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CONTROL OF THERMAL CONDUCTANCE IS INSIGNIFICANT TO THERMOREGULATION IN SMALL REPTILES[1]

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Five small species of Australian scincid lizard (<20 g) heated more slowly than they cooled when exposed to step-function changes in ambient temperature. This is the reverse of the pattern typical of larger reptiles. Interestingly, this pattern was predicted by extrapolation from an earlier study that described the relationship between thermal time constant and body mass in reptiles. The reverse pattern is unlikely to represent an adaptive response, so physiological control over thermal conductance is apparently insignificant or lacking in small skinks, and perhaps other small reptiles also, in which thermoregulation must depend primarily on behavioral strategies. As most reptiles weigh <20 g, the importance of regulatory changes in thermal conductance as a mechanism for thermoregulation may have been overrated by some authors as a generalization applicable to the reptilia as a whole.

INTRODUCTION

After decades of study, the regulation of body temperature in active reptiles has become accepted as a primarily behavioral achievement, augmented significantly by two important physiological strategies— panting and changes in thermal conductance (see reviews by Templeton [1970]; White [1973]; Heatwole [1976]; Bartholomew [1982]). Most work on these two physiological contributions to reptilian thermoregulation has been undertaken on larger reptiles (>20 g). In this paper we present data that show that regulatory changes in thermal conductance are unlikely to be of significance in the thermal relations of small reptiles. This is relevant because most reptiles are small; Pough (1980) pointed out that 80% of all species are <20 g.

The evidence for changes in thermal conductance has come from experiments demonstrating hysteresis between rates of heating and cooling in relatively large rep-

tiles in response to step changes in ambient temperature. A convenient measure of the rate of change of core temperature in response to such a step is the thermal time constant, τ, which is derived from the slope of the exponential rate of heating or cooling. Useful discussions of the use of τ have been given by Bakken (1976) and Smith (1976). Rapid heating and slower cooling have been found in Agamidae, Scincidae, Varanidae, Iguanidae, and Crocodilia (reviewed by Grigg, Drane, and Courtice 1979) and in the Colubridae (Dmi'el and Borut 1972). In many (but not all) studies, control experiments were undertaken on dead animals, which invariably show no hysteresis between heating and cooling.

Concerning the mechanism of hysteresis, changing heart rates during heating and cooling pointed toward changes in peripheral circulation being responsible for changes in thermal conductance (Bartholomew and Tucker 1963, 1964). Subsequently, this was confirmed in *Amblyrhynchus cristatus* (Morgareidge and White 1969) and in *Crocodylus johnstoni* (Grigg and Alchin 1976), where peripheral perfusion was found to increase during heating and decrease during cooling. The skin is thus envisaged as a site of heat exchange or insulation, depending on circumstances.

The usual biological interpretation of the observed hysteresis is that changes in thermal conductance are regulatory mechanisms by which reptiles are able to enhance heating, retard cooling, and hence

minimize the time that need be spent in the otherwise nonproductive behavior of basking.

Whether these generalizations apply to very small reptiles has received comparatively little attention. McKenna and Packard (1975) found more rapid heating than cooling in a teiid (mean 6 g) and an iguanid (mean 9 g). They attributed the difference to changes in thermal conductivity mediated by the cardiovascular system and concluded that "even the smallest lizards have the physiological capability to control rates of heat exchange with the environment." Against this, Crisp, Cook, and Hereward (1979), investigating the impact made on heat exchange by color in small *Lacerta* (2–7 g), found no differences between thermal time constants of heating and cooling and concluded that there was no evidence of physiological thermoregulation. Subsequently, Clausen and Art (1981) examined rates of heating and cool-

ing in 3–6-g *Anolis*. They found faster heating than cooling in still air but presented no control data. As it took us almost 2 mo to achieve a satisfactory system to heat and cool dead or rubber lizards without hysteresis, their results must be treated with caution. Nevertheless, they concluded that in moderate convection lizards <3 g may cool more rapidly than they heat. In his recent review, Bartholomew (1982) discounted the importance of physiological mechanisms in thermoregulation by small reptiles, but clearly more data are needed.

