storage and mixing motion. Convection is an important mechanism of energy transfer between a solid surface and a fluid (Kreith, 1969). It occurs as either free convection, where mixing occurs as the result of density differences caused by thermal gradients, or forced convection where mixing is caused by some external agency, such as the wind.

When the rate of heat flow in a system does not vary with time, the temperature at any point within the system is constant and steady state conditions prevail. Under these conditions, the rate of heat influx at any point must be equal to the rate of heat efflux and no change in internal energy can take place. In transient or unsteady state situations, internal energy (i.e. energy storage) results in temperature changes at different points with time. Newton's law, given by Eq. 1, is a linear relationship between the flux of heat energy across the boundary layer and the difference between the surface temperature of the object and its surroundings.

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$$q_c = h_c A \Delta T \tag{1}$$

where q_c is the rate of heat transfer by convection

A is the area

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- ΔT is the difference between the surface temperature Ts and fluid temperature at some specified location (usually at a distance from the surface).
- h_c is the average thermal convective conductance (also called the "surface coefficient of heat transfer" or "the convective heat transfer coefficient").

The numerical value of h_c in a system depends on the geometry of the surface, the velocity and physical properties of the fluid and often the temperature difference ΔT . Newton's law does not define a phenomenological law of convection, rather it defines h_c .

Models of heat exchange between animals and their environments are generally aimed at assessing the role of different mechanisms of energy flow (i.e. radiation, convection, conduction) on the energy balance and temperature of animals (Porter and Gates, 1969; Rapp, 1973; Mitchel, 1976; Gebremedhin, 1987; Stevenson, 1985a). While convection is not necessarily the dominant mode of thermal energy transport, it represents one of the most common models used in determining the heating and cooling rates of reptiles (Mitchel, 1976; Turner, 1987). Heating and cooling rates are determined by transferring an animal stabilized at an initial temperature to a different temperature and allowing it to equilibrate again. Such a process is intended to determine the rate of heat transfer at a specified temperature difference. However, the practice of determining heating and cooling rates based on changes in temperature (°C x min⁻¹) at the mid-point between initial and final temperatures, depends on the magnitude of ΔT , and comparisons between different ΔT 's are difficult. To make results more comparable, the thermal time constant Tau, is frequently used. Tau can be calculated from Newton's law of cooling as will be discussed later.

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The Thermal Time Constant and Newton's Law of Cooling

The driving force in Newton's law of cooling is the change in temperature between the surface temperature of the object and the environmental temperature taken some distance from the object. Since Newton's law originally described the time/temperature relationships during the cooling of red-hot blocks of iron, its application to animal systems necessarily involves assumptions and modifications (Morrison and Tietz, 1957; Henshaw, 1968; Strunk, 1971, 1973):

- 1. There are no heat sources or sinks within the animal's body.
- 2. All conditions are transient (temperature changes with time).
- 3. Heat capacity, mass and area are constant.
- 4. The core temperature of the animal is uniform and equals the surface temperature (i.e. the thermal conductivity of the animal tissue is extremely large relative to that of the environment). If resistance to heat flow in the animal's body is significant, thermal gradients will appear and the internal temperature will no longer be uniform.

These conditions assure that all thermal resistance occurs in the boundary layer where convection takes place. Using assumptions one to four, the heat transfer from an animal can be expressed:

$$q_c = -mC_p \frac{dT_B}{dt}$$
(2)

where q_c is the average rate of heat flow from the body

- m is the mass
- C_p is the specific heat capacity of the body
- dT_B/dt is the rate of change in body temperature change with time.

Heat lost from the body (Eq. 2) must equal the heat transferred to or from the fluid across the boundary layer. Thus, substituting Eq. 2 in Eq. 1 gives:

$$\frac{dT_B}{dt} = \frac{h_c A}{m C_p} (T_B - T_A) \tag{3}$$

$$= -\frac{1}{\tau} (T_B - T_A) \tag{4}$$

The solution of this gives:

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$$\frac{T_B - T_A}{T_B - T_A} = e^{\frac{-\Phi}{\tau}}$$
(5)

$$=e^{-\lambda\theta}$$
(6)

where $(T_{Bi} - T_A)$ is the difference between the initial body temperature and the fluid temperature.

The value, τ , is the thermal time constant and is expressed (from Eq. 3) as:

$$\tau = \frac{mC_{p}}{h_{c}A} \tag{7}$$

Tau (Eq. 7) is composed of three "animal" terms and one "environmental" term. If the mass, area, and specific heat of the animal are considered constants, and the environmental, term h_{e} , is held constant, then any differences that arise between rates of heating and cooling must be due to some change in the animals's thermal conductivity (i.e. some physiological property). If the rates of heating and cooling remain the same when the animal and environmental terms are held constant, then it must be considered that the animal has no control over its thermal conductivity. California (

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Model Considerations and Limitations

When using simple models to make predictions about an animal's relationship with its environment, it is necessary to remember that it is almost impossible to describe physical or physiological phenomena exactly. Approximations are necessary (Strunk, 1971). Also much of the physiology needed to form a truly analytical model of heat transfer is either not understood or poorly understood (Strunk, 1971; Huey and Stevenson, 1979). Finally, the practice of lumping everything into the conductance (fluid velocity, radiant heat, evaporation etc.) obscures important physical and physiological variables (Strunk, 1971). It must be remembered that animals modelled as simple geometric shapes (cylinders, spheres) and treated as if they were equivalent to Newton's blocks of iron bear little resemblance to the originals. Discussing these modelled animals as though they were alive provides little insight into actual reptile thermal ecology. The importance of these "Newtonian animals" (Strunk, 1971) lies in their ability to emphasize the generality of certain relationships between animals and their environments and to illustrate the proper use of Newton's Law in this context.

Part 2. The Effects of Experimental Variables on Tau

Variables affecting the determination of Tau have been divided into three categories: environmental factors (evaporation, air velocity etc.), animal properties (changes in thermal conductivity, absorption, metabolism etc.) and uncontrolled effects (animal restraint, placement of temperature probes).

Environmental Influences

The importance of the environmental term, h_{σ} has often been overlooked in both experimental design and interpretation. For example, fluctuations in air velocity (forced convection) can cause the instantaneous value of the heat flow to vary unpredictably with time. Such changes in heat flow may artificially enhance or reduce the thermal time constant, and lead to erroneous conclusions regarding an animal's ability to thermoregulate. The effects of evaporation and wind velocity on the thermal time constant have either been ignored or poorly controlled. By not accounting for them, it is difficult to know whether variations in Tau result from changes in the animal's conductivity or from these environmental conditions.

Evaporation

Because water vapour pressure has seldom been controlled or measured in experimental determinations of heating and cooling rates, the degree to which it has affected published rates is difficult to determine. For example, the rate of temperature change during heating in air for the desert iguana at a water vapour pressure of 46.7 mm Hg was 92.5% higher than at 7.2 mm Hg (Weathers, 1969). Weathers (1972) suggested that water vapour pressure might have influenced heating/cooling ratios reported for the lizard <u>Amphibolurus</u> by Bartholomew and Tucker (1963).

Experimentally, changes in water vapour pressure can affect body temperatures in two ways. The first is through condensation of water on the animal's surface and the second is by evaporative water loss. Water vapour condenses on an animal (or other object) if its surface temperature is below the dew point of the surrounding air (Weathers, 1970, 1972; Weathers and White, 1971; Mckenna and Packard, 1975). Since condensing water liberates heat, the animal's body temperature will be artificially increased. Claussen and Art (1981) noticed that when water droplets condensed on the surface of the lizard, <u>Anolis carolinensis</u>, at high humidity, the heating rate increased about four times compared to conditions of lesser humidity. Weathers (1972) suggested that low cooling to heating ratios reported for

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live pond turtles <u>Trachemys scripta</u> and <u>Chrysemys picta</u> (Spray and May, 1972) were due to condensation resulting from changes in relative humidity which ranged from 50 to 100%.

Evaporative water loss decreases body temperature by absorbing heat from the animal's body and the surroundings. As a result, the heating rate will decrease, and the time constant will increase. Weathers and White (1971) found that high rates of evaporative water loss from wet pond turtles heating in air not only prevented the turtle's body temperature from reaching ambient temperature but kept it at an average 2.9°C below ambient temperature. Stevenson (1985b) indicated theoretically that evaporative water loss could lower an animal's body temperature by as much as 20°C if water was present on the skin. Mckenna and Packard (1975) attributed differences between the heating and cooling rates of dead <u>Cnemidophorus sexlineatus</u> and <u>Sceloporus undulatus</u> lizards to evaporative water loss: the water vapour pressure of the experimental heating chamber was almost twice as high as that in the cooling chamber.

Evaporative water loss can also occur as the result of pulmo-cutaneous activity. However, available evidence suggests that evaporation from the skin or lungs is unlikely to significantly affect heating or cooling (Bartholomew and Tucker, 1963; Dmi'el and Borut, 1972; Licht and Bennett, 1972; Spray and May, 1972; Smith and Adams, 1987).

Air Velocity

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Air velocity also affects the rate of temperature change during heating and cooling. As the velocity of a fluid increases, the rate of convective heat transfer increases until it overrides physiological adjustments. For example, heating both live and dead animals in air at a velocity of 240 cm/sec was almost twice as fast as heating the animals in still air (Bartholomew and Tucker, 1963). The effect of wind velocity is greatest in small animals and decreases with increasing body mass. Since small increases in wind velocity can dramatically

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enhance forced convective heat loss of small lizards (Porter and Gates, 1969), regressions used to predict thermal time constants for small reptiles (less than 10 g) may not be accurate due to experimental differences in the air velocities used (Fraser and Grigg, 1984).

Animal-Initiated Changes in Thermal Conductivity and Their Effect on Tau

Animals are obviously very different from Newton's blocks of red-hot iron. When iron cools it can neither generate nor store energy. However, reptiles are capable of some heat generation through metabolic activity and some heat storage through changes in their thermal conductivities. These adjustments affect the convective heat transfer coefficient, h_e , which in turn affects the determination of Tau. Differences in the rates of heating and cooling car. be used to quantify a reptile's ability for physiological thermoregulation (Boland and Bell, 1980).

