

Thermal Relations of Some Australian Skinks (Sauria: Scincidae)

ALBERT F. BENNETT AND HENRY JOHN-ALDER

Preferred body temperature (PBT) was measured in 19 species of Australian skinks of the genera *Ctenotus*, *Egernia*, *Eremiascincus*, *Hemiergis*, *Leiopisma*, *Sphenomorphus* and *Tiliqua*. Field-active body temperature (FBT) and critical thermal minimum (CTMin) and maximum (CTMax) were also measured for some species. PBT ranged from 17.6 C in *H. decresciensis* (diurnal measurement) to 35.6 C in *C. regius* but was intragenerically conservative. PBT was greater in the evening than during the day in nocturnally-active species (*Eremiascincus*, *Hemiergis*). Feeding state did not affect PBT of *T. rugosa*. FBT was very similar to PBT for most species. CTMin ranged from 3.5 C in *T. rugosa* to 11.4 C in *C. taeniolatus* and CTMax ranged from 38.6 C in *H. decresciensis* to 45.5 C in *C. uber*. Limits of thermal tolerance were examined in relation to PBT. CTMax is positively correlated with PBT with a slope of 0.426 C CTMax/1.0 C PBT (significantly different from 1.0). CTMin is independent of PBT and averages 5.5 C. These correlations hold if FBT is substituted for PBT. Thermal tolerance range is not constant among these species and critical thermal limits do not parallel PBT or FBT.

THE skink fauna of Australia is notable for both its size and ecological diversity. Over 260 species occur on the continent (Cogger, 1983), about one-fifth of the total described species of this family (Cogger et al., 1983). The fauna, all species of which belong to the relatively advanced subfamily Lygosominae, is subdivided into three distinct groups by Greer (1979). Even within each of these closely related groups, the species have diversified into numerous different habitats and niches (Greer, 1976). The *Sphenomorphus* group, for example, contains the genera *Ctenotus* (arid-land, diurnally-active heliotherms, ecologically similar to small teiids and lacertids), *Eremiascincus* (desert-

dwelling, nocturnally-active sand swimmers), *Hemiergis* (small, mesic, cryptozoic lizards) and *Sphenomorphus* (a diverse genus which includes diurnally-active, high altitude water skinks).

This ecological diversification has been accompanied by a similar diversification of thermal relations. Habitats ranging from alpine meadows to rainforests to sandy deserts present very different constraints on and opportunities for thermoregulation and impose very different extreme temperatures. Several studies have been undertaken on different aspects of the thermal biology of Australian skinks (see refs. Tables 1-3; Licht et al., 1966b; Brattstrom, 1971; Spellerberg, 1972b, d). These have usually concen-

TABLE 1. PREFERRED BODY TEMPERATURES OF SOME AUSTRALIAN SKINKS. Values reported are means and standard errors; averages of minimum and maximum values of each individual are given in parentheses. When only one individual was available, mean value of all observations is reported. *Hemiergis* were not identified individually, so mean minimum and maximum values could not be calculated.