All authors apparently agree that the mass of a reptile is the dominant determinant of its thermal time constant. Grigg et al. (1979) compiled data on thermal time constants of 12 species (five families) of "lizard-shaped" reptiles heating and cooling in air and in water. Animals ranged in size from about 20 g to 40 kg, and over this wide range some very clear and consistent patterns emerged (fig. 1). First, for any size,
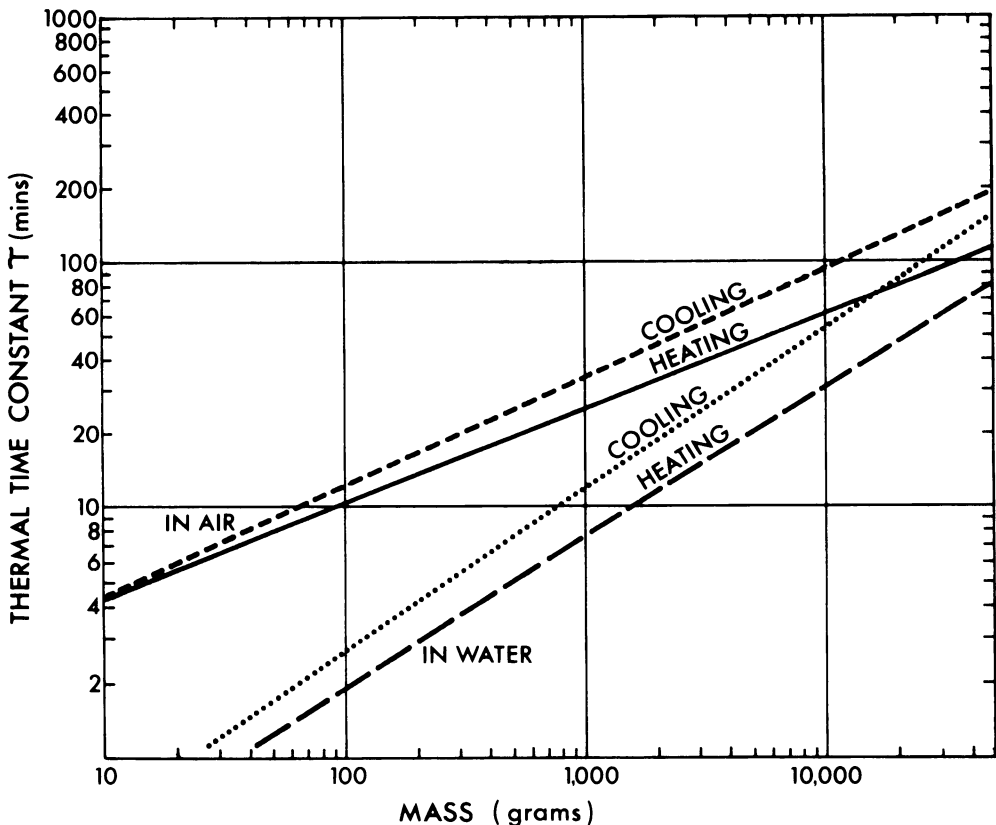

FIG. 1.—Summary figure showing the relationship between body mass and thermal time constants of 12 species (five families) of lizard-shaped reptiles (from Grigg et al. 1979).

time constants of heating and cooling were shorter in water than in air, as expected from the physical properties of water. Second, in both air and water, reptiles of these sizes heat faster than they cool. Third, strongly predictable relationships exist between thermal time constant and body size for a given set of circumstances. Finally, no taxonomic differences emerged.

The emergence of such strong relationships begs extrapolation, either upward toward larger reptiles (e.g., large crocodiles or dinosaurs; Grigg [1977]), or downward. Considering that 80% of reptile species weigh less than 20 g (Pough 1980), it seems useful to ask what the data may predict about the importance of changes in thermal conductance to small reptiles, which constitute the dominant size class. Interestingly, these regression relationships predict that reptiles 10 g or less, heating and cooling in air, will heat more slowly than they cool or, at best, heat and cool at the same rate. Either of these predictions suggests that regulatory alteration of thermal conductance is an insignificant factor in the thermoregulation of small (and, hence, most) reptiles.

Accordingly, the present study was undertaken to measure rates of heating and cooling in small reptiles and to compare the findings with these predictions.

MATERIAL AND METHODS

Five small thermophilic skinks were studied: *Lampropholis guichenoti, L. delicata, L. mustelina, Ctenotus taeniolatus,* and *Sphenomorphus tympanum.* Preferred body temperatures, as determined on a laboratory gradient, are known for only two of the species; *L. guichenoti* (33.75 ± 0.36 C; Fraser [unpublished]) and *S. tympanum* (39.5 C; Vernon and Heatwole [1970]; Heatwole [1976]). However, Greer (1980) has shown that Australian diurnal and surface-active skinks are thermophilic, having CTMAX values above 39.5 C. Of the five species in our study, only *L. mustelina* has a lower CTMAX, 38 C. The animals were maintained after capture in aquaria at 25 C for at least 6 wk prior to experimentation and were fed on either *Dacus* spp. pupae or cockroaches. Photoperiod and humidity were maintained at constant levels (12L:12D cycle, about 47% humidity). All animals used in experiments appeared to be healthy.