Changes in Heart Rate and Circulation and Their Effect on Heat Transfer

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Differences between heating and cooling rates have been linked to changes in heart rate and peripheral blood flow (Bartholomew and Tucker, 1963; Bartholomew et al. 1965). The observation that heart rates are faster during heating than cooling has been made in representatives from the Agamidae, Varanidae, Scincidae, and Crocodylia (Bartholomew and Tucker, 1963; Morareidge and White, 1969; Bartholomew and Tucker, 1968; Weathers, 1970; Spray and May 1972; Smith 1976a). However, the effect of changes in heart rate on heat transfer is not clear and its importance may vary among species. For example, Spray and May's (1972) work with turtles found no consistent differences in heart rates between heating and cooling. When atropine was administered to increase heart rate, body temperature did not increase. Similar results have been reported for <u>Pseudemys floridana</u>, <u>Chelvdra serpentina</u> (Weathers and White, 1971) and <u>Alligator mississippiensis</u> (Smith, 1976a). Weathers and White (1971) suggest that in turtles, heart rate may partly depend on respiratory activity, apenic periods being associated with low heart rates while active ventilation is associated with high heart rates. In snakes, heart rates may be stimulated by increases in blood temperature from the head region, or by increased muscular or neural activity and are not always accompanied by changes in body temperature (Webb and Heatwole, 1971). Morareidge and White (1969) found that peripheral vascular responses of the Galapagos marine iguana may be independent of heart rate. Finally, Smith (1976a,b) showed that while heart rate in the American crocodile was greater during warming than cooling, changes in blood flow rather than heart rate were important in altering rates of heating and cooling.

This suggests that heart rates may respond to physiological demands other than heating and cooling (Weathers and White, 1971; Fraser and Grigg, 1984; Turner 1987), and that changes in heart rate alone are not sufficient to effect heat exchange. However, changes in heart rate, coupled with peripheral circulation and cutaneous vasomotor responses could make the absorption and transfer of energy effective processes (Rauch, 1978). Peripheral vasodilation and tachycardia (rapid heart rate that starts and stops abruptly) result in increased blood flow and a higher rate of heat transfer between the core and surface. Peripheral vasoconstriction and bradycardia (slow heart rate) result in decreased heat flow between the core and surface. As a result, the skin may facilitate or impede heat exchange by acting as an insulating shell. Bartholomew and Tucker (1963) found that while the heart rate of <u>Amphibolurus barbatus</u> decreased to 1/5 the initial value during cooling, the thermal conductance did not change. Therefore, changes in heart rate were of secondary importance to peripheral vasodilation was found to promote the transport of heat from the surface of the animal to its core (Morareidge and White, 1969), and more blood was circulated than was

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necessary for oxygen transport alone (Baker and White, 1970). Finally, Smith (1976a) reported that <u>Alligator mississippiensis</u> was able to control its rate of heat exchange with the environment by altering its cutaneous vascular responses.

The ability of reptiles to control their rate of heat exchange by altering their thermal conductivies appears to increase with body mass. This may result from the observation that as mass increases so does integument thickness (Smith 1976a). A thicker integument would provide a better insulating shell and allow reptiles to shorten the amount of time they spend basking while lengthening the time they spend at their preferred body temperatures.

Metabolism

While cardiovascular adjustments modify heat transport, metabolism can directly increase the rate of heating and decrease the rate of cooling. Bartholomew et al. (1965) concluded that, based on a constant metabolic rate, endogenous heat production could entirely account for the observed differences in heating and cooling rates at 30°C in <u>Tiliqua</u> <u>scincoides</u>. Heliothermic varanid lizards should be able to elevate body temperature as much as 2°C above ambient (Bartholomew and Tucker, 1964). Extrapolations of skin thickness and metabolic heat production suggest that a two-metric-ton marine crocodile should be able to increase its body temperature 6.9°C in 35°C water (Smith et al., 1984). Stevenson (1985b) incorporated metabolic heat generation into a model of the steady state heat transfer from an animal's body and concluded that metabolic heat production would increase the body temperature by less than 1°C. Significant amounts of internal heat production would partially free a reptile from external heat sources, and allow it greater freedom to exploit its environment As a result, the degree to which metabolic heat production contributes to differences in heating and cooling rates has received considerable attention. However, published estimates of endogenous heat production have been questioned on several grounds. The first is that the correlation between the variable chosen (e.g. fat utilization, heart rate, oxygen consumption) and metabolism is not very good. For example, estimates of fat consumption of denning rattlesnakes suggested that if the snakes formed a snake-ball they should be able to increase their body temperature 15°C above ambient (White and Lasiewski, 1971). However, upon excavation, it was found that these snakes do not "ball up" and their body temperatures were found to average 5°C which is close to the snakes' critical thermal minimum (Brown et al., 1974). While variations between reported oxygen consumption or heart rate and body temperature may result from differences in the techniques used to measure them (Greenwald, 1971), they may also result from other factors such as acclimation and digestive status (Buikema and Armitage, 1969). Finally, heart rate or oxygen consumption and metabolism can vary considerably among individuals of the same species and within a individual over time (Bartholomew and Tucker, 1963; Buikema and Armitage, 1969). Therefore, the sources of variance between the variable and metabolism must be accounted for, before these rates can be used with certainty.

The second reason that metabolic estimates have been questioned results from the calculation of metabolism itself. By solving the heat transfer equations incorporating a constant metabolic heat term, Strunk (1971, 1973) showed that endogenous heat production should have no effect on heating and cooling thermal time constants. This is contrary to the analysis of Bartholomew and Tucker (1963) and implies that their conclusion that a constant metabolic rate influences the thermal time constant may be erroneous.

Changes in Emissivity

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An ideal thermal solid (a solid that absorbs all electromagnetic radiation incident upon it) at absolute zero would appear black. Most surfaces do not approximate ideal thermal solids (black bodies) and emit less IR radiation than the ideal. The ratio of the emissive power emitted by a surface to the emissive power which would have been emitted by an ideal thermal solid is called the emissivity of the surface.

At all temperatures above absolute zero (-273°C) every object emits a spectrum of differing wavelengths and intensities related to its surface area, surface emissivity, and the fourth power of its absolute temperature. Thus, radiative heat absorbed from a higher temperature object (e.g. sun) will not increase the rate at which an animal's temperature will change but will effect its equilibrium temperature. Stevenson (1985b) concluded from his heat transfer model that a reptile could, depending on size, attain a body temperature that ranged from 2 to 20°C above ambient – larger animals could attain the higher temperature.

Since some animals can change their skin colour, it is possible that these changes may differentially alter the reflectance and absorption of incident radiation (Crisp et al; 1972). Alterations in skin emissivity may affect rates of radiant heat exchange so that a highly absorptive surface combined with a high surface to volume ratio would allow small heliothermic reptiles to make rapid temperature changes. However, available evidence suggests that for species tested thus far, overall interspecific differences in integument reflectance are slight, and changes in colour are unlikely to significantly affect heating and cooling rates (Crisp, et al, 1972; Spellerberg, 1972).

Uncontrolled Parameters

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Variables such as animal restraint and the location of temperature probes in the animal's body have been shown to influence rates of heating and cooling (Bethea, 1972; Smith 1976a). While these variables can not be modelled (i.e. restraint does not affect all species in the same way), they should be recognized as a source of experimental variance.

Restraint

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The use of thermistors for recording temperature usually requires restraint to prevent the animal tangling the thermistor leads. However, restraint stresses the animal and may alter normal physiological processes such as blood circulation, which may in turn affect heat flow (Smith, Allison, and Crowder, 1974; Boland and Bell, 1980). Decreased heating rates have resulted from changes in the vascular system induced by disturbance or stress (Smith, 1976a). Boland and Bell (1980) showed that in <u>Crocodylus porosus</u>, bradycardia caused by disturbance reduced the rate of heating to a small fraction of its expected value, and Bethea (1972) found that <u>Terrapene ornata</u> had a much higher heart rate at room temperature when completely restrained. Radiotelemetry offers a partial solution to these problems because the animals need not be restrained. This allows responses to sudden alterations in heat flow in a less stressful manner. However, transmitters must often be surgically implanted to prevent regurgitation. The surgery may result in post operative shock, or persistently affect behaviour (Fitch and Shirer, 1971).

Location of Temperature Probes

Since the calculated rate of heating and cooling depends on the measured difference between the animal's body temperature and the ambient temperature, body temperature must be measured accurately. Most body temperatures used in heating and cooling experiments are taken from a single location, usually the cloaca/colon or oesophagus. While single location temperature measurements in small animals may result in reasonable estimates of body temperature, with little tissue lag (Spray and Belkin, 1972), this is not the case for larger animals. Significant oesophageal, nasal and cloacal temperature differences have been recorded in individual Iguana iguana, (Spray and Belkin, 1972), Thamnophis radix (Dill, 1972) and Thamnophis sirtalis parietalis (Vincent, 1975). Temperatures taken from

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a single location are unlikely to adequately describe a living reptile since they do not take into account possible variations, unequal values of specific heat, or thermal gradients within the animal (Smith, 1976a). Perhaps the greatest problem with single body temperatures is that they can introduce an unspecified error in whole body conductance values, which may influence the thermal time constant (Smith, 1976a). For example, in <u>Iguana iguana</u>, hysteresis can result from the differential heating rates between the heart and cloaca and need not result from changes in thermal conductivity (Spray and Belkin, 1973). Similar tissue lags have been reported in Australian pythons (Webb and Heatwole, 1971) and American alligators (Smith, 1976a).

Multiple temperature readings provide a more accurate description of a living animal. They may also provide an indirect measure of thermal conductance and blood flow based on the differential heating and cooling of different body regions (Smith, 1976a).

