

- termination in *Gekko japonicus* (Gekkonidae, Reptilia). Development, Growth and Differentiation 27:117–120.
- VIETS, B. E., A. TOUSIGNANT, M. A. EWERT, C. E. NELSON, AND D. CREWS, 1993. Temperature-dependent sex determination in the leopard gecko, *Eublepharis macularius*. Journal of Experimental Zoology 265:679–683.
- VIETS, B. E., M. A. EWERT, L. G. TALENT, AND C. E. NELSON, 1994. Sex-determining mechanisms in squamate reptiles. Journal of Experimental Zoology 270:45–56.

Accepted: 3 March 1998

Associate Editor: Allison Alberts

Herpetologica, 55(2), 1999, 212–222
© 1999 by The Herpetologists' League, Inc.

TEMPERATURE PREFERENCE IN GECKOS: DIEL VARIATION IN JUVENILES AND ADULTS

MICHAEL J. ANGILLETTA, JR.,¹ LYNDA G. MONTGOMERY,^{2,4} AND YEHUDAH L. WERNER³

¹Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

²Department of Otorhinolaryngology: HNS, University of Pennsylvania, Philadelphia, PA 19104, USA

³Department of Evolution, Systematics & Ecology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel

ABSTRACT: Field studies of nocturnal geckos have revealed that many species actively thermoregulate during both the day and the night. Data from laboratory studies indicate that geckos prefer body temperatures greater than those experienced during activity in the field, but data on diel patterns of temperature preference are inconsistent. We measured preferred body temperature (T_p) of five species of geckos (*Coleonyx mitratus*, *Eublepharis macularius*, *Hemidactylus turcicus*, *Oedura marmorata*, and *O. reticulata*) to determine the extent of within-day and between-day variation. Additionally, we compared T_p s of juveniles and adults of *O. marmorata* and *E. macularius*. Preferred body temperature increased from morning to evening hours within days but did not differ between days. Juveniles and adults had similar T_p s at all time periods. We hypothesize that a preference for higher T_p s toward the end of photophase initiates the thermoregulatory behavior observed in field-active geckos, and facilitates higher body temperatures during activity in early scotophase.

Key words: Gekkonidae; Body temperature; Diel variation; Thermoregulation

IN ectotherms, all physiological processes are affected by body temperature (T_b). Therefore, individuals that behaviorally thermoregulate can ensure an internal state that is conducive to maintenance and activity. Studies of the thermal biology of reptiles have served as the foundation for much of our understanding of the thermal physiology of ectotherms (Gans and Pough, 1982). The thermoregulatory behavior of many species has been investigated in the field and the laboratory (reviewed by Avery, 1982, and Huey, 1982). Field T_b s vary within and among individuals in a population (Beaupre, 1995;

Christian and Bedford, 1995, 1996; Christian and Weavers, 1996; Christian et al., 1983, 1985; Grant, 1990; Peterson, 1987). The observed variation in field T_b s is likely to have ramifications for metabolism (Beaupre et al., 1993a; Bennett and Dawson, 1976; Niewiarowski and Waldschmidt, 1992), digestion (Beaupre et al., 1993b; Waldschmidt et al., 1986), locomotory performance (Bennett, 1980, 1990; Greenwald, 1974), defensive behavior (Christian and Tracy, 1981; Goode and Duvall, 1989; Hertz et al., 1982; Scribner and Weatherhead, 1995), food consumption (Van Damme et al., 1991), and life history (Beaupre, 1995; Grant and Dunham, 1990).

Most species in the family Gekkonidae are active (out of cover) nocturnally. Al-

⁴ PRESENT ADDRESS: 174 Brattle Street, Arlington, MA 02174, USA.

though a few species thermoregulate at night using rock crevices or human-made heat sources (e.g., Werner, 1990a), the opportunity for heat gain during nighttime activity is limited. Thus, the availability of suitable microclimates plays a large role in determining the onset and cessation of foraging (Bustard, 1968). Body temperatures commonly experienced during activity are lower than T_b preferences (Angilletta and Werner, in press; Gil et al., 1994; Huey et al., 1989) and T_b s at which physiological processes are maximized (Autumn et al., 1994; Huey et al., 1989). Therefore, geckos may perform many activities at night but must depend on microclimates available only during the day to achieve T_b s necessary for digestion, growth, and repair. Indeed, several species have been observed to thermoregulate actively during the day (Avery, 1982; Greer, 1989; Werner and Whitaker, 1978). Daytime field T_b s are usually higher than nighttime field T_b s (Angilletta and Werner, 1998).