Individuals from each species of lizard were subjected to step changes in temperature so that their rates of heating and cooling could be determined. The apparatus was erected in a constant-temperature room (18.0 ± 1.0 C). Two identical polystyrene containers acted as reservoirs for hot or room-temperature air to which a lizard could be exposed alternately (fig. 2). Each reservoir was supplied with air from an identical hair dryer (Lady Sunbeam, Model AHD:62.230) equipped with a temperature selector dial. The reservoirs were maintained at 20.0 ± 0.3 C and 33.0 ± 0.3 C, respectively.

Individuals were heated and cooled contained in an aluminum cylinder from which escape was prevented by a piece of gauze over the free end. The size of the cylinder, together with that of pumps and flowmeters, depended on the size of the lizard under test. Pumps, etc., were selected and adjusted to achieve a linear velocity of air of 7 cm/s within the tube, measured with and without the lizard in the tube. The cylinder with a lizard inside could be moved easily between the hot and cold reservoirs. Aluminum was chosen for construction of the cylinders because of its high thermal conductivity. Hence both conductive and convective avenues of heat exchange were incorporated. The rate at which the cylinder equilibrated to the new ambient temperature was rapid and negligible when compared with the rate of temperature change of the lizards.

Deep body temperature of each lizard was monitored continuously during heating and cooling with a thermistor probe inserted into the intestine via the cloaca. A thermocouple taped to the surface was used to measure the temperature of the aluminum cylinder, and a second probe suspended 1 cm above the animal measured air temperature. For each lizard, note was taken of the snout–vent and tail length, and body weight was measured before and after each experiment.

For heating, a lizard was allowed to equilibrate in the cold reservoir (20 ± 0.3 C) then transferred quickly to the hot reservoir. Cooling was achieved by transferring
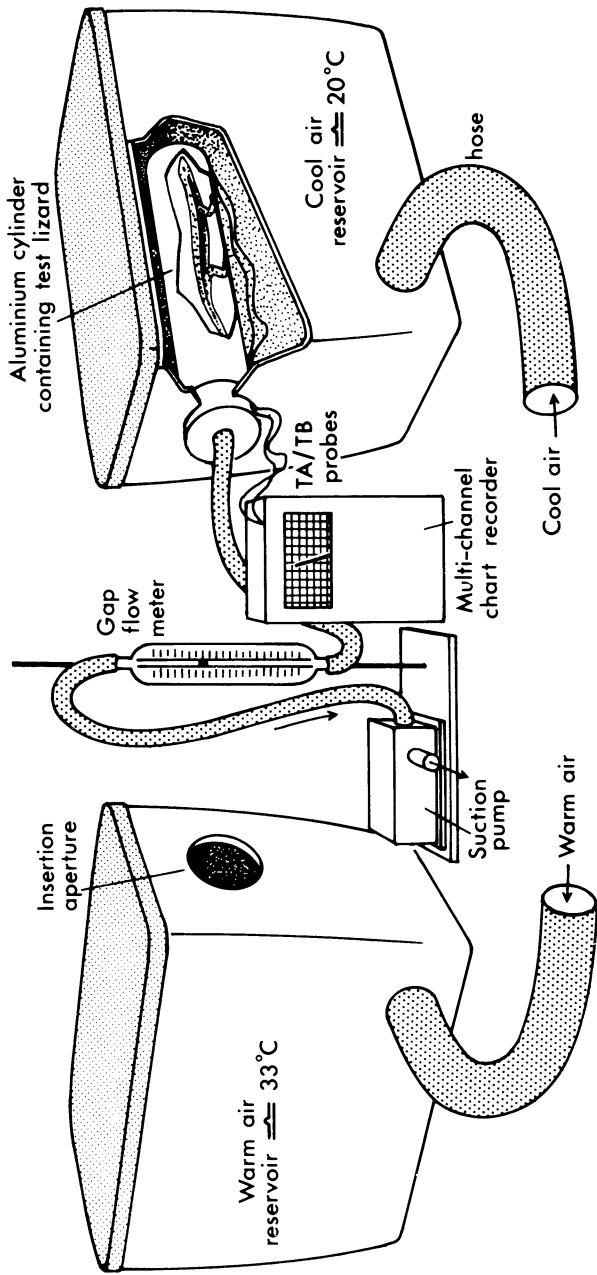
FIG. 2.—The apparatus in which small lizards were exposed to rapid, standardized step-function increases and decreases in ambient temperature

