

## Australian Geckos Do Not Display Diel Variation in Thermoregulatory Behavior

MICHAEL J. ANGILLETTA JR. AND YEHUDAH L. WERNER

Body temperature ( $T_b$ ) influences almost every aspect of a reptile's physiology and behavior (for reviews, see Huey, 1982; Lillywhite, 1987). For example,  $T_b$  can alter both auditory capacity (Werner, 1976, 1983) and locomotory performance (Bennett, 1980, 1990), thus facilitating or impairing escape from and defense against predators (e.g., Christian and Tracy, 1981; Hertz et al., 1982; Goode and Duvall, 1989), prey capture (Greenwald, 1974), and prey handling (Van Damme et al., 1991). Energy available for allocation to growth and reproduction is determined by digestive and metabolic processes, both of which are temperature-dependent (Bennett and Dawson, 1976; Waldschmidt et al., 1986; Van Damme et al., 1991). In viviparous species, the development of offspring depends on the  $T_b$  of the gravid mother (Bull, 1980). Thus,  $T_b$  can have both direct and indirect consequences for fitness. For many physiological processes (e.g., locomotion, feeding, digestion), the rate of function is maximal over some range of  $T_b$ s and decreases rapidly above and below this range (Huey, 1982).

Field studies of thermoregulation (e.g., Peterson, 1987; Christian and Weavers, 1996) indicate that many reptiles maintain relatively high and constant  $T_b$ s during activity. Presumably, thermoregulatory behavior allows animals to function over a range of  $T_b$ s that is conducive to the requisite physiological processes (e.g., locomotion, digestion). However, field  $T_b$ s do not indicate temperature preference. For many reptiles, tropical environments may provide stable thermal climates such that a narrow range of  $T_b$ s may be achieved with little effort (Shine and Madsen, 1996). In other cases, individuals may accept  $T_b$ s that are higher or lower than preferred temperatures due to constraints on their thermoregulation imposed by the environment (Huey and Slatkin, 1976). Clearly, field  $T_b$ s cannot be strictly interpreted as measures of  $T_b$  preferences in reptiles.

Preferred body temperature (Licht et al., 1966) has been used as an estimate of body temperature preferences in reptiles. Preferred body temperature ( $T_p$ ) is the  $T_b$  maintained by an organism free from all ecological constraints and is measured in a laboratory thermal gradient that provides a full range of equally accessible thermal environments. Measures of  $T_p$  are use-

ful because they indicate the temperature that an organism tries to attain during thermoregulation in nature (Hertz et al., 1993). Integrated measures of  $T_p$  and  $T_b$  have shown that  $T_p$  can provide information on temperature preferences of field-active animals (Christian and Bedford, 1995; Christian and Weavers, 1996). Additionally,  $T_p$  often reflects the temperature at which physiological processes are optimized (Dawson, 1975; Beiting and Fitzpatrick, 1979; Bauwens et al., 1995).

Nocturnal lizards of the family Gekkonidae tend to have bimodal distributions of  $T_b$ ; high  $T_b$ s during the inactive diurnal period and low  $T_b$ s during the active nocturnal period (Table 1). Although most activity occurs at night, many species actively thermoregulate during the day (Werner and Whitaker, 1978; Avery, 1982). High daytime  $T_b$ s may facilitate predator-avoidance by inactive geckos. Low nighttime  $T_b$ s reduce locomotory performance (Huey et al., 1989; Autumn et al., 1994), but they may also confer advantages to an ectotherm, including reduced energetic costs of locomotion (Bennett and John-Alder, 1984) and maintenance (Bennett and Dawson, 1976; Niewiarowski and Waldschmidt, 1992). In the nocturnal gecko *Teratoscincus przewalskii*, sprint speed is submaximal at  $T_b$ s experienced during activity, but the metabolic cost of running is substantially decreased (Autumn et al., 1994).

Werner et al. (1996) hypothesized that some geckos possess dual  $T_b$  preferences. Indeed, thermoregulatory rhythms are common in reptiles (for review, see Underwood, 1992). Many species of diurnal lizards, including anguids (e.g., Regal, 1967), iguanians (e.g., Engbretson and Hutchison, 1976; Roth and Ralph, 1976; Cowgell and Underwood, 1979), lacertids (e.g., Spellerberg, 1974; Rismiller and Heldmaier, 1982), scincids (e.g., Myhre and Hammel, 1969), and xantusiids (e.g., Regal, 1967) prefer lower  $T_b$ s during scotophase. However, the extent to which lower nighttime  $T_b$ s of geckos reflect a distinct preference or a thermal constraint is unclear. Although data on field  $T_b$ s of geckos are abundant, these data are usually reported without quantitative data on temperature availability. Only a few studies (Sievert and Hutchison, 1988; Gil et al., 1994; Autumn and DeNardo, 1995) exist in which  $T_p$ s of geckos