Although field T_b s are integral to determining the consequences of the thermal environment for an organism's ecology, they can not be interpreted strictly as body temperature preferences. Studies of the thermoregulatory behavior of lizards, in well-characterized thermal environments, have revealed that available microclimates often prevent animals from attaining desired T_b s (Gil et al., 1994; Grant and Dunham, 1988). The extent to which variation in field T_b represents changes in body temperature preference or changes in the availability of thermal microclimates is often unclear. Geckos experience increased T_b s during daytime "inactivity", and, in some reports, animals clearly avoided surrounding microclimates that were cooler (*Hoplodactylus maculatus* in Werner and Whitaker, 1978; *Phyllodactylus reissi* in Werner et al., 1996). In other cases, high daytime T_b s may reflect the warmer environment during photophase, rather than any temperature preference.

Preferred body temperature (sensu Licht et al., 1966) is a more appropriate measure of body temperature preference than field T_b s (Hertz et al., 1993). Preferred body temperatures (T_p s) of geckos

indicate that daytime field T_b s experienced by geckos may be the result of temperature selection (Angilletta and Werner, 1998). However, unlike studies of diurnal lizards (reviewed by Avery, 1982; Underwood, 1992), few investigations have recorded T_p s of geckos during photophase (e.g., Autumn and DeNardo, 1995; Gil et al., 1994; Sievert and Hutchison, 1988). Further, studies of diel variation in T_p s have yielded inconsistent results. In the geckos *Tarentola mauritanica* (Gil et al., 1994) and *Gekko gecko* (Sievert and Hutchison, 1988), T_p varied within or between photophase and scotophase (Gil et al., 1994), but in other species it did not (Angilletta and Werner, 1998). More studies of T_p are needed in order to determine the extent to which the T_b s experienced by geckos in the field correspond to those that they prefer.

We studied variation in T_p s of five species of geckos in a laboratory thermal gradient to address three questions. (1) Does T_p vary during the hours of potential thermoregulation (i.e., throughout photophase)? (2) Are short term measurements of T_p reliable, or does T_p vary between days? (3) Do daily patterns of T_p differ between juveniles and adults of a species?

MATERIALS AND METHODS

Species Description and Provenance

Coleonyx mitratus Peters.—This forest-dwelling terrestrial eublepharid is restricted to western Central America. Most specimens observed in the field were moving on the forest floor at night or found beneath rocks and logs during the day (Dial and Grismer, 1992; Tyle and Stephens, 1993). Our specimens (five adults) originated from Nicaragua and were received on 21 June 1993 from Glades Herp, Inc. (Fort Myers, Florida). [Voucher specimens: HUI-R 18876–18882.]

Eublepharis macularius Blyth.—This cursorial eublepharid inhabits rocks and clay from southern Transcaспia and Iraq to northwestern India and is widespread in Pakistan (Minton, 1966). Our specimens (10 females of 8–12 yr of age and five juveniles of 2–5 wk of age) came from the

Center for Reptile and Amphibian Propagation (Boerne, Texas). [Voucher specimens: HUI-R 18885–18900.]

Hemidactylus turcicus *Linnaeus*.—This scansorial gekkonine is found in a variety of habitats, including houses, in southwestern Asia and the Mediterranean area. *Hemidactylus turcicus* has been gradually colonizing the southern United States (Selcer, 1986). Our specimens (eight adults) were collected at The University of Texas (Austin, Texas) in June of 1994 by Gad Perry. [Voucher specimens: HUI-R 18883–18884, 19010.]

