

Australian Geckos Do Not Display Diel Variation in Thermoregulatory Behavior

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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; Beitinger 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 ± 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 ± 1.33 C) and *Nephruirus stellatus* (25.07 ± 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 ± 0.67 C, $n = 5$), and the nocturnal *P. hasselquistii* had the lowest T_p (28.7 ± 0.41 C, $n = 17$), whereas the T_p of *P. guttatus*, which is active diurnally and nocturnally, was intermediate (30.9 ± 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.

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