TABLE 1. MEAN DAYTIME ( $DT_b$ ) AND NIGHTTIME ( $NT_b$ ) BODY TEMPERATURES OF GECKOS ACTIVE IN THE FIELD. Standard error or range is in parentheses after  $T_b$ . The list contains only those species for which all information was available.

| Species                            | $DT_b$ (C)   | n   | $NT_b$ (C)   | n  | Source  |
|------------------------------------|--------------|-----|--------------|----|---|
| <i>Christinus marmoratus</i>       | 19.6 (0.72)  | 5   | 14.1 (0.27)  | 7  | Froudust, 1970                                  |
| <i>Gehyra punctata</i>             | 32.9 (0.42)  | 7   | 20.6 (2.82)  | 5  | Froudust, 1970                                  |
| <i>Gehyra variegata</i>            | 26.6         | 15  | 20.8 (1.53)  | 6  | Werner and Werner, unpubl. data; Williams, 1965 |
| <i>Hoplodactylus maculatus</i>     | 22.1 (15–33) | 101 | 11.3 (10–13) | 15 | Werner and Whitaker, 1978                       |
| <i>Phyllodactylus kofordi</i>      | 29.5 (0.50)  | 3   | 21.9 (0.37)  | 17 | Werner et al., 1996                             |
| <i>Phyllodactylus microphyllus</i> | 26.1 (0.77)  | 28  | 20.4 (0.24)  | 33 | Werner et al., 1996                             |
| <i>Phyllodactylus reissi</i>       | 29.8 (0.64)  | 5   | 22.3 (0.48)  | 12 | Werner et al., 1996                             |
| <i>Strophurus spinigerus</i>       | 23.1 (1.25)  | 14  | 16.0 (0.98)  | 3  | Froudust, 1970                                  |
| <i>Underwoodisaurus milii</i>      | 22.9 (1.62)  | 4   | 19.4 (2.96)  | 5  | Froudust, 1970; Williams, 1965                  |

were measured during both photophase and scotophase.

In this study, the  $T_p$  of geckos was measured to determine whether low nighttime  $T_b$ s reflect temperature preferences, rather than environmental constraints. We hypothesized that geckos possess dual  $T_b$  preferences, with high  $T_p$ s during the day and low  $T_p$ s at night. This hypothesis was tested by measuring 24-h  $T_b$  selection of six species of Australian geckos in a laboratory thermal gradient.

#### MATERIAL AND METHODS

**Study organisms.**—Six species of geckos were collected throughout Western Australia (WA) by YLW during fall 1993. Four of the six species are suspected of being composite; therefore, individuals were collected from well-defined populations. Voucher specimens have been deposited in the Zoological Museum of the Hebrew University of Jerusalem (identification numbers are reported in parentheses). *Christinus marmoratus* (HUI-R 18954–18965) were collected during September/October 1993 from trees and rocks, between Bunbury and Denmark, southwestern WA. *Gehyra punctata* (HUI-R 18909–18922) were taken on 17–18 September 1993 from under small slabs on one large granite outcrop between Gallowa and Barnong Station, west-central WA. *Gehyra variegata* (HUI-R 18923–18933) were collected during September/October 1993 from granite outcrops 6–17 km north of Mt. Magnet township, central WA. *Oedura marmorata* (HUI-R 18934–18944) were collected during September/October 1993, from granite outcrops 6–8 km north of Mt. Magnet township, central WA. *Oedura reticulata* (HUI-R 18949–18953) were collected during 1–5 November 1993, in eucalyptus groves in the Bungalbin Hills area, approximately 100 km north-

east of Southern Cross township, southern WA. *Nephrurus stellatus* (HUI-R 18945–18948) were collected on 3 November 1993 on a sand track in the Bungalbin Hills area, approximately 100 km northeast of Southern Cross township, southern WA.

**Animal care and procedure.**—Once collected, all geckos were transported to the University of Western Australia, Nedlands, where they were maintained at 25 C with a 12:12 h light cycle. Groups of 2–5 conspecifics were housed in 38-liter aquaria with a sand substrate and pieces of tree bark for refuge. All animals had access to mealworms and water ad libitum. On 18 December 1993, the geckos were transported by air to the California Academy of Sciences, San Francisco, where they were maintained temporarily until they could be accepted in Philadelphia. In February 1994, the geckos were transported to the University of Pennsylvania, Philadelphia, where they were kept under conditions described above. There, the geckos were initially fed wax moth larvae and crickets and later meal worms, three times per week.