Part 3. Creating the Basic Model

Classification of Data from the Literature

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> To reduce the confusion and ambiguity caused by the interpretation of data generated under different environmental conditions, I modelled the literature data under an arbitrary set of reference conditions: free convection in air at an average fluid temperature of 30°C.

> Based on the completeness of the experimental conditions reported (e.g. fluid velocity, chamber dimensions, etc.), the literature data were classified into one of three groups. Papers reporting the most complete experimental information are given in Table 1. Papers in which some experimental data are not reported, but where reasonable assumptions could be made regarding them are given in Table 2. With the exception of one paper (Smith, 1976b), all literature data cited in Tables 1 and 2 corresponds to measurements taken in air. Papers reporting measurements made in water often had missing environmental information

Species	Fluid	Fluid velocity Temp. range Refo °C		Reference
<u>Sphenamorphus</u> quo <u>yi</u>	air	0	20-39	Spellerberg (1972) ³
<u>Cnemidophorus</u> sexlineatus &	air	0	20-40	McKenna & Packard (1985) ²
<u>Sceloporus</u> undulatus	air	0	20-40	
<u>Gallotia galloti</u>	air	0	5-35	Gonzalez & Porcell (1986)
<u>Varanus</u> spp.	air	230-300 m/s	20-40	Bartholomew & Tucker (1964) ^{3,4}
<u>Tiliqua scincoides</u>	air	136 cm/s	20-40	Bartholomew et al. (1965) ³
<u>Dipsosaurus</u> dorsalis	air 0 90 ft/min 200 ft/min 400 ft/min		20-40	Weathers (1970)
<u>Scinicid</u> spp.	air	7 cm/s	20-3 3	Fraser & Griggs (1984)
Amphibolurus barbatus	air	air 0 58 cm/s 240 cm/s		Bartholomew & Tucker (1963) ³
<u>Alligator</u> mississippiensis	air	300 cm/s	15-35	Smith (1976b)
	water	10 l/min		
<u>Alligator</u> mississippiensis	air	300 cm/s	15-35	Smith (1984)
Trionyx spinifer	air	10 cm/s	15- 35	Smith et al. (1981) ¹
<u>Chrysemys picta</u> Trachemys scripta	air air	0 0	20-40 20-40	Spray & May (1972) ^{1,3}
Terrapene ornatu Pituophis nelanoleucus	air air	20 cm/s 0.2 m/s	20-40 15-33	Licht & Heldmaier (1985)
Lacerta viridis	air	20 1/hr.	20-3 8	Rismiller & Heldmaier (1985)

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Table 1. Summary of the Most Complete Environmental Data. (Cont'd.)

- 1. Denotes data from the same paper occuring in Table 1 and 2
- 2. Data originally reported as halftimes; converted to Tau by the method described by Glidewell (1981).
- 3. Data originally reported as °C/min; converted to Tau by the method described by Smith (1976b).
- 4. Average fluid velocity used.
- 5. Tank size: assume a 1.0 m long tank, and a fluid velocity of 0 m/sec.

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Species	Fluid	Fluid Velocity	Temp. Range ℃	Reference
<u>Anolis</u> carolinensis	air	?	1-20	Claussen & Art (1981) ^{3,5}
<u>Crocodylus</u> johnstoni	air	?	21-33	Grigg & Alchin (1976) ^{3,5}
<u>Alligator</u> mississippiensis	air	300 cm/sec	15-35	Smith (1976a) ⁵
<u>Gophenus</u> berlandieri	air	?	20-40	Voight & Johnson (1977) ^s
<u>Spalerosophis</u> <u>cliffordi</u> ml/min	air	150-500	15-35	Dmi'el & Bourt (1972) ^{2,5}
<u>Terrapene</u> <u>ornata</u>	air	?	10-30	Bethea (1972) ^{2,5}

 Denotes data from the same paper occuring in more than one Table.
Data originally reported as halftimes; converted to Tau by the method described by Glidewell (1981).

3. Data originally reported as °C/min; converted to Tau by the method described by Smith (1976b).

4. Average fluid velocity used.

5. Free convection assumed.

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and incomplete descriptions of the experimental apparatus used (i.e. tank sizes, water volumes etc.). However, since many reptiles are aquatic or semi-aquatic, an attempt was made to model these data. Papers falling into this category are listed in Table 3. Other papers (Stebbins and Barwick, 1968; Weathers and White, 1971; Crisp et al., 1972; Muth, 1977; Grigg et al., 1979; Boland and Bell, 1980) were considered, but their experimental design (i.e. radiant heating, field studies, etc.) gave results that were not amenable for use in the proposed model.

Heat Transfer Theory and Animal Body Shape and Size

Under conditions of free and forced convection, estimation of the heat transfer coefficient depends upon a characteristic dimension. Diameter is used for free convection while length is used for forced convection (Kreith, 1969). The characteristic dimension can be predicted from an animal's mass when no other physical dimensions are known. In order to estimate lengths and diameters for the animals reported in the literature, the mass, length and diameter of both live and dead reptiles of the same species or family were measured. Data from each reptile class were modelled separately. However, because few Crocodilians were available, their data were pooled with those of the Lacertilia. Animals used for these regressions (Table 4) were obtained from the Canadian Museum of Nature and Exotarium Import Inc., St. Eustache Quebec.

Diameter was calculated from the circumference measured at the mid-point of the animal's body. Regression formulas for circumference are given in Table 5. Two calculations of length (snout-vent, and length based on volume where Length = 4π vol/circumfrence squared) were made to determine which was the better descriptor of an animal's mass. To calculate volume, the animal was suspended in a weighed container of water. A weight was

Table 3. Summary of Environmental Data and Assumptions Made for Water Data.						
Species	Fluid	Fluia Velocity	Temp Range °C	Reference		
<u>Crocodylus</u> johnstoni	water	?	21-33	Grigg & Alchin (1976) ³		
<u>Alligator</u> mississippiensis	water	?	15-35	Smith & Adams (1978) ^s		
<u>Trionyx</u> spinifer	water	?	15-35	Smith et al. (1981) ^{1,4}		
<u>Chrysemys scripta</u>	water	?	10-30	Gildewell et al. (1981) ²		
<u>Terrapene ornata</u>	water	?	15-35	Adams & DeCarvalho (1984)		
<u>Pseudemys scripta</u> <u>& floridana</u>	water	?	20-40	Spray & May (1972) ^{1,3,6}		

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Denotes data from the same paper occuring in more than one Table. Data originally reported as halftimes; converted to Tau by the method described by 2. Glidewell (1981).

Data originally reported a °C/min; converted to Tau by the method described by *3*. Smith (1976b).

4. For tank size assume length, width and height are equal.

For tank size assume length equals three times width, width equals height. 5.

6. For tank size assume a height of eight inches.

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Table 4. Spe	cies Used i	n Modelling Body Shape.		
Lacertilia Chelonia				
<u>Amphilolurus barbatus</u>	D	<u>Chelydra serpentina</u>	D&L	
Anolis carolinensis	D	<u>Chrysemys floridana</u>	L	
<u>Callisaurus</u> draconoides	D	Chrysemys picta	D&L	
<u>Cnemidophorus sexilineatus</u>	D	<u>Chrysemys</u> scripta	D&L	
Diposaurus dorsalis	D	<u>Clemmys gutta</u>	L	
<u>Gallotia gallori</u>	D&L	<u>Coura amboinensis</u>	L	
Iguana iguana	D	<u>Emydoidea blandingi</u>	L	
Sceloporus undulatus	D	<u>Geochelone carbonaria</u>	L	
<u>Sceloporus</u> spp.	D	<u>Gopherus berlanderi</u>		
<u>Tiliqua</u> scincoides	D&L	Gopherus spp	L	
Varanus gouldii	D	<u>Mauremys japonica</u>	L	
		<u>Terrapene ornata</u>	D&L	
		<u>Trionyx</u> spinifer	D&L	
Serpentes		Crocodylia		
Boa constrictor	L	Alligator mississippiensis		
Elaphe obsoleta obsoleta	L	<u>Camin</u> <u>crocodilus</u> L		
<u>Pituophis</u> spp.	D			
Thamnophis sirtalis	L			

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Table 5. Regression Formulas for Circumference. $log C = a + b log m$					
Group	N	а	b	r value	
Lacerta/Crocodylia	43	2.368	0.347	0. 992	
Chelonia	44	2.541	0. 326	0. 992	
Serpentes	19	3.157	0.415	0. 965	

Note: Circumference is based on the equation $c = \pi d$, where the circumference, c, is in cm and N is the number of observations.

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tied to the animal to ensure that it remained completely submerged. The submerged animal did not touch the sides or bottom of the container. The mass of the water displaced by the weight and string used to suspend the animal were measured in the same way. The total mass of water displaced was the difference in mass with and without the animal (minus the mass of water displaced by the string and weight). Animal volume was then calculated according to the formula:

$$V = \frac{m}{d} \tag{8}$$

where volume = mass of water displaced by animal/density of the water at the measuring temperature

Volumes of live terrestrial reptiles were not determined. Preliminary modelling indicated that snout-vent length rather than the length calculated from the volume was the best descriptor of the animal's mass. Regressions relating snout-vent length to mass were calculated by the least squares method and are given in Table 6. Snout-vent length, circumference, and volume (where available) were plotted against mass for lizards/ crocodiles, turtles and snakes (Fig. 1, 2, and 3). These regressions were then used to estimate characteristic dimensions (length and diameter) for the reptiles reported in the literature.

Justification for Using Cylinders to Model Animal Shape

For many simple geometries (spheres and cylinders), the analytical and experimental evaluations of the heat transfer coefficients are well documented (Krieth, 1969). These simple forms are commonly used to represent convection from animals (Porter and Gates, 1969; Mitchell, 1976). In particular, the cylinder has been used extensively by Porter and

Table 6. Regression Formulas for Snout-Vent Length. $log L = a + b log m$					
Group	N a b		Ь	r value	
Lacerta/Crocodylia	43	2.532	0.345	0.992	
Chelonia	44	2.277	0.366	0.989	
Serpentes	19	3.104	0.302	0.958	

Note: L is the snout vent length in cm, mass is in Kg, N, is the number of observations.