Oedura marmorata *Gray*.—This rupicolous diplodactyline inhabits arid and semi-arid regions of northern and western Australia. *Oedura marmorata* is commonly found in exfoliating rocks, emerging at night to forage on open rock faces, but it is occasionally seen on trees (Cogger, 1992; Storr et al., 1990). All specimens of this species-complex (14 adults, five juveniles) were collected by Y. L. Werner on granite outcrops, 6–8 km north of Mt. Magnet township, Western Australia, during September and October of 1993. In the daytime, individuals were found under exfoliations, where presumably they could thermoregulate. [Voucher specimens: HUI-R 18934–18944.]

Oedura reticulata *Bustard*.—This arboreal diplodactyline is endemic to the semi-arid and sub-humid southwestern interior of Western Australia. *Oedura reticulata* is active at night but is sometimes found basking on smooth-barked eucalypts in late afternoon (Werner, personal observation). Our specimens (12 adults) were collected by N. and Y. L. Werner in eucalypt groves in the Bungalbin Hills area, 125 km northeast of Southern Cross township. [Voucher specimens: HUI-R 18949–18953.]

Animal collection and holding in Western Australia, and export to the United States, occurred with permission from the Department of Conservation and Land Management of Western Australia (SF001 105), and the Australian Nature Conservation Agency (PWS-P935483), respectively. All voucher specimens are deposited

in the Zoological Museum of the Hebrew University of Jerusalem.

Animal Care

Oedura reticulata and *O. marmorata* were first imported to the California Academy of Sciences (San Francisco, California), where they were maintained for a few weeks until they could be accepted in Philadelphia. Other species were received in Philadelphia, directly from their sources (listed above). In Australia and Philadelphia, geckos were housed in 38 l glass aquaria, as groups of 3–4. The room temperature was a constant 25 C and the photoperiod was 12L:12D. In Australia, mealworms were provided ad libitum. In Philadelphia, the diet comprised wax moth larvae and crickets, ad libitum.

Procedure

We measured the T_p of geckos in a 1 m thermal gradient consisting of five parallel runways, separated by opaque walls and covered with vented plexiglass lids. One end of the gradient was heated by incandescent bulbs, shielded to prevent confounding the effects of light and heat (Sievert and Hutchison, 1988). The other end of the gradient was cooled by a chilled water bath directly below the floor. The gradient provided a range of substrate temperature, measured with copper-constantan thermocouples, from 5 C to 45 C. Fluorescent lighting on a 12L:12D light cycle was distributed uniformly along the top of the gradient. Half of the width of each runway was sheltered by pieces of grey egg-packing carton, to allow geckos to thermoregulate under cover.

Measurements of T_p were made between 7 July and 24 August 1994. On 10 August, the gradient had to be relocated to a manually controlled environment; fluorescent lighting was usually turned on at 0730 h (rarely, as early as 0445 h or as late as 0900 h) and was turned off between 1730 h and 1800 h. Air temperature was recorded in the room whenever T_p s were recorded. Average air temperature did not vary significantly within days (28.4 ± 1.0 C, 28.4 ± 1.0 C, 28.6 ± 1.0 C, and 28.8 ± 1.0 C for time periods 1–4, respective-

ly), but did vary considerably among days (28.6 ± 1.0 C, range = 25.5–32.5 C).

The geckos were not fed for approximately three days before measurement of T_p . The last 1–2 days of fasting were spent in the thermal gradient, to acclimate animals to the experimental conditions; acclimation was necessary to reduce the probability of measuring acute thermal preferences (sensu Reynolds and Casterlin, 1979). After the acclimation period, T_b was measured once during each of four time periods of each day (0700–1000 h, 1000–1300 h, 1300–1600 h, 1600–1900 h), typically at 0730, 1100, 1400, and 1730. Measurements were made for 1–2 days. Body temperature was measured rectally with a quick-reading mercury thermometer (C. Miller and Weber, Inc., Queens, New York). Data were discarded if excess chasing or handling was used to acquire T_b .