The thermal gradient was 1 m in length and divided into five parallel tracks, each 25.4 cm wide. The walls, separating adjacent tracks, were opaque plexiglass, and the floor was 0.64-cm thick aluminum, covered with 1 cm of fine sand. The substrate was heated at one end by three incandescent lights, underneath the gradient and shielded to prevent the confounding effects of light as a heat source (see Sievert and Hutchison, 1988, 1989). The opposite end of the gradient was cooled by a chilled water bath in direct contact with the metal floor. The entire set-up was contained in an environmental chamber at 25 C, resulting in a stable range of substrate temperatures from 5–45 C. Temperatures at the extremes of the gradient were beyond the min-

imum and maximum temperatures chosen by the individuals in the experiment.

Lizards were fasted for 48 h prior to being placed in the thermal gradient. Individuals were fitted with a copper-constantan thermocouple (0.5-mm diameter) inserted through the cloaca into the rectum and secured with a harness of cloth tape. The thermocouple wires were 92 cm long, allowing movement throughout the gradient. The harnesses did not come in contact with the legs and did not seem to constrain the mobility of the lizards. Lizards were placed in the gradient between 1200 h and 1300 h and allowed to habituate to the experimental conditions until the onset of photophase at 0800 h the next day, to reduce the probability of measuring acute thermal preferences (see Reynolds and Casterlin, 1979). Body temperature was recorded each minute and averaged hourly by a Campbell data logger (Model CR10) for a period of 24 h, beginning at the onset of the first complete photophase and ending at onset of the next photophase. Trials in which thermocouple wires became tangled or detached were excluded from the dataset.

*Statistical analysis.*—The experiment involved repeated measures of the  $T_b$  of each individual; therefore a repeated-measures analysis was used. The analysis of variance with repeated measures (ANOVAR) assumes that successive measurements within individuals are not correlated (Potvin et al., 1990). We could not use Mauchly's test of sphericity to assess whether the data met this assumption because the variance-covariance matrix was nearly singular. Therefore, we used the multivariate analysis of variance with repeated measures (MANOVAR) to test for the between-subjects effect of species and the within-subjects effect of hour on  $T_p$ . MANOVAR makes fewer assumptions about the form of the covariance matrix (Potvin et al., 1990). However, MANOVAR still assumes that the dependent variables (i.e., the hourly  $T_b$ s) are normally distributed and that their variances and covariances are homogeneous (compound symmetry of the variance covariance matrix). We were unable to assess adequately the normality of the dependent variables due to the sample sizes, but the  $F$ -test is usually robust to deviations from normality (Lindeman, 1974). The singularity of the variance-covariance matrix precluded use of the multivariate Box M test to determine whether the assumption of compound symmetry was met. Therefore, we examined each dependent variable separately for homogeneity of variance using the univariate Cochran's test. Where the assumption was

violated, we examined the data to ensure that there were no correlations between the means and the variances, to avoid spurious significant effects.

To determine whether  $T_p$  differed between photophase and scotophase, we made planned comparisons between  $T_p$ s selected during photophase and those selected during scotophase for each species. We made the same comparison using the data for all six species to achieve greater statistical power. The Tukey-Kramer method was used to make unplanned comparisons when significant effects were found in the MANOVAR. The Tukey-Kramer method corrects the critical values and standard errors for unequal sample sizes among groups (Sokal and Rohlf, 1981). We accepted a type I error rate of 0.05 for all statistical tests.

## RESULTS

Data were obtained for a total of 36 geckos, ranging from three to nine individuals per species. The variances were homogeneous for 18 of 24 of the dependent variables. Log-transformation tended to increase the heterogeneity of the variances, such that untransformed data were used in the MANOVAR. In each case in which the variances were heterogeneous, there were no correlations between the means and variances. The results of the MANOVAR demonstrated no significant effect of hour on  $T_p$  (Wilk's  $\lambda = 0.13$ ,  $F = 2.28$ ,  $df = 23$ ,  $P = 0.11$ ). The effect of species on  $T_p$  was highly significant (MS = 1353.86,  $F = 6.98$ ,  $df = 5$ ,  $P = 0.0002$ ). No significant interaction was found between species and hour (Wilk's  $\lambda = 0.001$ ,  $F = 1.06$ ,  $df = 115$ ,  $P = 0.42$ ).