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Fig. 1. Measurements of the physical characteristics (circumference (cir), length (len), area, and volume (vol)) of lizards and crocodiles that allow body dimensions to be predicted from the mass.



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₹ # Fig. 2. Measurements of the physical characteristics of snakes that allow body dimensions (circumference, length and area) to be predicted from the mass.





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Fig. 3. Measurements of the physical characteristcs of turtles that allow body dimensions to be predicted from the animal's mass.

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MASS (kg)

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TINU **APPROPRIATE** Gates (1969) and Spotila et al. (1972) to model heat transfer. It is assumed that a cylinder can adequately describe a reptile under Newton's law of cooling and that the principle component of heat transfer is radial (from its centre out). The cylinder was chosen for this model because it most closely resembles the shape of the animals under consideration.

Determining the Physical Properties of the Fluid:

Theory of Forced Convection for Cylinders

Forced convection is usually reported with the animal's body parallel to the direction of the wind flow (i.e. head to tail). Data concerning the effect of forced convection on cylinders are not available (Kreith, 1969). However, the effect that forced convection has on flat plates is well understood, and, since a flat plate is equivalent to an unwrapped cylinder, it can be used to determine the coefficient of heat transfer for cylinders.

The equation for the coefficient of heat transfer under forced convection (Kreith, 1969) is:

$$Nu_{*} = 0.664 Pr^{1/3} Re^{1/2}$$
(9)

$$Nu_L = h_c \frac{L}{k} \tag{10}$$

$$Pr = C_{\rho} \frac{\mu}{k} \tag{11}$$

$$Re = \rho V \frac{L}{\mu} \tag{12}$$

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where Nu is the Nusselt number, defined as the ratio of heat transmitted via convection to the heat transmitted via conduction in a fluid; h_c is the coefficient of heat transfer; k is the thermal conductivity of the fluid; L is the characteristic dimension; V is the velocity of the free stream fluid; μ is the dynamic viscosity of the fluid; ρ is the density of the fluid; Pr is the Prandlt number and is the ratio of two molecular transport properties, the kinematic viscosity (which affects the velocity distribution) and the thermal diffusivity (which affects the temperature profile); and Re is the Reynolds number defined as an indication of the ratio of inertial to viscous forces.

Rearranged, the equation gives a value for h_c:

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$$h_c = \frac{(0.664kPr^{1/3}Re^{1/2})}{L}$$
(13)

Free Convection for Horizontal Cylinders

The equation for the coefficient of heat transfer under free convection for a horizontal cylinder in liquids and gases is given by Kreith (1969) as:

$$N_{\mu\nu} = 0.53 (Gr_p Pr)^{1/4}$$
(14)

$$Gr = \frac{g\rho^2\beta(T_s - T_{\infty})D^3}{\mu^2}$$
(15)

(for GrPr between 10^4 and 10^9) where Gr is the Grashof number, and represents the ratio of buoyant to viscous forces, β is the coefficient of thermal expansion, D is the characteristic dimension, T, is the surface temperature and T ∞ is ambient temperature taken some distance from the surface.

Rearranged, Eq. 14 gives a value for h_c under free convection:

$$h_c = 0.53k \frac{(Gr_D Pr)^{1/4}}{D}$$
(16)

For Eq. 14 and 16, the fluid properties vary across the boundary layer with time. Kreith (1969) has indicated that a reasonable approximation of the heat transfer can be obtained if the physical properties of the fluid are evaluated at the arithmetic mean of the average boundary layer temperature.

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Average Fluid Temperatures Across the Boundary Layer

Different fluid properties (density, viscosity etc.) can greatly influence the calculation of Tau via the heat transfer coefficient h_c . Thus, accurate comparisons of Tau can only be made when all data are referenced to the same environmental conditions. The reference conditions used here are: free convection in air at an average fluid (boundary layer) temperature of 30°C.

To obtain an average fluid temperature of 30°C, a body at 15°C (time = 0) would have to be placed in a chamber heated to a temperature of 35°C. The instant the body is placed in the chamber the initial temperature difference across the boundary layer is 20°C; and the mid-point between the initial body temperature and maximum environmental temperature is 25°C (Fig. 4). For a passive body, the temperature and the resulting average boundary layer temperature increase with time until they equal that of the free stream fluid at T_{w} . The arithmetic mean of the average boundary layer temperature, (T_{BL}), then becomes

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Fig. 4. The physical properties of the fluid in the boundary layer are determined at the average boundary layer temperature.

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Temperature Distribution in the Boundary Layer

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$$T_{BL} = \left(\frac{\left(T_{B} + T_{\bullet}\right)}{2} + T_{\bullet}\right)$$
(17)

Similarly, to get an average of 30°C for cooling, an initial body temperature of 45°C, and a T_{∞} of 25°C are needed.

Effects of Humidity on the Thermal Time Constant

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While humidity has no effect on the animal properties (specific heat, area, mass) that constitute the thermal time constant, it can affect the value of Tau via the process of condensation (Weathers, 1972). However, it is not clear whether, in the absence of condensation, differences in humidity between heating and cooling chambers (Table 7) can affect the thermal time constant.

The ratio of time constants for an animal being heated or cooled in an at different humidities is given by substituting Eq. 14 into Eq. 18 where $(h_c)_1$ is the surface coefficient at high humidity, and $(h_c)_2$ is the surface coefficient at low humidity. For free convection, (Eq. 16) the ratio of heat transfer coefficients and the time constants are given by

$$\frac{\tau_1}{\tau_2} = \frac{h_{c_1}}{h_{c_1}} \tag{18}$$

$$=\frac{k_2(GrPr)_2^{1/4}}{k_1(GrPr)_1^{1/4}}$$
(19)

$$=\frac{k_2(C_{\rho_1}\rho_2^2\mu_1k_1)^{1/4}}{k_1(C_{\rho_1}\rho_1^2\mu_2k_2)^{1/4}}$$
(20)

Animal	Heating		Cooling		Author
	RH%	Temp. °C	RH%	Temp. °C	
snake	39%	33	48%	15	1
lizards	-	39.9	-	18.7	2
turtles	_*	30	_*	10	3
turtles	33%	35	84%	15	4
alligators	70%	35	70%	15	5
lizards	-	38	-	20	6
lizards	13.77 (mm Hg)	40	7.35 (mm Hg)	20	7
snakes	-	35	-	15	8
turtles	.*	35	_*	15	9
lizards	26% >9 5 %	40 30	59% >95%	20 10	10
lizards	35-40%	35	35-40%	5	11
turtles	-	40	•	20	12
lizard	-	40	-	20	13
tu rt le	-	32	-	4	14
liazard	-	40	-	20	15
crocodiles	-	34	-	21	16'
lizard	75-80% 75-80%	39 20	75-80% 75-80%	20 1	17 17
lizard	-	40	-	20	18
alligators	.*	35	_*	15	19
turtles	•	40	-	20	20
lizard	-	33	-	20	21
alligators	70%	35	70%	15	22

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no values given
 * animals tested in water
 ¹ temperatures represent an average

Cont'd.

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Table 7. Relative Humidities and Temperatures of Meating and Cooling Chamber. (Cont'd.)			
Authors:	1. Licht and Bennett, 1972		
	2. Weathers, 1970		
	3. Smith et al. 1981		
	4. Glidewil et al. 1981		
	5. Smith 1976a		
	6. Rismiller and Heldmaier, 1985		
	7. McKenna and Packard, 1975		
	8. Dmi'el and Borut, 1972		
	9. Adams and DeCarvalho, 1984		
	10. Claussen and Art, 1981		
	11. Gonzalez and Porcell, 1986		
	12. Voight and Johnson, 1977		
	13. Bartholomew et al., 1965		
	14. Bethea, 1972		
	15. Bartholomew and Tucker, 1964		
	16. Grigg and Alchim, 1976		
	17. Spellerberg, 1972		
	18. Bartholomew and Tucker, 1963		
	19. Smith and Adams, 1987		
	20. Spray and May, 1972		
	21. Fraser and Grigg, 1984		
	22. Smith, 1976b		

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The values of the heat capacity, thermal conductivity and viscosity of air are relatively insensitive to changes in humidity, Therefore:

$$\frac{h_{c_1}}{h_{c_2}} = \left[\frac{\rho_1^2}{\rho_2^2}\right]^{1/4}$$
(21)

Similarly using (Eq. 11) it can be shown that for forced convection the ratio of the heat transfer coefficients is given by Eq. 22.

$$= \left[\frac{\rho_1}{\rho_2}\right]^{1/2}$$
(22)

For both free and forced convection, the ratio of surface coefficients (thermal time constants) is a function of the square root of the ratios of the densities of air.

The Effect of Humidity on the Density of Moist Air

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Density tables for air (Weast, 1983) indicate that density changes with humidity. To see if changes in density have an effect on the thermal conductance, Eq. 21 is evaluated for relative humidities of 40% and 80% at a film temperature of 30°C. These humidities were chosen as representative of those quoted in the literature (Table 7). For a relative humidity of 80% and dry bulb temperature of 30°C, the dew point is 26°C; for a relative humidity of 40% and a dry bulb temperature of 30°C, the dew point is 16°C (Weast, 1983).

The density of humid air can be determined from the general relation (Weast, 1983):

$$\rho_{air} = 1.2929 \left[\frac{273.13}{T} \right] \left[\frac{B - 0.3783e}{760} \right]$$
(23)

where ρ is the density of the air; T the absolute temperature of 303.13°K (i.e. 30°C); B the barometric pressure in 6mm, assumed at 760 mm Hg; and e the vapour pressure of the air moisture in mm.