Species	No. of animals	Body temperature °C		Collecting locality
<i>Ctenotus atlas</i>	1	35.5	(34.5–36.6)	Swan Reach, S.A.
<i>C. regius</i>	13	35.6 ± 0.46	(33.5–37.3)	Waikerie, S.A.
<i>C. robustus</i>	6	34.4 ± 0.75	(33.4–35.1)	Modbury, S.A.
<i>C. taeniolatus</i>	6	35.3 ± 0.67	(33.4–37.8)	Armidale, N.S.W.
<i>C. uber</i>	6	35.3 ± 0.53	(33.2–37.2)	Swan Reach, S.A.
<i>Egernia striolata</i>	6	32.7 ± 1.08	(31.3–33.1)	Swan Reach, S.A.
<i>E. whitii</i>	5	34.1 ± 0.67	(32.9–34.9)	Kosciusko Nat. Park, N.S.W.
	12	33.6 ³		
<i>Eremiascincus fasciolatus</i>	10	21.2 ¹ ± 1.17	(18.0–23.9)	Innamincka, S.A.
	10	24.4 ² ± 1.61	(19.5–29.4)	
<i>E. richardsoni</i>	1	24.6 ¹	(22.4–27.5)	Swan Reach, S.A.
	1	27.3 ²	(26.3–29.1)	
<i>Hemiergis decresciensis</i>	7	17.6 ¹ ± 0.58		Para Wirra, S.A.
	7	24.8 ² ± 1.37		
<i>H. peroni</i>	10	20.3 ¹ ± 1.57		Thompson's Beach, S.A.
	10	23.5 ² ± 1.40		
<i>Leiolopisma entrecasteauxii</i>				
Form A	3	32.5 ± 1.03	(30.2–34.1)	Kosciusko Nat. Park, N.S.W.
Form B	4	33.9 ± 0.78	(33.0–35.2)	Kosciusko Nat. Park, N.S.W.
	10	31.0 ³		
<i>Sphenomorphus kosciuskoi</i>	8	29.8 ± 1.08	(27.2–32.1)	Kosciusko Nat. Park, N.S.W.
	7	30.8 ⁴		
<i>S. quoyi</i>	7	28.8 ± 0.40	(28.3–29.7)	Armidale, N.S.W.
	12	29.6 ⁴		
	23	31.1 ⁵		
<i>S. tympanum</i>	8	29.6 ± 0.72	(27.4–32.0)	Kosciusko Nat. Park, N.S.W.
(Cool temperate form)	16	29.8 ⁴		
	16	29.1 ³		
<i>Tiliqua cassurinae</i>	1	31.2	(27.8–33.0)	Kosciusko Nat. Park, N.S.W.
	6	32.6 ³		
<i>T. rugosa</i>	10	31.9 ± 0.75	(29.4–34.3)	Wilmington, S.A.
	13	33.8 ⁶ ± 0.31	(31.2–36.0)	
	10	32.6 ⁷ ± 0.62		

¹ 0900–1600 h.

² 1600–2200 h.

³ Rawlinson, 1974.

⁴ Spellerberg, 1972c.

⁵ Veron and Heatwole, 1970.

⁶ Licht, Dawson, Shoemaker and Main, 1966.

⁷ Wilson, 1974.

trated on a single species or genus or have examined a single thermal factor (e.g., critical thermal maximum). This present work was undertaken to explore the thermal relations of a number of different species and to analyze correlations among preferred body temperatures (PBT), field-active body temperatures (FBT) and critical thermal limits (critical thermal maximum, CTMax and critical thermal minimum, CTMin).

MATERIALS AND METHODS

A list of species examined and collecting localities in South Australia and New South Wales is given in Table 1. The species *Leiolopisma entrecasteauxii* and *Sphenomorphus tympanum* are each divided into two recognized forms, respectively Forms A and B and Cool Temperate and Warm Temperate Forms, which may deserve specific status (Jenkins and Bartell, 1980;

Cogger, 1983). Animals were collected during Oct. to Dec., 1983, during the austral spring. Collection was made by hand or slip-noose, except for *Eremiascincus fasciolatus*, which were caught in pit-fall traps. Body temperature at capture was measured for some individuals with a quick registering Schultheis thermometer. For the cryptozoic *Hemiergus* spp., which are too small for such a measurement, the soil surface temperature at the midpoint of the body was used as an estimate of body temperature. Animals were returned to the University of Adelaide where PBT was measured, usually within two weeks of capture. In the meantime, lizards were housed in 30-l glass terraria equipped with incandescent light bulbs set on a LD 12:12 photoperiod to permit behavioral thermoregulation. Smaller lizards were fed *Tenebrio* larvae and termites; the larger *Tiliqua rugosa* was fed mixed fruit and dog food.