Planned comparisons indicated that there was no significant difference between  $T_p$  during photophase and  $T_p$  during scotophase for all species (MS = 15.66,  $df = 1$ ,  $F = 0.37$ ,  $P = 0.54$ ). When the same comparisons were made for each species independently, none was significant. Therefore, mean  $T_p$ s for the 24-h cycle are reported in addition to mean  $T_p$ s of each species during photophase and scotophase (Table 2). For the remainder of the text, all means reported are the grand means of the mean  $T_p$ s of individuals,  $\pm$  one standard error.

Unplanned comparisons among the six species of geckos revealed significant differences in  $T_p$ . *Gehyra punctata* and *G. variegata* had significantly higher  $T_p$ s than both *Christinus marmoratus* and *Nephrurus stellatus*. No other species differed significantly in  $T_p$ .

TABLE 2. MEAN  $T_p$ s FOR THE SIX SPECIES OF AUSTRALIAN GECKOS. Mean  $T_p$ s are presented for the hours of photophase ( $DT_p$ ), scotophase ( $NT_p$ ), and the complete diel cycle ( $T_p$ ). The means reported are the grand means of the mean  $T_p$ s of the individuals. Standard error is in parentheses after  $T_p$ .

| Species                      | $DT_p$ (C)   | $NT_p$ (C)   | $T_p$ (C)    | n |
|------------------------------|--------------|--------------|--------------|---|
| <i>Gehyra punctata</i>       | 33.75 (0.93) | 33.21 (1.15) | 33.48 (0.98) | 9 |
| <i>Gehyra variegata</i>      | 34.00 (0.74) | 33.45 (0.80) | 33.72 (0.69) | 9 |
| <i>Oedura marmorata</i>      | 30.97 (2.70) | 32.98 (1.14) | 31.97 (1.86) | 5 |
| <i>Oedura reticulata</i>     | 31.01 (0.56) | 29.82 (0.77) | 30.41 (0.65) | 5 |
| <i>Christinus marmoratus</i> | 27.59 (1.69) | 27.83 (1.29) | 27.71 (1.33) | 5 |
| <i>Nephruirus stellatus</i>  | 24.19 (3.21) | 25.95 (0.89) | 25.07 (2.05) | 3 |

#### DISCUSSION

None of the six species of geckos displayed diel variation in  $T_p$ . Even when data for all six species were combined, no significant differences in  $T_p$  were observed between photophase and scotophase. Previously, Autumn and DeNardo (1995) noted no significant difference between  $T_p$  of *Eublepharis macularius* measured during photophase and scotophase. However, diel variation in  $T_p$  of other lizards is common. For example, in the Moorish gecko, *Tarentola mauritanica*,  $T_p$  gradually increased during photophase and decreased during scotophase (Gil et al., 1994). In contrast,  $T_p$  of *Gecko gecko* (Sivert and Hutchison, 1988) was significantly higher for 2 h during scotophase (2400–0200 h) than for 1 h during photophase (1300–1400 h). In diurnal lizards,  $T_p$  decreases during scotophase (reviewed by Underwood, 1992). A decrease in  $T_p$  at the onset of scotophase may encourage diurnal lizards to seek cooler shelters as photophase draws to an end (Underwood, 1992). In the geckos examined here, no such trend in  $T_p$  was evident.

It is necessary to establish that the lack of a diel cycle of  $T_p$  observed in this study was not an artifact of acclimation to laboratory conditions. Lizards, including geckos, can undergo seasonal acclimatization of thermoregulatory behavior (Christian et al., 1983; Christian and Bedford, 1995; Sivert and Hutchison, 1989). These factors may affect diel cycles of  $T_p$  in lizards (e.g., Rismiller and Heldmaier, 1982), but their effects on  $T_p$  in geckos is unknown. One way to assess whether the thermoregulatory behavior we observed was representative of natural behavioral patterns is to compare the  $T_p$ s we observed with those reported for the same species by other investigators. Licht et al. (1966) measured the  $T_p$ s of *G. punctata*, *G. variegata*, and *C. marmoratus* during photophase. The  $T_p$ s reported by the two studies were not significantly different for any of the species (*G. punctata*:  $t = 1.14$ ,  $P > 0.05$ ; *G. variegata*:  $t = 2.29$ ,  $P$

$> 0.05$ ; *C. marmoratus*:  $t = 0.08$ ,  $P > 0.05$ ). Thus, the behavior observed in our study is consistent with that observed elsewhere and is unlikely to be due to the conditions under which our animals were maintained prior to the experiment.