Statistical Analyses

Age class and time period comparisons.—We used a Multivariate Analysis of Covariance with Repeated Measures (MANCOVAR) to examine the effects of species, age class, and time period on the T_p of *E. macularius* (10 adults, five juveniles) and *O. marmorata* (14 adults, five juveniles). When T_b s were recorded for an individual on two consecutive days, T_b s for each time period were averaged between days to yield a single T_b per individual for each of the four time periods. Because ambient temperature was not controlled during part of the study, air temperature was used as a covariate in the analysis. The slopes of the relationship between the air temperature and T_p s were examined for homogeneity among treatment groups, prior to employing MANCOVAR.

MANCOVAR makes few assumptions about the form of the covariance matrix (Potvin et al., 1990), but the analysis does assume that the dependent variables (i.e., T_p s for the four time periods) are normally distributed and that their variances and covariances are homogeneous (compound symmetry of the variance covariance matrix). The singularity of the variance-covariance matrix precluded the 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 Levene'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. The Chi-square goodness of fit test was used to examine the assumption of normality. When main effects or interactions were significant, we used Tukey's honest significant difference test to determine the significance of pairwise comparisons of group means. All statistical analyses were performed with Statistica for Windows (Statsoft, 1995).

Within-day and between-day comparisons.—We used Analysis of Covariance with Repeated Measures (ANCOVAR) to examine the effects of species, day, and time of day on T_p . Air temperature was used as a covariate in the analysis. Because we were missing records for one or more time periods for some individuals, we averaged the first two time periods (0700–1000 h and 1000–1300 h) and the second two time periods (1300–1600 h and 1600–1900 h) to yield a single T_b for morning (M) and evening (E) periods of each day. It is unlikely that pooling time periods masked any diel variation in T_p , because T_p did not differ significantly between periods 1 and 2 ($t = -1.71$, $df = 44$, $P > 0.05$) or between periods 3 and 4 ($t = 0.78$, $df = 50$, $P > 0.05$). The resulting data set contained T_b s for 48 individuals, comprising five *C. mitratus*, nine *E. macularius*, eight *H. turcicus*, 14 *O. marmorata*, and 12 *O. reticulata*. We tested the assumptions of ANCOVAR using the methods described above. Post hoc comparisons of groups means were made using Tukey's honest significant difference test.

RESULTS

Age Class and Time Period Comparisons

The variances in T_p of the groups were not homogeneous for two of the four time periods (1000–1300 h and 1300–1600 h), however the means and variances were not correlated ($R^2 = 0.35$ and 0.05 , respective-

TABLE 1.—Summary of the MANCOVAR of the effects of species, age class, and time of day on preferred body temperature (T_p).

| Source | df | MS | F | P |
|--|------|------------------|-------|----------|
| A. Between-subjects effects: | | | | |
| Species | 1,29 | 536.22 | 86.08 | 0.000000 |
| Age class | 1,29 | 0.04 | 0.01 | 0.934231 |
| Species \times age class | 1,29 | 0.20 | 0.03 | 0.858479 |
| | | Wilk's λ | F* | P |
| B. Within-subjects effects: | | | | |
| Time | 3,25 | 0.81 | 1.95 | 0.147789 |
| Species \times time | 3,25 | 0.92 | 0.68 | 0.574767 |
| Age class \times time | 3,25 | 0.92 | 0.68 | 0.571657 |
| Species \times age class \times time | 3,25 | 0.94 | 0.50 | 0.682986 |

* Approximate multivariate F ratio corresponding to Wilk's λ .

ly; $P > 0.05$ for both). Overall, T_p was not significantly related to air temperature (Wilk's $\lambda = 0.49$, $F_{16,70} = 1.17$, $P > 0.05$). MANCOVAR revealed significant effects of species on T_p (Table 1). *Oedura marmorata* had a significantly higher T_p than *E. macularius*. While the main effect of time was not significant ($P = 0.14$), post hoc comparisons of T_p among time periods indicated that the T_p of *O. marmorata* for period one (32.7 ± 0.08 C) was signifi-

cantly lower than that for period four (34.8 ± 1.1 C; Fig. 1). No significant differences in T_p were found between juveniles and adults (Table 1). Also, no significant interactions were found.