Labels within figure:

Aluminium cylinder containing test lizard

Cool air reservoir ≏ 20°C

hose

TA/TB probes

Multi-channel chart recorder

Cool air

Gap flow meter

Insertion aperture

Suction pump

Warm air

Warm air reservoir ≏ 33°C

the animal initially at a body temperature of 33.3 ± 0.3 C to the cold reservoir.

To assess the variability of rates of heating and cooling in individuals, a series of heating and cooling tests were carried out on two *L. guichenoti.* The experiment involved heating and cooling the live lizards four times, killing the animals in liquid nitrogen, and repeating the procedure on the dead animals. This method was not adopted throughout with all the lizards, as it was thought that continual heating and cooling trials would cause dehydration and hence change the physiological condition of the animals. Therefore, all other animals were heated and cooled once and killed; then the heating and cooling were repeated on the dead animals.

Before any experimentation on live animals was begun, extensive tests were required to develop a system which had no intrinsic hysteresis. This step appears to have been neglected by some previous workers. In our first attempts, we found that the apparatus induced asymmetric rates of heating and cooling in a rubber model of a lizard. A new system was then built and modified until no hysteresis could be detected in the rates of heating and cooling dead or rubber lizards.

Rates of heating and cooling were determined by plotting the difference between ambient temperature and deep body temperature semilogarithmically over time. A least-squares regression equation was then calculated for each lizard heating and cooling and used to generate thermal time constants (Bakken 1976; Smith 1976; Grigg et al. 1979). For all species of *Lampropholis* and *Ctenotus taeniolatus,* an analysis of variance was performed on the time constants for each species. Student-Newman-Keuls (SNK) tests were used to rank the means, and paired *t*-tests were used where an analysis of variance was inappropriate.

RESULTS

All three species of *Lampropholis* and also *Ctenotus taeniolatus* took longer to heat than to cool (table 1) ($P < .05$; Anova paired *t*-tests, SNK tests). No significant differences were found between heating and cooling rates of dead animals ($P > .05$). Typical results are shown in figure 3 for *L. delicata* alive and dead. Though variable,

the heating rates of live lizards was generally slower than rates of heating and cooling dead lizards (SNK test). It could be that a dead, limp lizard was in closer contact with the aluminum cylinder than a live lizard, but apart from this we have no explanation. Because of the small sample size of *Sphenomorphus tympanum* ($n = 2$), it is difficult to establish a trend, although the rates of heating and cooling were not significantly different as indicated by paired *t*-tests ($t = 7.33$, $P > .05$) (table 1).

The time constants of repeated heating and cooling trials of *L. guichenoti* (table 2) suggest that the rate of heating varies more between trials on an individual lizard than does cooling rate. For many of the small skinks, up to 2% or 3% of body weight was lost after a heating and cooling trial, which suggests that evaporative cooling may be a very important factor in the thermal physiology of small lizards. Hence, repeated heating and cooling trials are practically impossible without a buffer period between all trials in which the lizard could recoup any water loss it may have suffered. (Authors will supply original data if requested.)

There is a strong correlation between the thermal time constants and mass ($r^2 = .94$ heating, $r^2 = .98$ cooling). Figure 4 presents the pooled relationships between the thermal time constant and body mass for the five species of skink being heated and cooled. Regression lines extrapolated from figure 1 are included for comparison.

DISCUSSION

These data suggest that small skinks and, possibly, other small reptiles are unable to enhance heat gain or retard heat loss by effecting changes in thermal conductance. This supports the opinion expressed by Bartholomew (1982) that, in small reptiles, physiological modification of rates of heat exchange is of negligible importance compared with behavioral adjustments. The results, though variable, suggest that 1–10-g skinks cool faster than they heat, as predicted by the generalization described by Grigg et al. (1979) and summarized in figure 1. Such a finding may in part be explained if there were differences in the animals' posture during heating and cooling, as both conductive and convective heat exchange