Although geckos frequently experience low body temperatures during nighttime activity, it is clear that they possess higher temperature preferences than the  $T_b$ s would indicate. Preferred body temperatures of geckos are typically higher than nighttime  $T_b$ s ( $NT_b$ s). The  $T_p$ s of three species of geckos during scotophase were 3.2–4.2 C higher than  $T_b$ s for the same species (Huey et al., 1989). Likewise, the  $T_p$  of *Tarentola mauritanica* ( $31.56 \pm 0.17$  C,  $n = 151$ ) was significantly higher than  $T_b$ s during activity in the field ( $T_b = 24.8 \pm 0.51$  C,  $n = 30$ ; Gil et al., 1994). In our study,  $T_p$  was relatively high ( $> 30$  C) for all species, except *C. marmoratus* ( $27.71 \pm 1.33$  C) and *Nephruirus stellatus* ( $25.07 \pm 2.05$  C). We compared  $T_p$  of *G. punctata*, *G. variegata*, and *C. marmoratus* to  $T_b$ s obtained from the literature (Table 1). The  $T_p$  of *G. punctata* was not different ( $t = 0.59$ ,  $P > 0.05$ ) from the daytime  $T_b$  ( $DT_b$ ) for this species but was much higher ( $t = 13.08$ ,  $P < 0.001$ ) than the nighttime  $T_b$  ( $NT_b$ ). The  $T_p$  of *G. variegata* was significantly higher ( $t = 10.34$ ,  $P < 0.001$ ;  $t = 18.76$ ,  $P < 0.001$ ) than both  $DT_b$  and  $NT_b$ . Preferred body temperature of *C. marmoratus* was also significantly higher ( $t = 6.08$ ,  $P < 0.01$ ;  $t = 10.20$ ,  $P < 0.001$ ) than both  $DT_b$  and  $NT_b$ . Further, geckos can attain relatively high  $NT_b$ s in the presence of unusual sources of heat. For example, two species of Hawaiian geckos attained  $NT_b$ s that were similar to  $DT_b$ s, by basking near electric lamps and inside deep rock crevices (Werner, 1990).

Although geckos do not prefer  $T_b$ s experienced during nighttime activity, they do possess lower  $T_p$ s than diurnal lizards (Huey et al., 1989). We compared  $T_p$ s published for species of gekkonids with those for iguanians and diurnal scincids (Table 3). The homogeneity of

TABLE 3. MEAN  $T_p$  OF DIURNAL AND NOCTURNAL LIZARDS. Mean  $T_p$  is the grand mean of the  $T_p$ s of the species, and n is the number of species.

| Taxon     | $T_p$ (C) | SE   | n  | Sources                        |
|-----------|-----------|------|----|--------------------------------|
| Iguanians | 36.2      | 0.44 | 21 | 2, 4, 6, 9, 10, 11, 12, 13, 15 |
| Gekkonids | 31.0      | 0.72 | 17 | 5, 7, 8, 12, 14, 16            |
| Scincids  |           |      |    |                                |
| Diurnal   | 33.2      | 0.33 | 24 | 1, 3, 9, 12                    |
| Nocturnal | 25.0      | 0.81 | 4  | 3                              |

(1) Bartholomew et al., 1965; (2) Bennett, 1972; (3) Bennett and John-Alder, 1986; (4) Bradshaw and Main, 1968; (5) Brattstrom, 1965; (6) Dewitt, 1967; (7) Gil et al., 1994; (8) Huey et al., 1989; (9) Licht, 1964; (10) Licht, 1968; (11) Licht and Basu, 1967; (12) Licht et al., 1966; (13) Moberly, 1968; (14) Sievert and Hutchison, 1988; (15) Wilson, 1971; (16) present study.

variances assumption required by ANOVA was not upheld (Bartlett's statistic = 6.84,  $df = 2$ ,  $P < 0.05$ ), so the nonparametric Kruskal-Wallis test was used in the analysis. The mean  $T_p$  of gekkonid species is significantly lower ( $\chi^2 = 14.42$ ,  $df = 2$ ,  $P < 0.001$ ) than those of diurnal lizards. We hypothesize that a decrease in the  $T_p$  of geckos was associated with the evolution of nocturnality. An analysis of changes in  $T_p$  and activity patterns in lizards, using comparative methods (Harvey and Pagel, 1991), would be a fruitful undertaking and would allow one to explore the validity of this hypothesis. Interestingly, the mean  $T_p$  of nocturnal scincids is significantly lower ( $t = 9.15$ ,  $df = 25$ ,  $P < 0.001$ ) than that of diurnal scincids (Table 3). The fact that lower  $T_p$ s are associated with nocturnality in both geckos and scincids is consistent with the notion that  $T_p$  is linked to activity pattern in lizards.