Preferred body temperature was measured in photo-thermal gradients with wooden sides and flooring, housed in a controlled temperature room. Each gradient measured $1.5 \times 0.21 \times 0.23$ m with a sand substrate approximately 2 cm deep. The heat source was provided by both a 275 W heat lamp and a strip of heating tape under the sand at one end of the gradient. This arrangement provided a range of surface temperatures, grading gradually from >50 C directly beneath the lamp to the ambient temperature of the environmental chamber (15 C for species with thermal preferenda below 30 C and 20–25 C for species with higher preferenda). The gradients were covered with galvanized steel screening supported on a wooden frame to prevent lizards from escaping. Additional lighting (fluorescent) was provided from the ceiling of the environmental chamber. All lights and heat strips were turned on at 0600 h and off at 1800 h South Australian Standard Time, except as noted below.

Lizards were placed in gradients at approximately 1500 h on the day before measurement, giving them time to explore the gradient before the beginning of the scotophase. The lizards had no access to food for two days before measurement. Only one lizard occupied each gradient. Body temperatures was taken approximately every two hours during the photophase, commencing at 0900 h and continuing until 1600 h or disappearance of the lizards beneath the sand. During surface active periods, all lizards placed themselves at intermediate positions in the gradient and did not retreat to walls

or corners. The environmental chamber was isolated and the animals were undisturbed by human presence except during the short measurement periods. For larger lizards (>5 g), temperatures were measured cloacally with a quick-registering Schultheis thermometer. For smaller animals, temperatures were taken with a small, sheathed thermocouple connected to a Wescor model TH-65 thermocouple thermometer. During measurements on *Hemiergus* spp., the sand surface was covered with paper towelling and three to four animals were placed in each gradient; they never emerged from under this cover. Body temperatures of *Hemiergus* were estimated by measuring sand temperature under the midpoint of the body. During measurements on *Eremiascincus* and *Hemiergus*, gradient heat lamps and the heat strips were left on and measurements were continued until 2200 h.

Critical thermal limits (non-lethal loss of righting response) were measured according to standard techniques. For measurement of CTMax, animals were first put in an environmental chamber at 35 C for 1 h prior to experimentation. Each animal was then placed in a plastic container with a 250 W incandescent bulb mounted above it, so that body temperature increased approximately 1 C/min. When the animal appeared uncoordinated, it was placed on its back every subsequent minute to determine loss of righting response. When an animal first failed to right, cloacal body temperature was taken immediately with a thermocouple or quick-registering thermometer and the lizard was placed in cool water. All revived within 10 sec and survived indefinitely after the measurement. For determination of CTMin, animals were put at 15 C for 1 h prior to experimentation. Each was placed on aluminum foil or an enamel pan placed on crushed ice. Body temperature fell about 1 C/min and was recorded when the first loss of righting response occurred. Animals were then placed in warm water and all recovered rapidly and survived indefinitely. Each individual was used only once for determination of either CTMin or CTMax, except for *Eremiascincus richardsoni*, for which both measurements were made on a single animal.

The effect of feeding on PBT was determined for *T. rugosa*. Ten animals were fasted for three days and placed singly in gradients. Body temperatures were measured hourly. At 0930–1030 on the second day of the experiment, each animal was fed approximately 20 g (mean = 21.4

TABLE 2. FIELD ACTIVE BODY TEMPERATURES. Means, standard errors and ranges are reported.

Species	N	FBT °C	Reference
<i>Ctenotus atlas</i>	23	34.5 ± 0.83	Pianka, 1969
<i>C. regius</i>	3	36.4 ± 0.41 (35.7–37.1)	This study
<i>C. robustus</i>	3	35.0 ± 0.67 (34.4–36.3)	This study
<i>Egernia whitii</i>	—	33.1 (30.8–33.5)	Heatwole, 1976
	74	34.0 ± 0.37 (31.3–35.6)	Johnson, 1977
<i>Hemiernis decresciensis</i>	8	20.3 ± 0.70 (17.3–23.0)	This study
<i>H. peroni</i>	12	23.6 ± 0.68 (19.2–27.0)	This study
<i>Sphenomorphus kosciuski</i>	4	28.2 ± 0.82 (25.8–29.6)	This study
	37	30.9 (16.9–36.0)	Spellerberg, 1972c
<i>S. quoyi</i>	112	28.1 (22.2–33.9)	Veron and Heatwole, 1970
	42	30.0 (17.4–34.2)	Spellerberg, 1972c
<i>S. tympanum</i>	12	29.3 ± 0.74 (25.2–33.0)	This study
(Cool temperate form)	83	30.2 (16.3–34.5)	Spellerberg, 1972c
<i>Tiliqua rugosa</i>	10	34.3 ± 0.34 (32.4–35.9)	This study
	72	32.7 ± 0.31	Licht, Dawson, Shoemaker and Main, 1966
	—	23.1 to 36.1 ¹	Warburg, 1965