TABLE 1
SUMMARY OF THERMAL TIME CONSTANTS FOR HEATING AND COOLING IN FIVE SPECIES OF SKINK

SPECIES (n)	WEIGHT (g) Before	After	ALIVE τ_h	ALIVE τ_c	DEAD τ_h	DEAD τ_c	ALIVE $\frac{\tau_h}{\tau_c}$	DEAD $\frac{\tau_h}{\tau_c}$
Lampropholis								
guichenoti (15)	1.189 ± .296	1.149 ± .297	3.744 ± .753	3.206 ± .459	3.260 ± .592	3.171 ± .593	1.190 ± .273	1.031 ± .089
L. delicata (10)	.939 ± .172	.828 ± .328	4.129 ± .955	3.238 ± .621	3.406 ± .777	3.069 ± .556	1.301 ± .338	1.137 ± .190
L. mustelina (7)	2.501 ± .420	2.413 ± .379	4.694 ± .875	4.180 ± .924	4.687 ± .635	4.509 ± .844	1.133 ± .128	1.049 ± .067
Ctenotus taeniolatus								
(10)	4.979 ± .867	4.888 ± .873	6.189 ± 1.214	5.485 ± .948	6.247 ± 2.172	6.385 ± 1.907	1.130 ± .118	.973 ± .099
Sphenomorphus								
tympanum (2)	12.76 ± 1.633	12.48 ± 1.584	11.00 ± 1.061	10.85 ± .495	9.025 ± .389	8.350 ± .495	1.02 ± .141	1.08 ± .014

NOTE.—Values given as $\bar{X}$ ± SD. Thermal time constants in minutes.

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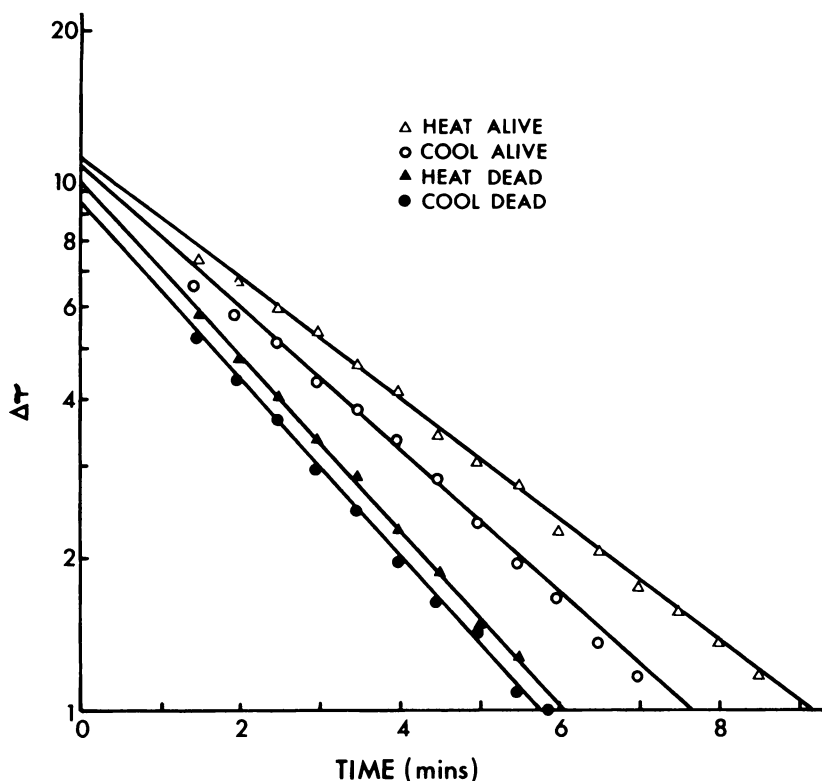
FIG. 3.—Heating and cooling of *Lampropholis delicata,* alive and dead

could be involved. The more rapid heat exchange rates of many of the dead lizards reinforces this possibility. As the preferred temperature of these species is at the high rather than the low end of the temperature steps, it is unlikely that the more rapid

TABLE 2

THERMAL TIME CONSTANTS OF RESPONSES OF *Lampropholis guichenoti* TO REPEATED STEP-FUNCTION
INCREASES AND DECREASES IN AIR TEMPERATURE