If geckos have evolved lower thermal preferences in response to nocturnal activity, it would seem that this response was only partial. The  $T_p$ s of geckos are typically higher than  $T_p$ s experienced while nocturnally active. The lack of diel variation in  $T_p$  of most geckos and thermoregulation during the day suggest that any response to the thermal conditions imposed by nocturnality may be a compromise between activities during the cooler conditions of scotophase and the warmer conditions of photophase. Data for three species of *Ptyodactylus*, which differ in their activity patterns, is consistent with the hypothesis that  $T_p$  of geckos is influenced by both daytime and nighttime activities (Arad et al., 1989). The diurnal *P. puisieuxi* had the highest  $T_p$  ( $33.5 \pm 0.67$  C,  $n = 5$ ), and the nocturnal *P. hasselquistii* had the lowest  $T_p$  ( $28.7 \pm 0.41$  C,  $n = 17$ ), whereas the  $T_p$  of *P. guttatus*, which is active diurnally and nocturnally, was intermediate ( $30.9 \pm 0.76$ ,  $n = 10$ ). Activities such as

digestion and locomotion to avoid predators may constrain geckos from a complete adaptation of their  $T_p$  to nighttime temperatures and force an evolutionary compromise. Attempts to test hypotheses about the coadaptation of physiological performance and thermoregulatory behavior in geckos will benefit from careful consideration of the natural patterns of activity for the species in question.

#### ACKNOWLEDGMENTS

We thank the Western Australian Museum for hospitality and advice; N. Werner for indispensable help on all collecting expeditions; P. Withers, A. Roberts, and S. Davies for help with field expeditions; Y. Martin for animal care in Australia; A. Bauer and J. Vindum for vital help in bridging Perth and Philadelphia; A. Angilletta, P. Igic, J. Mayr, and P. Nealen for assistance with handling geckos during the study; P. Niewiarowski for use of his data logger; A. Dunham for advice on several issues, including the design of the thermal gradient; S. Beaupre, P. Nealen, P. Petraitis, and J. Roper for statistical advice; J. Saunders for partial personal support of YLW, materials, and other logistic support (research award DC-00510 of NIDCD); and S. Beaupre, B. Casper, P. Nealen, P. Petraitis, R. Winters, and three anonymous reviewers for improving previous versions of the manuscript. Animal collection and holding in Western Australia and export to the United States occurred under permits SF001105 from the Department of Conservation and Land Management of Western Australia and PWS-P935483 from the Australian Nature Conservation Agency, respectively. All work was performed in accordance with the regulations and recommendations of the Institutional Animal Care and Use Committee of the University of Pennsylvania.

#### LITERATURE CITED

- ARAD, Z., P. RABER, AND Y. L. WERNER. 1989. Selected body temperature in diurnal and nocturnal forms of *Ptyodactylus* (Reptilia: Gekkoninae) in a photothermal gradient. *J. Herpetol.* 23:103-108.
- AUTUMN, K. AND D. F. DENARDO. 1995. Behavioral thermoregulation increases growth rate in a nocturnal lizard. *Ibid.* 29:157-162.
- , R. B. WEINSTEIN, AND R. J. FULL. 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiol. Zool.* 67: 238-262.
- 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.