¹ Monthly averages.

g, range = 16.7–26.0) of a puree of bananas, apples and oranges. Animals were weighed before and after feeding to determine intake. Temperatures were subsequently measured hourly from 1100–1700.

RESULTS

Thermal preferences are reported in Table 1. Our measurements extend the range of PBTs previously reported for Australian skinks, with values ranging from 17.6 C (measured diurnally) in *Hemiernis decresciensis* to 35.6 C in *Ctenotus regius*. Values of PBT measured in this study are quite similar to those previously reported for some of these species, indicating that these values are relatively independent of the exact methodology used in their determination (Huey, 1982).

The cryptozoic lizards (*Eremiascincus* spp. and *Hemiernis* spp.) had the lowest PBTs of all species examined. *Eremiascincus* were intermittently surface-active beginning at about 1600 h; *Hemiernis* never emerged from under cover. PBT is greater in the late afternoon and evening than during the day in *E. fasciolatus* and both species of *Hemiernis* (P 's < 0.01, Student's t -tests). The same trend occurred in *E. richardsoni*, but the small sample size prevents it attaining statistical significance. The low PBTs of *Hemiernis* spp. support the suspicion of Licht et al. (1966) that their measurements of PBT of *H. quadrilineatum*

may have been too high because of the high minimum temperature of their gradient (25 C).

Field-active body temperatures measured for these species are reported in Table 2. In general, these are very similar to PBTs, being insignificantly different ($P > 0.2$, t -test) in all species except *H. decresciensis* measured diurnally ($P = 0.01$), *H. peroni* measured diurnally ($P = 0.05$) and *T. rugosa* ($P < 0.01$). In these latter species, FBT exceeded PBT. Field temperatures of *T. rugosa* are reported to vary between 23.1 and 36.1 C throughout the activity season (Warburg, 1965).

Critical thermal limits are reported in Table 3. *Ctenotus* have the greatest CTMax (about 45 C) and the *Hemiernis* spp., the lowest (38.6 C). The CTMin ranged from 3.5 C in *T. rugosa* to 11.4 C in *C. taeniolatus*.

T. rugosa did not significantly change its preferred body temperature after feeding. Mean body temperatures before and after feeding were 31.9 C (± 0.75 S.E., $N = 10$, 70 measurements) and 32.0 C (± 0.83 S.E., $N = 10$, 70 measurements), respectively ($P > 0.5$, paired Students' t -test).

DISCUSSION

Preferred body temperatures of skinks are generally lower than those of most other groups of lizards (Brattstrom, 1965; Licht et al., 1966;

TABLE 3. CRITICAL THERMAL LIMITS AND PREFERRED TEMPERATURES OF AUSTRALIAN SKINKS. Data from this study (mean [N, SE]) unless referenced.