Within-day and Between-day Comparisons

The assumption of normality was not met in one case, T_p of *O. marmorata* during the evening of day two, but the deviation from normality was slight ($\chi^2 = 4.07$, $df = 1$, $P = 0.04$). The variances in T_p of the species were not homogeneous for one of the four time periods (D1M), however the means and variances were not correlated ($R^2 = 0.04$, $P > 0.05$).

Preferred body temperature covaried significantly with air temperature (Wilk's $\lambda = 0.47$, $F_{16,110} = 1.92$, $P < 0.05$). ANCOVAR indicated that T_p varied significantly with time of day (Table 2). Average evening T_p was 1.3 C higher than average morning T_p (Fig. 2). No significant difference in T_p was found between days (Table 2). Only *O. reticulata* had similar T_p s during morning and evening periods (Table 3).

The effect of species on T_p was highly significant (Table 2). Tukey's test identified significant pairwise differences among the species. *Oedura marmorata* and *O. reticulata* had higher T_p s than the other species, with T_p of *O. marmorata* being significantly higher than that of *O. reticulata* (Table 3). All other species had statistically indistinguishable T_p s. For the purpose of

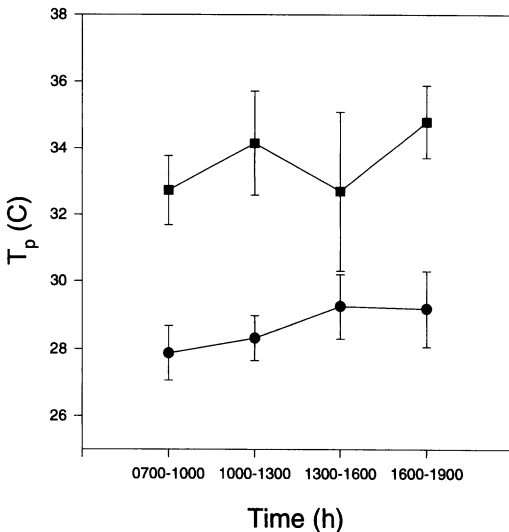


FIG. 1.—Preferred body temperature (T_p) of *Oedura marmorata* (squares) and *Eublepharis macularius* (circles) measured at four time periods during photophase. Error bars represent the 95% confidence intervals of the means. Preferred body temperature of *O. marmorata* during the first time period (0700–1000 h) was significantly lower than that during the fourth time period (1600–1900 h).

TABLE 2.—Summary of the ANCOVAR of the effects of species, day, and time of day on preferred body temperature (T_p).

| Source | df | MS | F | P |
|------------------------------------|----|--------|-------|----------|
| Between-subjects effect: | | | | |
| Species | 4 | 212.53 | 18.66 | 0.000000 |
| Within-subjects effects: | | | | |
| Day | 1 | 20.24 | 2.53 | 0.119389 |
| Time | 1 | 26.75 | 6.01 | 0.018497 |
| Species \times day | 4 | 8.33 | 1.04 | 0.398172 |
| Species \times time | 4 | 8.38 | 1.88 | 0.131534 |
| Day \times time | 1 | 0.18 | 0.06 | 0.808873 |
| Species \times day \times time | 4 | 1.28 | 0.43 | 0.787544 |

comparing T_p s of the species used in this study with those of other species, we computed the average T_p of each species. Average T_p s are the grand means of the mean T_p s of individuals of each species.

DISCUSSION

Methodology

Two methods of measuring T_b have been used in studies of T_p : manual, using quick-reading cloacal thermometers (e.g., Autumn and DeNardo, 1995; Huey et al., 1989) and automated, using fixed thermocouples (e.g., Angilletta and Werner, 1998; Licht et al., 1966). Animals fixed with thermocouples may behave differently than "unimpaired" animals. The pres-