At 80% RH with $T_{dew} = 26^{\circ}$ C, 0.3783e = 9.55 mm Hg;

$$\frac{(B-0.3783e)}{760} = 0.987 \tag{24}$$

At 40% RH with $T_{dew} = 16^{\circ}C$, 0.3783e = 5.16 mm Hg;

$$\left[\frac{B-0.3783e}{760}\right] = 0.993 \tag{25}$$

Therefore, for free or forced convection;

$$\frac{h_{c_{i}}}{h_{c_{i}}} = \left[\frac{\rho_{1}}{\rho_{2}}\right]^{1/2}$$
(26)

$$= \left[\frac{0.9874}{0.993}\right]^{1/2}$$
(27)

Results

As calculated here, changes in relative humidity between 40-80% will change the surface conductance and the thermal time constant by less than 0.5%. In the absence of condensation, changes in relative humidity between heating and cooling chambers will have an insignificant affect on Tau.

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Integration of Heat Transfer Theory and Literature Data

By using either the equation for free or forced convection in air or water (Eq. 9 and 14 respectively), Tau can be calculated for each study using the experimenter's original conditions.

Tau values taken from the literature, Tau_L , are given by;

$$\mathbf{r}_{L} = \left(\frac{mC_{p}}{h_{c}A}\right)_{L}$$
(28)

These 'literature' time constants are not directly comparable because each is representative of its own environmental conditions. However, by calculating what the h_c would be under the reference set of conditions it is possible to normalize them and make different time constants comparable. The reference Tau_R is given by:

$$\tau_R = \left(\frac{mC_p}{h_c A}\right)_R \tag{29}$$

To calculate h_c for the reference conditions, the ratio of Tau_R and Tau_L is given by

$$\frac{\tau_L}{\tau_R} = \frac{\left(\frac{mC_p}{h_c A}\right)_L}{\left(\frac{mC_p}{h_c A}\right)_R}$$
(30)

For a given animal, the mass, specific heat, and area remain constant; therefore, the ratios of Taus are given by the ratios of the surface conductances. The reference Tau is calculated according to:

$$\tau_R = \tau_L \left(\frac{h_{c_L}}{h_{c_R}} \right) \tag{31}$$

where τ_R is the reference (corrected) time constant $(h_c)_L$ is the calculated surface conductance based on original data; τ_L is the experimental time constant based on original data; $(h_c)_R$ is the surface conductance calculated for the reference conditions.

Part 4. Results and Discussion

Results of Modelling Literature Data

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Rates of heating and cooling for data sets containing the most complete environmental conditions (Table 1) were plotted under the reference conditions (Fig. 5A and B). Except for one data set (Smith, 1976b), all data represent conditions in air. For comparison, the same data are plotted without environmental corrections (Fig. 6A and B). Data sets from Table 2 (where assumptions had to be made prior to modelling) were combined with the data cited in Table 1 and are given in Fig. 7A and B. Uncorrected data from both Tables are presented in Fig. 8A and B. In all cases, the modelled data show a better fit than the unmodelled data and the most complete data sets (Table 1) gives the best fit.

Corrected data show that all species can be modelled. When the necessary environmental data are reported, water data also fit the model quite well.

The Relationship Between Tau and Small Animal Mass

Based on the model presented here, certain relationships between mass and Tau can be addressed. Among these is whether very small (20 g or less) animals have control over their thermal conductances. This point has received considerable attention in the literature, and has produced a number of conflicting answers. For example, the heating/cooling curves of Grigg et al. (1979) suggest that small (less than 46 g) animals should cool more rapidly than they heat. Smith and Adams (1976) report a similar

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Fig. 5A and B. The thermal time constant for heating and cooling, calculated using data from Table 1, shows a linear relationship with mass on a log log plot. Under reference conditions, the modelled data fit closely along the regression line.

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Fig. 6A and B. Thermal time constants of the original data (Table 1). Increased scatter around the regression lines for heating and cooling data results from differences in experimental conditions present in the original data.

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Fig. 7A. Thermal time constants calculated from the combined data of Tables 1 and 2. The correlation coefficient (r = 0.845) is lower than that of the best modelled data (Fig. 1; r = 0.922). This decrease is largely due to the assumptions that had to be made prior to modelling (Table 2).

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10. 114 Fig. 7B. Thermal time constants calculated from the combined data of Tables 1 and 2. The correlation coefficient (r = 0.841) is lower that that of the best modelled data (Fig. 1; r = 0.901). This decrease is largely due to the assumptions that had to be made prior to modelling (Table 2).



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MASS (kg)

Fig. 8A and 8B. Heating and cooling data taken from the literature (Tables 1 and 2) without accounting for environmental conditions exhibits greater scatter about the regression line than the same data after modelling.

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result for alligators weighing approximately 42 g. Work by Fraser and Grigg (1987) indicates that small skinks and possibly other small reptiles (1-10 g) are unable to enhance heat gain or retard heat loss by effecting changes in their thermal conductance. These authors, and others (White, 1973; Smith, 1976b; Smith and Adams, 1978), support the opinion that physiological control of heating rates in small reptiles is secondary to behavioral adjustments. Against this, Claussen and Art (1981) suggest that lizards larger than 13 g should heat more rapidly than they cool as should small lizards tested in air. When modelled, the best data (Table 1) shows that the intersection point falls below 1 g (Fig. 9A and B) and indicates that even very small animals heat faster than they cool. For the same data unmodelled, the intersection point falls at about 3 g. If it is assumed that small reptiles would gain as much as large reptiles from the benefits associated with a high constant body temperature (i.e. enhanced predator avoidance, greater exploitation of habitat, etc.), then the ability to influence their thermal conductances is not unexpected. The ability of very small animals to control their conductivities suggests that small size does not necessarily act as a limitation for physiological thermoregulation. However, the large surface to volume relationship of small animals suggests that they are subject to rapid heat loss which would increase with even slight changes in air velocity. To counter this, small animals may have a more effective circulatory system that would increase heat transfer between the core and surface. This would allow these animals to maintain a preferred body temperature even though they lack effective insulation and internal heat production (McKenna and Packard, 1975; Turner, 1987). While this is an interesting question, the important question remains as to whether time constants measured in seconds have any ecological significance.

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- Fig. 9A. Calculated regression lines for data reporting the most complete environmental conditions (Table 1). This graph shows that even very small animals have control over their thermal conductivities.
- Fig. 9B. Calculated regression lines for the combined data in Tables 1 and 2. By incorporating assumptions regarding environmental conditions (Table 2), the combined data is shown to have less scatter than the unmodelled data.

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Thermal Time Constant Ratios and Physiological Thermoregulation

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Ratios of heating to cooling thermal time constants appear quite frequently in the literature (Weathers, 1970; Spray and May, 1972; Smith, 1976a,b; Glidewell et al, 1981) and are used to determine how well a reptile can control its rate of heat transfer. For example, a decreasing ratio of Tau warming to Tau cooling with increasing mass implies an increased ability to physiologically thermoregulate in larger animals (Smith, 1976b). A cooling to heating ratio of one indicates that a reptile cannot modify its heat transfer characteristic, and will heat and cool at the same rate. A cooling to heating ratio greater than one indicates that the animal takes longer to cool than heat and is able to modify its rates of heat exchange. To determine whether the ability to control rates of heat exchange is a function of mass, heating and cooling rates for small and large reptiles were compared (Table 8). These data represent both terrestrial and aquatic animals, and were selected because heating and cooling rates were known for each animal. Further, because these examples (from Table 1) contain the most complete environmental conditions, it is expected that they would best show any trends. Unfortunately, no suitable snake or turtle data were available, and the results best apply to lizard-shaped reptiles.

The corrected (modelled) cooling to heating thermal time constant ratios (Fig. 10) shows that the ability to alter rates of heat exchange is independent of mass. This result is similar to that reported by Gonzalez and Porcell (1986). While statistically no relationship between mass and cooling/heating ratios exists (r = 0.18), a slight trend in this direction is indicated by the modelled data. While the same mechanisms of heat transfer (i.e. changes in thermal conductivities) are utilized by both small and large reptiles, identical heating/cooling ratios will have different consequences for both

Species	Reference		
Amphibolurus barbatus	Bartholomew and Tucker, (1964)		
<u>Varanus punctatus</u>	Bartholomew and Tucker, (1964)		
Varanus gouldii			
<u>Varanus acanthurus</u>			
<u>Varanus varius</u>			
<u>Tiliqua scicoides</u>	Bartholomew, Tucker and Lee, (1965)		
<u>Dipsosaurus</u> <u>dorsalis</u>	Weathers, (1970)		
<u>Sphenomorphus</u> squoui	Spellerberg, (1972)		
Sphenomorphus tympanum			
<u>Sphenomorphus</u> kosuiskoi			
<u>Sceloporus undulatus</u>	McKenna and Packard, (1975)		
<u>Cnemidophorus</u> sexlineatus			
<u>Alligator mississippiensis</u>	Smith, (1976b)		
Lampropholis guichenoti	Fraser and Grigg, (1984)		
<u>Alligator mississippiensis</u>	Smith, et al., (1984)		
<u>Gallotia galloti</u>	Gonzalez and Porcell, (1986)		

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Fig. 10. Cooling to heating thermal time constant ratios of 'lizard-shaped' reptiles indicates that the ability to alter rates of heat exchange is independent of mass. Thermal time constants are based on modelled data from Table 1.





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57 1 groups. For example, a large animal will derive greater benefit from the same cooling/heating ratio than a small animal. Thermal inertia will permit the large animal to extend its cooling time, perhaps for many hours. The small animal, with its lack of insulation and small size may have the same ratio as the big animal but will be able to extend its cooling time for only a few seconds (Fig. 10). If there is no ecological advantage for small animals to prolong their preferred body temperature for even a few moments, the question arises as to why these animals are as equally efficient at doing so as animals many times their size. One other curious result is the apparent ability of a few small animals to have accelerated cooling rates (Fig. 10). The reason for this is unclear and needs further investigation.