ALIVE		DEAD		ALIVE $\dfrac{\tau_h}{\tau_c}$	DEAD $\dfrac{\tau_h}{\tau_c}$
τ_h	τ_c	τ_h	τ_c		
		Animal 1 (1.31 g before; 1.2 g after)			
3.50	3.30	3.10	3.70	1.06	.84
3.87	3.13	3.45	3.50	1.24	.99
4.45	3.27	3.40	3.37	1.36	1.01
4.35	3.40	3.38	3.35	1.28	1.01
$\bar{X} = 4.04$	$\bar{X} = 3.28$	$\bar{X} = 3.23$	$\bar{X} = 3.48$	$\bar{X} = 1.24$	$\bar{X} = .99$
		Animal 2 (1.42 g before; 1.35 g after)			
4.86	4.30	4.13	4.33	1.13	.95
4.60	4.26	4.27	4.33	1.08	.99
5.00	4.40	4.01	4.28	1.14	.94
4.98	4.32	4.03	4.35	1.15	.93
$\bar{X} = 4.86$	$\bar{X} = 4.32$	$\bar{X} = 4.11$	$\bar{X} = 4.33$	$\bar{X} = 1.13$	$\bar{X} = .95$

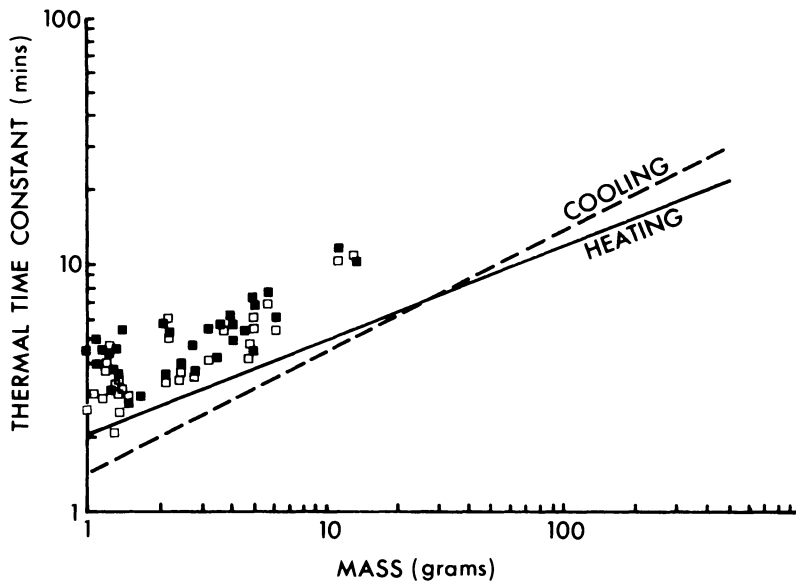NOTE.—Weight changes during the procedure are indicated.

FIG. 4.—The relationship between body mass and thermal time constant in five species of skink heating (solid squares) and cooling (open squares). The lines from fig. 1 are transferred and extrapolated for comparison.

cooling rate reflects an attempt by the lizard to avoid a high temperature. It is possible that the slow heating is an effect of evaporative cooling. Whatever the reason for the difference, it is unlikely to reflect any adaptive ecological response.

Time constants for both heating and cooling are longer than would be predicted by Grigg et al. (1979) for lizards less than 10 g. One possible explanation is that these results are extrapolated from regression lines, in which case data falling on either side of the lines could be expected. Low air velocity during the trials may offer an alternative explanation for the departure from expectations. The present study was carried out at flow rates of approximately 7 cm/s, much lower than those used by many other workers (Bartholomew and Tucker 1963, 1964; Bartholomew and Lasiewski 1965; Bartholomew, Tucker, and Lee 1965; Spellerberg 1972). Because it is rare for a lizard to expose itself to high wind velocities, it is more reasonable to use low wind velocities when studying heating and cooling rates.

Terrestrial turtles constitute the only other group of reptiles in which the rate of heating is known to often be slower than the rate of cooling (Bethea 1972; Spray and May 1972; Craig 1973). These results have been explained with varying degrees of success, by relating them to the thermal ecology of turtles.

Small size, while apparently presenting a limitation to control of thermal conductance, confers an advantage in allowing rapid heat exchange. This enables many small skinks to be active opportunistically throughout the year, taking advantage of limited winter warmth when available. A number of strategies, such as the behavioral selection of a preferred temperature on a thermal gradient and an increase of this temperature after feeding, are common to both small and large reptiles (Hudson and Bertram 1966; Regal 1966; Moll and Legler 1971; Lang 1979; Fraser and Grigg, in preparation). However, whereas small and large reptiles are similar in their behavioral thermoregulatory strategies, the present study confirms that they differ markedly in their capacity to thermoregulate by physiological means.

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