Species	CTMin °C	PBT °C	CTMax °C
<i>Ctenotus regius</i>	8.7 (3, 0.35)	35.6	45.1 (3, 0.29)
<i>C. taeniolatus</i>	11.4 (2, 0.12)	35.3	44.7 (3, 0.24)
<i>C. uber</i>	9.1 (3, 0.53)	35.5	45.5 (3, 0.18)
<i>Egernia cunninghami</i>	4.7 ¹	33.3 ²	41.9 ¹
<i>E. saxatilis</i>	4.5 ¹	34.0 ³	41.8 ¹
<i>E. striolata</i>	6.1 (3, 0.47)	32.7	44.2 (3, 0.13)
<i>E. whitii</i>	4.0 ¹	34.1	42.8 ⁴
<i>Eremiascincus fasciolatus</i>	9.0 (3, 0.50)	24.4	41.2 (3, 0.32)
<i>E. richardsoni</i>	7.3 (1)	27.3	42.0 (1)
<i>Hemiergis decresciensis</i>	6.8 ¹	24.8	38.6 (4, 0.34)
<i>H. peroni</i>	9.6 (2, 0.12)	23.5	38.8 ⁴
<i>Leiopisma entrecasteauxii</i>	2.5 ¹	32.5	42.8 ⁴
<i>L. metallicum</i>	2.7 ¹	29.0 ⁵	40.0 ¹
<i>L. ocellatum</i>	3.0 ¹	30.7 ⁵	40.1 ¹
<i>L. trilineatum</i>	3.0 ¹	31.9 ⁵	43.5 ¹
<i>Pseudemoia spenceri</i>	2.8 ¹	31.0 ⁵	42.3 ¹
<i>Sphenomorphus kosciuskoi</i>	2.5 ¹	29.8	40.2 ¹
<i>S. quoyi</i>	6.0 ¹	28.8	40.8 ⁶
<i>S. tympanum</i>			
Cool temperate form	2.9 ¹	29.6	39.8 ¹
Warm temperate form	6.1 ¹	29.0 ⁷	40.0 ¹
<i>Tiliqua nigrolutea</i>	5.2 ¹	34.8 ⁵	42.5 ¹
<i>T. rugosa</i>	3.5 (3, 0.18)	31.9	43.0 (3, 0.26)

¹ Spellerberg, 1972a.² Licht et al., 1966.³ Heatwole, 1976.⁴ Greer, 1980.⁵ Rawlinson, 1974.⁶ Veron and Heatwole, 1970.⁷ Spellerberg, 1972c.

Avery, 1982). However, not all skinks have low thermal preferenda. *Ctenotus*, for example, are quite thermophilic and have PBTs and FBTs around 35°C (Table 1, this study; Pianka, 1969: mean FBT = 34.6°C for 14 spp.). What is exceptional about skinks is the extraordinary breadth of their thermal preferenda, even within a single group of the subfamily Lygosominae (e.g., the *Sphenomorphus* group). Although the range of values within the family is quite broad, PBT is conservative at the generic level, as has been noted for most lizard genera (Huey, 1982).

For instance, all five species of *Ctenotus* measured have PBTs within 0.6°C of 35.0°C; the three species of *Sphenomorphus* measured by us have PBTs within 0.8°C of 29.0°C. The genera examined here may be ranked in the following order of increasing thermal preference: *Hemiergis*, *Eremiascincus*, *Sphenomorphus*, *Tiliqua*, *Leiopisma*, *Egernia* and *Ctenotus*.

Preferred thermal levels are sometimes influenced by feeding state or by time of day. An increment in PBT after feeding has been reported for several species of reptiles (Lang, 1979;

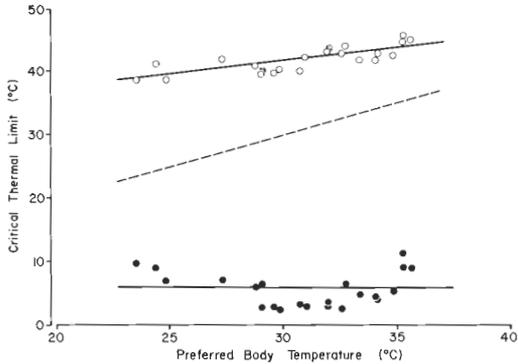


Fig. 1. Preferred body temperature and critical thermal limits of Australian skinks. Data from Table 3. Open circles = CTMax with solid regression line; closed circles = CTMin with mean value of observations; dashed line is PBT isotherm.