- BARTHOLOMEW, G. A., V. A. TUCKER, AND A. K. LEE. 1965. Oxygen consumption, thermal conductance, and heart rate in the Australian skink *Tiliqua scincoides*. *Copeia* 1965:169-173.
- BAUWENS, D., T. GARLAND, A. M. CASTILLA, AND R. VAN DAMME. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49:848-863.
- BEITINGER, T. L., AND L. C. FITZPATRICK. 1979. Physiological and ecological correlates of preferred temperature in fish. *Am. Zool.* 19:319-329.
- BENNETT, A. F. 1972. The effect of activity on oxygen consumption, oxygen debt, and heart rate in the lizards *Varanus gouldii* and *Sauromalus hispidus*. *J. Comp. Physiol.* 79:259-280.
- . 1980. The thermal dependence of lizard behaviour. *Anim. Behav.* 28:752-762.
- . 1990. Thermal dependence of locomotor capacity. *Am. J. Physiol.* 250:R253-R258.
- , AND W. R. DAWSON. 1976. Metabolism, p. 127-224. *In: Biology of the Reptilia*. Vol. 5. C. Gans and W. R. Dawson (eds.). Academic Press, New York.
- , AND H. B. JOHN-ALDER. 1984. The effect of body temperature on the locomotory energetics of lizards. *J. Comp. Physiol.* B155:21-27.
- , AND ———. 1986. Thermal relations of some Australian skinks (Sauria: Scincidae). *Copeia* 1986: 57-64.
- BRADSHAW, S. D., AND A. R. MAIN. 1968. Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. *J. Zool. Lond.* 154:193-221.
- BRATTSTROM, B. H. 1965. Body temperatures of reptiles. *Am. Midl. Nat.* 73:376-422.
- BULL, J. J. 1980. Sex determination in reptiles. *Q. Rev. Biol.* 55:3-21.
- CHRISTIAN, K. A., AND G. S. BEDFORD. 1995. Seasonal changes in thermoregulation in the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. *Ecology* 76:124-132.
- , AND C. R. TRACY. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* 49:218-223.
- , AND B. W. WEAVERS. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecol. Monogr.* 66:139-157.
- , C. R. TRACY, AND W. P. PORTER. 1983. Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology* 64:463-468.
- COWGELL, J., AND H. UNDERWOOD. 1979. Behavioral thermoregulation in lizards: a circadian rhythm. *J. Exp. Zool.* 210:189-194.
- DAWSON, W. R. 1975. On the physiological significance of the preferred body temperatures of reptiles, p. 443-473. *In: Perspectives in biophysical ecology*. D. M. Gates and R. B. Schmerl (eds.). Springer-Verlag, Berlin, Germany.
- DEWITT, C. B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. *Physiol. Zool.* 40:49-66.
- ENGBRETSON, G. A., AND V. H. HUTCHISON. 1976. Parietectomy and thermal selection in the lizard *Sceloporus magister*. *J. Exp. Zool.* 198:29-38.
- FROUDIST, J. 1970. Thermoregulation in geckos, with respect to its possible influence on nocturnal habits. Unpubl. bachelor's thesis, Univ. of Western Australia, Nedlands.
- GIL, M. J., F. GUERRERO, AND V. PEREZ-MELLADO. 1994. Diel variation in preferred body temperatures of the Moorish gecko *Tarentola mauritanica* during summer. *Herpetol. J.* 4:56-59.
- GOODE, M. J., AND D. DUVAL. 1989. Body temperature and defensive behaviour of free-ranging prairie rattlesnakes, *Crotalus viridis viridis*. *Anim. Behav.* 38:360-362.
- GREENWALD, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974:141-148.
- HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford.
- HERTZ, P. E., R. B. HUEY, AND E. NEVO. 1982. Fight versus flight: body temperature influences defensive responses of lizards. *Anim. Behav.* 30:676-679.
- , ———, AND R. D. STEVENSON. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142:796-818.
- HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles, p. 25-74. *In: Biology of the Reptilia*. Vol. 12. C. Gans and F. H. Pough (eds.). Academic Press, New York.
- , AND M. SLATKIN. 1976. Cost and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51:363-384.
- , P. H. NIEWIAROWSKI, J. KAUFMANN, AND J. C. HERRON. 1989. Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? *Physiol. Zool.* 62:488-504.
- LICHT, P. 1964. The relation between thermoregulation and physiological adjustments to temperature in lizards. Unpubl. Ph.D. diss., Univ. of Michigan, Ann Arbor.
- . 1968. Response of thermal preference and heat resistance to thermal acclimation under different photoperiods in the lizard *Anolis carolinensis*. *Am. Midl. Nat.* 79:149-158.
- , AND S. L. BASU. 1967. Influence of temperature on lizard testes. *Nature* 213:672-674.
- , W. R. DAWSON, V. H. SHOEMAKER, AND A. R. MAIN. 1966. Observations on the thermal relations of western Australian lizards. *Copeia* 1966:97-110.
- LILLYWHITE, H. B. 1987. Temperature, energetics, and physiological ecology, p. 422-477. *In: Snakes: ecology and evolutionary biology*. R. A. Seigel, J. T. Collins, and S. S. Novak (eds.). McGraw-Hill, New York.
- LINDMAN, H. R. 1974. Analysis of variance in complex experimental designs. W. H. Freeman and Co., San Francisco, CA.
- MOBERLY, W. R. 1968. The metabolic responses of the common iguana, *Iguana iguana*, to activity under restraint. *Comp. Biochem. Physiol.* 27:1-20.
- MYHRE, K., AND H. T. HAMMEL. 1969. Behavioral reg-