Metabolism and Its Implications for Reptile Thermal Ecology

Differences in rates of warming and cooling need not arise solely through changes in blood flow (Turner and Tracy, 1985). For smaller animals, (10 kg or less), circulatory changes are likely to account for heating/cooling differences (Turner and Tracy, 1985). In larger animals, however, hysteresis is thought to result from endogenous heat production (Bartholomew and Tucker, 1963, 1964; Smith, 1976a). If metabolic heat production occurs in significant amounts, it has important and diverse implications for reptile thermal ecology. For example, it could influence an animal's metabolic scope for activity (Bartholomew and Tucker, 1963), allowing the animal to better avoid predatory and exploit its environment. Significant internal heat production in the agamid lizard <u>Amphibolurus barbatus</u> could allow the animal greater independence at low temperatures and permit it to seek basking sites when its body temperature is 15 to 20°C below its eccritic level (Bartholomew and Tucker, 1963). At high body temperatures the maximum metabolic rate of varanid lizards may equal or considerably exceed the basal

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rate of a mammal of equal size (Bartholomew and Tucker, 1964). This suggests that reptiles could serve as a model for the evolution of homeothermy.

While the model presented here cannot predict the effects that metabolic heat will have on an animal, it can assess the degree to which constant and variable metabolic rates will influence differences between heating and cooling thermal time constants. It can also assess whether changes in thermal conductivity (with and without endogenous heat production) can form the basis of a model to describe the relationship from a variable to a constant body temperature.

The Effects of a Constant Metabolic Rate on Differences Between Heating and Cooling Thermal Time Constants

If a lizard maintained its maximum metabolism at all body temperatures during both heating and cooling, the rate of cooling would be decreased while the rate of heating would increase (Bartholomew and Tucker, 1963). Consequently, it would be expected that the animal would reach and maintain an equilibrium temperature higher than ambient temperature. If it is assumed that the metabolic rate (heat generated by the animal's metabolism per unit mass) of a reptile can be represented by a linear relationship with body temperature (i.e. $Q_{met} = a+bT$) then the heat transfer from the animal can be represented by the generalized Eq. A23 from Appendix A.

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$$T_{c} - T_{a} = [(T_{c_{1}} - T_{a}) - \frac{(a+bT_{a})mR_{T}}{1-bmR_{T}}]e^{-\frac{1-bmR_{T}}{mC_{p}R_{T}}} + \frac{(a+bT_{a})mR_{T}}{1-bmR_{T}}$$
(32)

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where T_c is the animal's body temperature,

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- T_{ci} is the initial temperature of the animal's body,
- T, is the ambient temperature,
- m is the mass of the animal,
- C_p is the specific heat of the animal,
- R_T is the resistance to heat transfer (i.e. $1/h_cA$ if the heat transfer is governed only by convection across the boundary layer).

This equation is different from that proposed by Bartholomew and Tucker (1963) and Strunk (1971). The reasons for the difference between the effect of metabolism identified in Eq. 34 and that given by Bartholomew and Tucker (1963) are the same as those identified by Strunk (1971). However, Eq. 34 also differs from that proposed by Strunk (1971). While Strunk indicated that metabolic heat generation affects the heat transfer from the core of the animal to its surface he neglected to consider that metabolic heat generation will also affect the heat lost by convection from the animal's surface.

From Eq. 34 it can be seen that the thermal time constant can be given by:

$$\tau = \frac{mC_{p}R_{T}}{1-bmR_{T}}$$
(33)

If the metabolic rate is constant, that is "b" equals zero, then it would have no effect on the thermal time constant. It is only when the metabolic rate varies with the animal's body temperature (b > 0) that Tau would be affected. The same observations were made by Strunk (1971).

The equilibrium temperature of the animal is the temperature that the animal's body assumes after it has been exposed to the ambient temperature for a long time (i.e.
it approaches infinity) and can be obtained from Eq. 34. It is a balance between the heat generated by metabolism and the heat lost by the animal to its environment.

$$T_{cr} = T_{a} + \frac{(a+bT_{a})mR_{T}}{1-bmR_{T}}$$
(34)

where T_{α} is the equilibrium body temperature of the animal.

The dependence of the above equation on both a and b, the two parameters that were assumed to determine the metabolic rate, indicates that the equilibrium body temperature will always exceed the ambient temperature if metabolic heat generation is significant. However, where metabolic heat production has been determined as being able to increase body temperatures above ambient, measured temperature differences between the animal and the environment have either not occurred, or been reproducible (Johnson, 1972; Brown et al., 1974). Until differences between the reptile's body and ambient temperature can be unambigously proven, calculated rates of heat production must be treated with great caution.

The Effect of a Variable Metabolic Rate on Differences Between

Heating and Cooling Time Constants

In the absence of metabolic heat production, an animal heats and cools as a passive body. The only way in which an animal can affect its heating and cooling rate is to alter the thermal resistance of its body. Thermal resistance is comprised of two components: the resistance to heat transfer across the boundary layer (h_c) and the thermal conductivity of the animal's insulation layer. The first is a function of environmental conditions and is outside the control of the animal. The second is a function of animal physiology (i.e. changes in cardiovascular activity) and is the only method by which differences in heating/cooling time constants can arise. In the presence

of a constant metabolic rate, differences in heating and cooling rates must be related to changes in the thermal conductivity of the skin.

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If metabolic rate changes linearly with body temperature, $(a+bT_c)$ then a variable metabolic rate will influence the thermal time constant (Eq. 33). For example, if "b" is positive Tau will be lengthened. While the equilibrium temperature will always be greater than ambient it remains a function of the ambient temperature and will be greater or less depending on whether "b" is positive or negative (Eq. 34). However, since a negative "b" implies that as body temperature decreases, metabolic rate increases, the effects of a negative "b" need not be considered further. Regardless of whether the animal is being heated or cooled, "b" does not change. While the metabolic rate will change as a function of temperature, the value of the slope between body temperature and metabolic rate does not because "b" is a constant. Since Tau is a function of "b" it can not have any effect on differences between heating and cooling curves. Therefore, any observed hysteresis must reflect the animal's ability to alter its thermal conductivity.

Constant and Variable Metabolic Rates and the Evolution of Homeothermy

The question arises as to whether a large body mass with a long thermal time constant and a low metabolic rate is indicative of an evolutionary line leading from variable to constant body temperatures (Bartholomew and Tucker, 1963; Smith, 1976b). Spotila et al. (1973) proposed that it was mathematically possible for a body of sufficient mass to be thermostable by virtue of its mass alone. However, large body size was found to be effective only under favourable environmental conditions where the effects of a high heat capacity could provide some of the advantages of homeothermy without the necessity of evolving thermoregulatory mechanisms such as fur, feathers or an increased

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metabolic rate. Consequently, there would seem little pressure to evolve true homeothermy when some of the advantages of a constant body temperature could be gained through purely physical means without altering basic reptilian metabolism (Spotila et al., 1973). However, constantly low body temperatures would occur under seasonally cold conditions regardless of the animal's mass. In fluctuating environmental conditions, large size may be a limiting factor, and other physical (insulation) and physiological (metabolic) changes may be more important than mass alone for the evolution of homeothermy (Bartholomew and Tucker, 1963; Spotila et al., 1973).

Insulation (integument thickness) increases with mass (Smith, 1976a) and could influence rates of heat exchange. However, in the absence of endogenous heat production, insulation was found to be insignificant in maintaining a high constant body temperature except over short term unfavourable climatic conditions (Spotila et al; 1973).

Consequently, for homeothermy to evolve some form of internal heat generation must be considered. If a constant metabolic rate is assumed (b=0), the equilibrium body temperature will always remain the same amount above ambient. But, because the equilibrium temperature is tied to the ambient it will fluctuate with ambient temperature and will never result in a constant high body temperature. Variable metabolic rate (a+bTc) is also tied to ambient temperature, and, for the same reason, will not result in a constant body temperature. From assumptions concerning metabolic rate (either constant or variable), it is obvious that differences between Tau heating and cooling can not be influenced by endogenous heat production, and, that differences between heating and cooling curves can only result from changes in the thermal conductivity of the integument layer. In spite of these observations, some form of internal heat production must be considered for homeothermy to develop. Further, this heat production must

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result from differences between the animal's body temperature and environmental temperature. The process by which this could occur in reptiles remains to be discovered, partly perhaps because much of the physiology involved may not be completely understood.

Dead Reptiles

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Rubber and dead animals have provided two different approaches to understanding reptilian heat transfer. The first is a test of experimental procedure. Dead or rubber animals should act as passive bodies. The absence of hysteresis during heating and cooling serves to verify that the methods used to heat and cool the animal do not contribute to differences in thermal time constants. Data reported without controls (Fraser and Grigg, 1984) or where the heating and cooling rates of dead animals are assumed to be equal (Bartholomew and Tucker, 1964) or are based on published literature values (Glidewell et al., 1981) must be treated with caution. When dead animals (data taken from papers in Table 1) are modelled under the same environmental conditions as live animals (Fig. 16), they are found to heat and cool as passive bodies and to do so more slowly than live animals.

The second use that dead reptiles serve deals with the observation that dead reptiles heat and cool more slowly than live ones (Bartholomew and Tucker, 1963; Strunk, 1971; Grigg et. al, 1976). This is due in part to large thermal gradients that exist between the core and the periphery (Bartholomew and Tucker, 1963). The presence of these thermal gradients coupled with the slower heating rates of dead animals may indicate the importance of circulation in heat distribution within the living animal (Grigg et al., 1976).

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Fig. 11. Dead reptiles (from Table 1) heat and cool as passive bodies.