Huey, 1982). This increment is generally considered to facilitate digestion and absorption. However, many other species, including lizards, snakes and turtles, do not show such an increment (Huey, 1982). *T. rugosa* falls into this latter group. No generalizations have yet emerged concerning factors, such as phylogenetic relationship or food type, that might account for the differences in post-prandial thermoregulation.

Many species of diurnally-active reptiles will voluntarily select lower body temperatures at night than during the day (Regal, 1967; Huey, 1982), although there are some exceptions. Such a nocturnal decrement has also been demonstrated in the nominally nocturnally-active lizard *Klauberina riversiana* (Regal, 1967). Our data on *Hemiergis* and *Eremiascincus* are the first to show a nocturnal increment in PBT. The timing of this increment coincides with normal activity times of these species. *Hemiergis* are rarely seen active out from under cover, but have been observed abroad in the late afternoon and early evening and are almost never seen during the day (B. Miller, pers. comm.; P. Rawlinson, pers. comm.). *Eremiascincus* are active at dusk and in the early evening (Greer, 1979) and are collected in pit fall traps only at these times (M. Thompson, pers. comm.).

The most interesting thermal relationships observed are those of the cryptozoic genera *Hemiergis* and *Eremiascincus*. The low PBTs of these species make it clear that low FBTs are not imposed on these lizards by habitat pref-

erence but rather are selected. In fact, both species of *Hemiergis* were diurnally collected in the field at temperatures significantly above diurnal PBT. Both *Hemiergis* and *Eremiascincus* prefer temperatures close to the middle of their tolerance range (CTMin to CTMax; Huey and Stevenson, 1979). This pattern is unusual for most lizards, which generally select temperatures closer to CTMax (Brattstrom, 1965; Huey, 1982). The nocturnal thermal safety margins of *Hemiergis* and *Eremiascincus* (=CTMax - PBT, Heatwole, 1970), 13.8-16.8 C, are among the highest reported (Heatwole, 1976; Huey, 1982).

E. fasciolatus is of particular interest because of its desert sand dune habitat, which extends through central Australia and encompasses some of the hottest deserts in the world (Greer, 1979). Diurnal surface temperatures must be very high. The diurnal PBT of this species is, however, among the lowest reported for lizards (21.2 C). Perhaps the lizards burrow through the sand to considerable depths during the day to avoid the heat; perhaps they take advantage of their very considerable thermal safety margin (diurnal: 20.0 C) and tolerate temperatures in excess of preferred levels. Somewhat surprisingly, the lower PBT is not accompanied by an ability to function effectively at lower body temperatures. These lizards are largely incapacitated by cold: their maximal speeds are less than 5 cm/s at 10 C (Huey and Bennett, unpubl.), which is only about 10 C below diurnal PBT. Their righting response is abolished at 9 C. A field study on the activity patterns and body temperatures of this species would be very useful to our understanding of thermoregulatory adaptations of lizards to desert environments.

A detailed analysis of the relationship between PBT or FBT and critical thermal limits is usually difficult for most groups of reptiles, as complete data sets are unavailable and little variability is evident among closely-related genera. We now have sufficient data for such an analysis for Australian skinks (Table 3, Fig. 1). Data reported are measurements made on adult animals during the austral spring or summer; if more than one critical temperature is available, the lowest CTMin and the highest CTMax are used. CTMax increases with PBT according to the following relationship:

$$\text{CTMax} = 28.3 + 0.439 \text{ PBT} \\ (N = 22, r^2 = 0.62, P < 0.001)$$

where CTMax and PBT are in °C. CTMax does not, however, parallel PBT, that is, the slope is

significantly lower than 1.0 ($P < 0.001$ by t-test, $SE\ b = 0.0765$). CTMin is not significantly dependent on thermal preferendum:

$$CTMin = 7.78 - 0.073\ PBT \\ (N = 22, r^2 = 0.009, P = 0.67)$$

where CTMin and PBT are in °C. Mean CTMin is $5.5\ C \pm 0.58\ SE$. As a consequence of these relationships, the differential between CTMax and CTMin increases with increasing thermal preferendum:

$$(CTMax - CTMin) = 20.9 + 0.499\ PBT \\ (N = 22, r^2 = 0.38, P = 0.003).$$

These relationships also hold for comparisons involving FBTs as well as PBTs, as they are quite similar in this group of lizards (Licht, Dawson, Shoemaker and Main, 1966; Tables 1 and 2, this study) ($N = 10$; CTMax vs FBT $r^2 = 0.70$, $P = 0.003$; CTMin vs FBT $r^2 = 0.05$; [CTMax - CTMin] vs FBT $r^2 = 0.45$, $P = 0.03$). These data demonstrate that the thermal tolerance range among these species is not constant. Critical thermal limits do not parallel either PBT or FBT. Rather, more thermophilic species have a broader tolerance range than the less thermophilic ones. Furthermore, they also regulate at body temperatures closer to their CTMax, so that they have smaller thermal safety margins (Heatwole, 1970) than do more cryophilic species.

The thermal tolerance of Australian skinks has been implicated as an important factor in their biogeographic distribution. Greer (1980) reported that cryptozoic or nocturnally-active skinks from the cooler periphery of the continent all have CTMax below 39.5 C. Species of similar habits in the interior and all diurnally-active, surface dwelling skinks regardless of habitat have CTMax above this temperature. Additional observations on CTMax in this study conform to Greer's division: *Ctenotus* spp., *Egernia striolata* and *T. rugosa* (diurnally-, surface-active species) and *Eremiascincus* spp. (semi-fossorial species from the arid interior) all have CTMax above 39.5 C and *H. decresciensis* (cryptozoic species from the coastal area) has a CTMax of 38.6 C (Table 3). In contrast, PBT appears more related to habit than habitat: all diurnally-active surface-dwelling species examined have PBTs $> 28\ C$ and cryptozoic forms, $< 28\ C$ (Tables 1 and 3). Spellerberg (1972a) reported that CTMin is an important distributional correlate, with CTMin being lower in Australian lizards inhabiting cooler environ-

ments. Statistical analysis of the data reported by Spellerberg for skinks and the new data in this study (Table 3) support this general correlation. Species were assigned to one or more of the zoogeographic subregions specified by Spellerberg (Eyrean, Bassian warm, Bassian cool, Bassian cold) and their CTMin compared. Analysis of variance indicated a significant difference among groups ($F_{3,41} = 7.08$, $P < .001$) and subsequent Student-Newman-Keuls analysis indicated that CTMin values of Eyrean and Bassian warm species were greater than those of Bassian cool and cold species, although no significant differences occur within either of these pairs. These data on thermal tolerance indicate that there are associations between critical thermal limits and the distribution of skink species within Australia. Whether these correlations are significant determinants of distribution is not known.

ACKNOWLEDGMENTS

We thank D. Bradford, C. Daniels, R. Huey, K. John-Alder, B. Miller, T. Schwaner and M. Thompson for assistance in collecting animals. R. Huey also helped with laboratory measurements and critically reviewed the manuscript. We thank B. Firth for access to his thermal gradients and R. Seymour and the Department of Zoology at the University of Adelaide for laboratory facilities. Animals were collected under South Australian National Parks and Wildlife Permit No. 918 and New South Wales National Parks and Wildlife Permit No. A216 to AFB. This study was supported by N.S.F. Grant PCM81-02331 to AFB.