- ulation of internal temperature in the lizard *Tiliqua scincoides*. *Am. J. Physiol.* 217:1490-1495.
- NIEWIAROWSKI, P. H., AND S. R. WALDSCHMIDT. 1992. Variation in metabolic rates of a lizard: use of SMR in ecological contexts. *Funct. Ecol.* 6:15-22.
- PETERSON, C. R. 1987. Daily variation in the body temperatures of free-ranging garter snakes, *Thamnophis elegans*. *Ecology* 68:160-169.
- POTVIN, C., M. J. LECHOWICZ, AND S. TARDIF. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ibid.* 71:1389-1400.
- REGAL, P. J. 1967. Voluntary hypothermia in reptiles. *Science* 155:1551-1553.
- REYNOLDS, W. W., AND M. E. CASTERLIN. 1979. Behavioral thermoregulation and the "final preference" paradigm. *Am. Zool.* 19:211-224.
- RISMILLER, P. D., AND G. HELDMAIER. 1982. The effect of photoperiod on temperature selection in the European green lizard, *Lacerta viridis*. *Oecologia* 53:222-226.
- ROTH, J. J., AND C. L. RALPH. 1976. Body temperature of the lizard (*Anolis carolinensis*): effect of parietalectomy. *J. Exp. Zool.* 198:17-28.
- SHINE, R., AND T. MADSEN. 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiol. Zool.* 69:252-269.
- SIEVERT, L. M., AND V. H. HUTCHISON. 1988. Light versus heat: thermoregulatory behavior in a nocturnal lizard (*Gecko gecko*). *Herpetologica* 44:266-273.
- \_\_\_\_\_, AND \_\_\_\_\_. 1989. Influences of season, time of day, light and sex on the thermoregulatory behaviour of *Crotaphytus collaris*. *J. Therm. Biol.* 14:159-165.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2d ed. W. H. Freeman and Co., New York.
- SPELLERBERG, I. F. 1974. Influence of photoperiod and light intensity on lizard voluntary temperatures. *Br. J. Herpetol.* 5:412-420.
- UNDERWOOD, H. 1992. Endogenous rhythms, p. 229-297. *In: Biology of the Reptilia*. Vol. 18. C. Gans and D. Crews (eds.). Univ. of Chicago Press, Chicago.
- VAN DAMME, R., D. BAUWENS, AND R. F. VERHEYEN. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. *Funct. Ecol.* 5:507-517.
- WALDSCHMIDT, S. R., S. M. JONES, AND W. P. PORTER. 1986. The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. *Physiol. Zool.* 59:376-383.
- WERNER, Y. L. 1976. Optimal temperatures for inner-ear performance in gekkonid lizards. *J. Exp. Zool.* 195:319-352.
- \_\_\_\_\_. 1983. Temperature effects on cochlear function in reptiles: a personal review incorporating new data, p. 149-174. *In: Hearing and other senses: presentation in honor of E. G. Wever*. R. R. Fay and G. Gourevitch (eds.). Amphora Press, Groton, CT.
- \_\_\_\_\_. 1990. Habitat-dependent thermal regimes of two Hawaiian geckos (Reptilia: Gekkonidae). *J. Therm. Biol.* 15:281-290.
- \_\_\_\_\_, AND A. H. WHITAKER. 1978. Observations and comments on the body temperatures of some New Zealand reptiles. *N.Z. J. Zool.* 5:375-393.
- \_\_\_\_\_, N. CARRILLO DE ESPINOZA, R. B. HUEY, R. ROTHENSTEIN, W. W. SALAS, AND F. VIDELA. 1996. Observations and comments on body temperatures of some Neotropical desert geckos (Reptilia: Sauria: Gekkoninae). *Cuadernos de Herpetologia* 10:62-67.
- WILLIAMS, C. K. 1965. Competition between species of lizards in the field viewed through the aspect of thermoregulation. Unpubl. bachelor's thesis, Univ. of Western Australia, Nedlands.
- WILSON, K. J. 1971. The relationships of activity, energy metabolism, and body temperature in four species of lizards. unpubl. Ph.D. diss., Monash Univ., Melbourne, Victoria, Australia
- (MJA) DEPARTMENT OF BIOLOGY, UNIVERSITY OF PENNSYLVANIA, PHILADELPHIA, PENNSYLVANIA 19104-6018; AND (YLW) DEPARTMENT OF EVOLUTION, SYSTEMATICS AND ECOLOGY, HEBREW UNIVERSITY OF JERUSALEM, 91904 JERUSALEM, ISRAEL. E-mail: (MJA) angillet@sas.upenn.edu. Send reprint requests to MJA. Submitted: 14 May 1997. Accepted: 29 Jan. 1998. Section editor: R. G. Bowker.