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Part 5. Modelling Animals Tested in Water

Modelling Animals Tested in Water as Conduction

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Free convection occurs when a body comes in contact with a fluid that is either warmer or cooler than itself. Heat flowing between the body and fluid gives rise to changes in fluid density. These density changes, often referred to as convection currents, require a large volume of fluid in which to form so that the temperature of the fluid being measured (T_{∞}) is not affected by the body (Kreith, 1969). However, in a number of papers (see footnotes Table 3), experimental design was such that it was unlikely that this independence of fluid and body temperatures could occur. For example, Grigg and Alchem (1976), tested alligators between 98-168 cm in length in a tank that was 120 cm long, 40 cm wide and 20 cm deep. As a result it is possible that neither free convection nor conduction was actually being measured. Papers where the fluid volume was judged to be insufficient to allow an unbiased temperature difference between the body and the fluid were modelled as free convection and conduction to see which model best fit these data.

Calculation of Conduction

When modelling heat transfer from an animal as conduction, several assumptions have to be made: there is no bulk motion of the fluid in which the animal is immersed, the animal's body temperature is assumed to be relatively uniform, temperature differences between the animal and its surroundings are responsible for the heat flux, and fluid temperature is measured at a large distance form the body. The Nusselt number (representing the ratio of heat transmitted via convection to the heat trans:-itted via conduction in a fluid) for convection has been found (Kreith, 1969; Strunk, 1971) to be constant at a value of 1. Thus a Nusselt number of 1 was assumed in this case. This assumption allows an equivalent surface conduction to be calculated from the Nusselt number (Nu = $h_c(k/L)$). Once the coefficient of heat transfer has been determined it can be substituted into the equation for the calculation of Tau (Eq. 7).

Results

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Under the assumption of free convection and conduction, data combined from Tables 1 and 2 (Fig. 9A and B) were used as a reference for the modelling of the water data (Table 3). When data were modelied under the reference conditions (i.e. free convection) the points fell above the regression line (Fig. 12A and B) indicating that the thermal time constant for these animals was too long. By modelling data from Table 3 as conduction (Fig. 13A and B) the points are relocated below the regression line indicating that the thermal time constant is now too short. However, compared with the same data (Table 3) modelled as convection, the fit is improved. In both cases (free convection and conduction), the regression coefficients are lower than those of the combined data from Tables 1 and 2 (Fig. 7A and B). However, the regression coefficients are improved over the same data unmodelled (Fig. 14). While conduction may best overall describe this data, it cannot do so completely and indicates that these data are probably a combination of convection and conduction. For reference, all the data (from Tables 1, 2, and 3) are plotted without corrections (Fig. 15A and B).

Aquatic Reptiles, Terrestrial Reptiles and Tau

An attempt to model water data (Table 3) was made so that it would be possible to make inferences about the thermoregulatory response of aquatic and semi-aquatic reptiles under standard reference conditions. This would allow comparisons between aquatic and terrestrial animals to determine whether differences exist between the two

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Fig. 12A and B. Water data, solid symbols, lie above the regression line when modelled as free convection. Data from Table 3.

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Fig. 14. Calculated regression lines for the combined data of Tables 1, 2, and 3. Corrected data from Table 3 modelled as conduction.

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Fig. 15A and B. Data taken from the literature (Tables 1, 2, and 3) exhibits considerable scatter around the regression line as indicated by the low correlation coefficient.

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groups (Gatten, 1974; Grigg and Alchim, 1976). However, such comparisons are difficult since the data from aquatic animals do not model well. In spite of this, some general comments may be possible. Fig. 12A and B, when modelled as free convection, the water data lies above but essentially parallel to the regression line for data in air. If the necessary corrections to these data could be made it is likely that they would collapse along the air regression line, suggesting that there is no significant difference in the thermoregulatory response of aquatic and terrestrial animals. Further support for this trend is found in the comparison of the heating and cooling curves (Fig. 12A and B). If it is assumed that, due to the high specific heat of water, aquatic reptiles should have better developed thermoregulatory responses, (Spray and May, 1972; Grigg and Alchin, 1976) then it might be expected that there would be a large difference between heating and cooling time constants. However, when these curves are compared, the water data points a! nost lie on top of each other, again suggesting that aquatic reptiles do not have better thermoregulatory responses than terrestrial forms.

The Turtle Question

Turtles are unique in that terrestrial forms appear adapted to retard heat gain and augment heat loss, while aquatic forms appear to have the opposite strategy (Spray and May 1972; Bethea, 1972; Weathers and White, 1971). Various ecological explanations have been offered to account for this observation (Spray and May, 1972; Bethea, 1972; Gatten, 1974; Glidewell et al., 1981). However, variations in the thermal response of terrestrial turtles have been reported. For example, <u>Gopherus berlandieri</u> has been reported to heat faster than it cools (Voight and Johnson, 1977), while <u>G. agassizii</u> (Voight and Johnson, 1977) and <u>Terrapene ornata</u> (Adams and DeCarvalho, 1984) evidently heat and cool at the same rate and <u>G. polyphemus</u> cools faster than it heats

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(Spray and May, 1972). Experimental difficulties encountered with the testing of animals in water makes it difficult to determine if any variation in thermal response truly exists within aquatic animals.

One possible explanation for this experimental variation in heating and cooling responses could result from alterations in the turtles's surface area caused by limb extension or retraction. Large variations in the data of <u>T</u>, <u>ornata</u> could have resulted from differences in head and limb extension during heating and cooling (Bethea, 1972). This hypothesis becomes more likely with the finding by Cranshaw et al. (1980) that head position has a major effect on heat transfer and may be the means by which turtles alter rates of heat exchange with the environment. If the degree to which the extension or retraction of the limbs is significant, it could affect the thermal time constant and may account for at least some of the variability in reported rates of heating and cooling. To test this, changes in turtle surface area resulting from limb extension or retraction were modelled to determine their effect on Tau.

Changes in Surface Area

In the calculation of Tau (Eq. 7), the animal terms of mass specific heat and area are assumed to be constant. By retracting its limbs while cooling a turtle could change its surface to volume ratio and possibly retard its cooling time. If turtles do change their surface area in this manner, then the value of Tau would also change by an amount equivalent to the change in surface area.

Preserved turtles, obtained from the Canadian Museum of Nature, were classified into three groups: terrestrial, aquatic and semi-aquatic (Table 9). The limbs (including head/neck) were measured according to Fig. 16. The surface area of the limbs was

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Table 9. Species Used in Determining Changes in Surface Area.				
Terrestrial Turtles	Semi-Aquatic Turtles			
Terrapene carolina carolina	Grapyemys geographica			
<u>Terrapene carolina boufi</u>	Chrysemys picta			
<u>Testudo marginata</u>	<u>Clemmys gutta</u>			
<u>Testudo graeca</u>	<u>Clemmys muhlenbergi</u>			
<u>Testudo</u> horsefield	Malaclemimys terrapin			
Geochelone carbonaria				
Geochelone chilensis				
Geochelone denticulata				
<u>Geochelone</u> spp.				
Aquatic Turtles				
Stemotherus odoratus				
<u>Chelydra serpentina</u>				
<u>Trionyx</u> spinifer				
Lisemys punctata				

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Measurements Used to Determine Changes in Body Area



modelled under two conditions: limbs fully extended and limbs fully retracted (Fig. 17A, 17B, and 18A). Regression equations (Table 10) were found to be very similar to each other, which suggests that there is very little difference between the groups. This is confirmed when all results are pooled (Fig. 18B).

Changes in Limb Area and Their Effects on Tau

From the equation for Tau (Eq. 7), the effect of changes in surface area can be calculated. If Tau_0 represents turtles with their legs extended and Tau_1 represents turtles with their legs retracted then:

$$\log A_0 = a_0 + b_0 \log M \tag{35}$$

$$\log A_1 = a_1 + b_1 \log M \tag{36}$$

where A is area; M is mass in kg; b is the slope.

From Table 9, $b_0 = b_1$, then

$$\log M = \frac{\log A_0 - a_0}{b_0}$$
(37)

$$\log A_{1} = a + b_{1} \frac{(\log A_{o} - a_{o})}{b_{0}}$$
(38)

$$=a_1 + \log A_0 - a_0 \tag{39}$$

$$\log A_1 - \log A_0 = a_1 - a_0 \tag{40}$$

$$\log \frac{A_1}{A_0} = a_1 - a_0 \tag{41}$$

$$\frac{A_1}{A_0} = 10^{(a_1 - a_1)}$$
(42)

$$\frac{\tau_0}{\tau_1} = \frac{A_1}{A_0} \tag{43}$$

$$= 10^{-(a_{0}-a_{1})}$$
(44)

$$= 10^{-0.2}$$

- Fig. 17A. Changes in surface area of aquatic turtles with their limbs extended and retracted.
- Fig. 17B. Changes in surface area of semi-aquatic turtles with their limbs extended and retracted.

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Classification	No.	a	<u>b</u>	r value
Terrestrial Turtles				
limbs retracted	29	2.901	0.684	0.997
limbs extended	2 9	2.797	0.668	0.997
Aquatic Turtles				
limbs retracted	26	2.666	0.679	0.995
limbs extended	26	2.953	0.670	0.998
Semi-Aquatic				
limbs retracted	36	2. 902	0.631	0.995
limbs extended	36	3.062	0.622	0.995
All Turtles				
limbs retracted	91	2.786	0.667	0.991
limbs extended	91	2. 997	0.652	0.997

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Fig. 18A. Changes in surface area of terrestrial turtles with this limbs extended and retracted.

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Fig. 18B. Changes in surface area of aquatic, semi-aquatic and terrestrial turtles with their limbs extended and retracted.





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Thus, Tau calculated with the limbs extended will be 60% of the Tau calculated with the legs retracted, and will result in a 40% decrease in the thermal time constant. As a result, both terrestrial and aquatic turtles can increase or decrease their heat transfer by radiation and convection by an amount equal to the surface area exposed. The degree to which changes in surface area have contributed to variations in heating and cooling time constants of terrestrial and aquatic animals is difficult to determine because limb position has generally not been controlled.

In spite of this, a general indication of the importance of turtle extremities in controlling heat transfer can be gained from anecdotal evidence. For example, Voight and Johnson (1977) report that Galapagos tortoises bask with head and limbs extended during the day but withdraw their extremities at night. By retracting their limbs, these animals could extend their cooling time 67% over the Tau with the legs extended, and cool slowly by convection. The advantage of turtles to extend or reduce their rates of heat exchange in this manner is obvious.