LITERATURE CITED

- AVERY, R. A. 1982. Field studies of body temperatures and thermoregulation, p. 93-166. In: *Biology of the Reptilia*, vol. 12. C. Gans and F. H. Pough (eds.). Academic Press, New York, New York.
- BRATTSTROM, B. H. 1965. Body temperatures of reptiles. *Am. Midl. Nat.* 73:376-422.
- . 1971. Critical thermal maximum of some Australian skinks. *Copeia* 1971:554-557.
- COGGER, H. G. 1983. Reptiles and amphibians of Australia. A. H. & A. W. Reed Pty. Ltd., Sydney, New South Wales, Australia.
- , E. E. CAMERON AND H. M. COGGER. 1983. Zoological catalogue of Australia. 1. Amphibia and Reptilia. Australian Govt. Publ. Service, Canberra, Australia.
- GREER, A. E. 1976. A most successful invasion. *The*

- diversity of Australia's skinks. *Aust. Nat. Hist.* 18: 428-433.
- . 1979. A phylogenetic subdivision of Australian skinks. *Rec. Aust. Mus.* 32:339-371.
- . 1980. Critical thermal maximum temperatures in Australian scincid lizards: their ecological and evolutionary significance. *Aust. J. Zool.* 28:91-102.
- HEATWOLE, H. 1970. Thermal ecology of the desert dragon *Amphibolurus inermis*. *Ecol. Monogr.* 40:425-457.
- . 1976. *Reptile Ecology*. University of Queensland Press, St Lucia, Queensland, Australia.
- HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles, p. 25-91. *In: Biology of the Reptilia*, vol. 12. C. Gans and F. H. Pough (eds.). Academic Press, New York, New York.
- , AND R. D. STEVENSON. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19:357-366.
- JENKINS, R., AND R. BARTELL. 1980. *A field guide to reptiles of the Australian high country*. Inkata Press, Melbourne, Victoria, Australia.
- JOHNSON, C. R. 1977. Thermoregulation in four Australian lizards of the genus *Egernia* (Sauria: Scincidae). *Zool. J. Linn. Soc.* 60:381-390.
- LANG, J. W. 1979. Thermophilic response of the American alligator and the American crocodile to feeding. *Copeia* 1979:48-59.
- LICHT, P., W. R. DAWSON AND V. H. SHOEMAKER. 1966. Heat resistance of some Australian lizards. *Copeia* 1966:162-169.
- , ———, AND A. R. MAIN. 1966. Observations on the thermal relations of western Australian lizards. *Copeia* 1966:97-110.
- PIANKA, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* 50:1012-1030.
- RAWLINSON, P. A. 1974. Biogeography and ecology of the reptiles of Tasmania and the Bass Strait area, p. 291-338. *In: Biogeography and ecology of Tasmania*. W. D. Williams (ed.). W. Junk Publishers, The Hague, The Netherlands.
- REGAL, P. J. 1967. Voluntary hypothermia in reptiles. *Science* 155:1551-1553.
- SPELLERBERG, I. F. 1972a. Temperature tolerances of southeast Australian reptiles examined in relation to reptile thermoregulatory behaviour and distribution. *Oecologia* 9:23-46.
- . 1972b. Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. I. The environment and lizard critical temperatures. *Ibid.* 9: 371-383.
- . 1972c. Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. II. Physiological aspects of thermoregulation. *Ibid.* 9:358-398.
- . 1972d. Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. III. Behavioural aspects of thermoregulation. *Ibid.* 11:1-16.
- VERON, J., AND H. HEATWOLE. 1970. Temperature relations of the water skink, *Sphenomorphus quoyi*. *J. Herpetol.* 4:141-153.
- WARBURG, M. R. 1965. The influence of ambient temperature and humidity on the body temperature and water loss from two Australian lizards, *Tiliqua rugosa* (Gray) (Scincidae) and *Amphibolurus barbatus* Cuvier (Agamidae). *Aust. J. Zool.* 13:331-350.
- WILSON, K. J. 1974. The relationship of oxygen supply for activity to body temperature in four species of lizards. *Copeia* 1974:920-934.

SCHOOL OF BIOLOGICAL SCIENCES, UNIVERSITY OF CALIFORNIA, IRVINE, CALIFORNIA 92717 AND DEPARTMENT OF BIOLOGICAL SCIENCES, RUTGERS UNIVERSITY, PISCATAWAY, NEW JERSEY 08854. Accepted 1 May 1985.