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Summary

A number of experimental conditions directly affect the coefficient of heat transfer and influence the thermal time constant Tau. Evaporation increases cooling rates and decreases heating rates; condensation has the opposite effect. Fluid velocity increases both heating and cooling rates, and its effect is greatest on small animals and decreases with increasing animal size. While heart rate is correlated with temperature change, it has little effect on rates of heat transfer. However, changes in cutaneous and peripheral blood flow allow reptiles to alter their thermal conductance and influence heat gain or loss. Available evidence suggests that changes in emissivity are unlikely to significantly affect heating and cooling rates for small reptiles. Restraint may affect an animal's physiological response during heating or cooling, which could affect its conductivity and thermal time constant. Single body temperature measurements, except in very small animals, may be misleading. Differential rates of heating between body regions may erroneously be interpreted as evidence of changes in thermal conductance.

Heat generated by metabolism could partially free a reptile from its dependance on environmental heat sources. However, the relationship between oxygen consumption, heart rate, etc. and metabolism is not well correlated and possible errors in the calculation of metabolic rate have resulted in erroneous predictions.

By modelling data collected from the literature under standard reference conditions, it was found that humidity, in the absence of condensation, had no significant effect on the thermal time constant. When sufficient environmental data are given, even animals tested in water can be modelled.

Reptiles weighing 20 g or less have control over their rates of heat exchange, and have heating cooling ratios comparable to those of animals many times their size. However, for

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very small animals, thermal time constants and heating/cooling ratios are often only a few seconds in duration and their ecological significance is not obvious.

A constant metabolic rate will not affect the thermal time constant but will result in a body temperature that always exceeds ambient. A variable metabolic rate will affect the thermal time constant but, because it affects both heating and cooling curves in the same manner, it can not account for differences between the curves. In both cases, differences between Tau heating and cooling can only be accounted for by changes in the animal's thermal conductivity.

It is not likely that homeothermy would evolve in a reptile with a low metabolic rate and a large body mass. Neither a constant nor variable metabolic rate would lead to the evolution of homeothermy because both are tied to ambient temperature and would not result in a constant body temperature. For homeothermy to occur, some form of internal heat generation must be considered. However, reptile physiology may not be well enough understood at present to predict what the relationship might be.

Dead animals heat and cool as passive bodies but, due to the presence of large thermal gradients, do so at a slower rate than live animals. This difference in rates of heating between dead and live animals may indicate the importance of circulation in heat distribution.

Some animals were tested in water but errors in experimental procedure resulted in data that were a mixture of both convective and conductive heat transfer. While conclusions based on these data are tenous, it seems unlikely that aquatic animals are better thermoregulators than terrestrial forms.

Turtles are unique in that they can alter their surface area by extending or retracting their limbs. Changes in limb surface area can significantly affect the thermal time constant. However, the effect that changes in surface area have on reported thermal time constants is difficult to determine because limb placement was not controlled or reported in the original literature.

Appendix A

Theory of Heat Loss from an Animal

In \cdot ler to solve the following equations describing heat loss from an animal, a number of assumptions must be made: 1, the animal can be represented by an isothermal core (i.e. the thermal conductivity throughout the core is infinite); 2, the isothermal core is covered with a thin layer of insulation (skin) with a thermal conductivity, k, and thickness L, that can not store or generate heat; 3, this layer is thin enough and the core is large enough that over the core/skin interface a cartesian coordinate system can be used to model heat transfer; 4, the heat generated by metabolism is uniformly distributed throughout the core.

Heat loss from the core can be described as (Kreith, 1969):

Internal energy of the core + heat generated by metabolism = heat flow from the core (Fig. A1).

$$q_{int} + q_{met} = q_{out} \tag{A1}$$

where q_{int} increase of internal energy

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q_{met} metabolic heat generated

q_{out} net heat flow from the animal

According to Kreith (1969), heat transfer from the body, q_{out} is equivalent to the reciprocal of the thermal resistance to heat transfer multiplied by the total temperature difference (i.e. core temperature minus the ambient temperature).

$$q_{out} = \frac{T_c - T_{\infty}}{R_T}$$
(A2)

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Fig. A1. In an isothermal body covered by an insulation layer, the heat generated by metabolism and the change in internal energy equals the heat lost (or gained) by the animal. The overall temperature change occurs across the insulation layer and the thermal boundary layer.



Temperature Distribution from the Animal

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$$=\frac{T_c - T_{\infty}}{R_s + R_f}$$
(A3)

where R_i is the thermal resistance of the skin

 \mathbf{R}_{t} is the thermal resistance of the fluid boundary next to the animal

 R_T is the total thermal resistance (skin and fluid)

From heat conduction theory,

$$R_s = \frac{L}{k_s A} \tag{A4}$$

where k_{s} is the thermal conductivity of the fluid

A is the surface area of the animal

L is the thickness of the insulation layer (skin)

and from convective heat transfer (Newton's Law of Cooling)

$$R_f = \frac{1}{h_c A} \tag{A5}$$

Therefore

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$$R_T = \frac{1}{A} \left(\frac{L}{k_s} + \frac{1}{h_c} \right) \tag{A6}$$

where h_e is the coefficient of heat transfer.

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The rate of increase in internal energy is given by

$$q_{int} = -mCp\left(\frac{dT_c}{dt}\right)$$
(A7)

where m is the mass of the body

- Cp is the specific heat of the core
- t is time
- T_c is the temperature of the core

The rate of metabolic heat generation (per unit mass of core) is assumed to be linearly related to the core temperature, T_c .

Therefore

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$$q_{max} = (a + bT_c)m \tag{A8}$$

where a and b are constants and m is the mass of the animal.

Heat transfer from the animal can be represented by

$$-mCp\frac{dT_c}{dt} + (a+bT_c)m = \frac{(T_c - T_{\infty})}{R_T}$$
(A9)

Let θ represent the temperature difference between the core and the surrounding fluid.

$$\Theta = T_c - T_{\infty} \tag{A10}$$

then

 $-mCp\frac{d\theta}{dt} + m(a+b\theta+bT_{\infty}) = \frac{\theta}{R_{T}}$ (A11)

therefore

 $-mCp\frac{d\theta}{dt} - \frac{\theta}{R_{\tau}} + bm\theta = -(a+bT_{\infty})m$ (A12)

and

$$-mCp\frac{d\theta}{dt} - \theta\left(\frac{1-bmR_T}{R_T}\right) = -(a+bT_{\infty})m$$
(A13)

therefore;

of

$$\frac{d\theta}{dt} + \theta \left(\frac{(1 - bmR_T)}{mCpR_T} \right) = \frac{(a + bT_{\infty})}{Cp}$$
(A14)

This is a first order linear differential equation that will have a complimentary solution

$$\Theta_c = C_1 e^{-\left(\frac{1-bmR_r}{mCpR_r}\right)^t}$$
(A15)

and a particular solution

$$\theta_p = N$$
 (A16)

where N is a constant.

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Substitution of Eq. A16 back into the differential equation (Eq. A1) yields

$$N\frac{1-bmR_{T}}{CpmR_{T}} = \frac{a+bT_{\infty}}{Cp}$$
(A17)

therefore

$$N = \frac{a + bT_{\infty}}{1 - bmR_{T}}mR_{T}$$
(A18)

and the solution ($\theta = \theta_c + \theta_p$) (Eq. A15 plus A16) becomes

$$\theta = C_1 e^{-\frac{1-bmR_T}{mCpR_T}t} + \frac{a \cdot b T_{\infty}}{1-bR_T}$$
(A19)

When applying the boundary condition, it is assumed that the animal has an initial core temperature, $(T_c)_i$ at time zero. Thus at t=0,

$$\boldsymbol{\theta} = \boldsymbol{\theta}_{i} = (T_{c})_{i} - T_{a} \tag{A20}$$

therefore

$$\theta_{i} = C_{1} \frac{a + b T_{\infty}}{1 - b m R_{T}} m R_{T}$$
(A21)

and

$$C_1 = \theta_i - \frac{a + bT_{\infty}}{1 - bmR_T} mR_T$$
(A22)
substituting C_1 in Eq. A19, the complete solution becomes

$$\Theta = \left(\Theta_{i} - \frac{a + bT_{\infty}}{1 - bmR_{T}}mR_{T}\right)e^{-\frac{1 - bmR_{T}}{mC_{P}R_{T}}} + \frac{a + bT_{\infty}}{1 - bmR_{T}}mR_{T}$$
(A23)

where

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$$R_T = \frac{1}{A} \left(\frac{L}{k_s} + \frac{1}{h_c} \right)$$
(A24)

The thermal time constant for the heating and cooling of the animal is

$$\tau = \frac{mCp\left(\frac{L}{k_s} + \frac{1}{h_c}\right)}{A - bm\left(\frac{L}{k_s} + \frac{1}{h_c}\right)}$$
(A25)

For the case where the metabolic heat generation is negligible (i.e. a=b=0), Eq. A23 becomes

$$T_{c} - T_{\infty} = [(T_{c})_{i} - T_{\infty}]e^{-\frac{At}{mCp\left(\frac{L}{k_{c}} + \frac{1}{k_{c}}\right)}}$$
(A26)

and the thermal time constant (Tau) becomes:

$$\tau = m C p \left(\frac{\frac{L}{k_s} + \frac{1}{h_c}}{\frac{A}{2}} \right)$$
(A27)

If it is further assumed that there is no thermal insulation layer around the animal (i.e. L=0) then Eq. A27 reduces to

$$\mathbf{T}_{c} - \mathbf{T}_{\infty} = [(\mathbf{T}_{c})_{i} - \mathbf{T}_{\infty}]e^{-\frac{h_{c}A}{mCp}t}$$
(A28)

where the thermal time constant is

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$$\tau = \frac{Cpm}{h_c A} \tag{A29}$$

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