ence of the thermocouple in the large intestine may initiate a thermophilic response, noted in reptiles during digestion (Autumn and DeNardo, 1995; Dorcas et al., 1997; reviewed by Peterson et al., 1993). Also, the thermocouple wire may restrict an animal's ability to locomote within a thermal gradient. We compared T_p s of *O. reticulata* and *O. marmorata* measured in this study with a quick-reading thermometer to those which were previously measured using thermocouples fixed in the cloaca by a cloth harness (Angilletta and Werner, 1998). One might expect to find that the T_p s reported by Angilletta and Werner (1998) were higher than those reported in this study, due to the proposed thermophilic response to the thermocouple wire. However, there was no significant difference between the T_p s reported in the two studies for either *O. marmorata* ($t = 1.16$, $df = 17$, $P = 0.26$) or *O. reticulata* ($t = 0.96$, $df = 15$, $P = 0.35$). In fact, the averages of T_p s determined by Angilletta and Werner (1998), using fixed thermocouples, were slightly lower than average T_p s given here. Thus, such methodological differences should not preclude us from comparing our results to those of other studies of T_p .

Specific Temperature Preferences

Previous studies reported comparable T_p s for four of the species studied here. Dial and Grismer (1992) measured T_p s of *C. mitratus* (25.7 ± 0.96 C, $n = 5$) and *E. macularius* (26.5 ± 0.91 C, $n = 4$), which were 1 C and 2 C lower than our results, respectively. Autumn and DeNardo (1995)

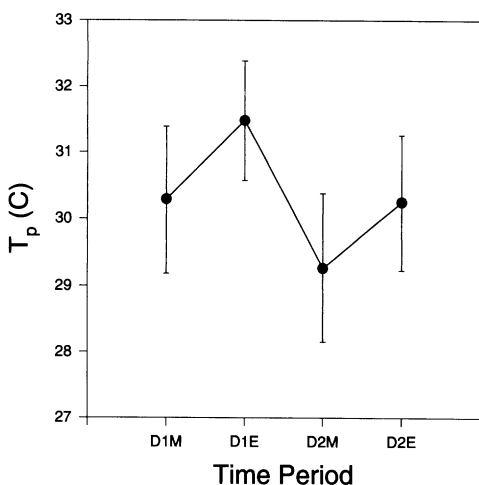


FIG. 2.—Preferred body temperature (T_p) for 48 geckos of five species. On both days (D1 and D2), T_p was significantly higher during the evening (E) than the morning (M) period. Error bars represent the 95% confidence intervals of the means.

TABLE 3.—Mean preferred body temperature (± 95 confidence interval) of five species of geckos for the morning (M T_p), evening (E T_p), and both time periods (Avg T_p). Mean T_p of each species is the grand mean of the individual mean T_p s. The number of individuals of each species (n) is given.

| Species | M T_p | E T_p | Avg T_p | n |
|-------------------------------|--------------------|--------------------|--------------------|-----|
| <i>Coleonyx mitratus</i> | 24.9 (± 3.1) | 28.1 (± 1.7) | 26.5 (± 2.4) | 5 |
| <i>Eublepharis macularius</i> | 27.7 (± 0.7) | 28.7 (± 0.7) | 28.2 (± 0.6) | 9 |
| <i>Hemidactylus turcicus</i> | 27.8 (± 1.7) | 29.1 (± 1.6) | 28.4 (± 1.5) | 8 |
| <i>Oedura marmorata</i> | 32.8 (± 0.8) | 34.1 (0.8) | 33.4 (± 0.8) | 14 |
| <i>Oedura reticulata</i> | 31.2 (± 1.4) | 31.1 (± 1.0) | 31.2 (± 0.8) | 12 |

reported a higher T_p for *E. macularius* (30.6 ± 0.29 C, $n = 12$) than those reported by Dial and Grismer (1992) and by us. As mentioned above, Angilletta and Werner (1998) found T_p of *Oedura reticulata* to be 1 C lower and that of *O. marmorata* to be 2 C lower (though these differences were not statistically significant). The differences between previously reported T_p s and those reported here do not alter the rank order of T_p among the four species. In fact, the differences are smaller than those often found between separate, but comparable, studies of a given species (Greer, 1989:Table 11).

Although most of the differences between T_p s obtained by the different investigators are insignificant, it is noteworthy that in all cases but one (T_p for *E. macularius* in Autumn and DeNardo, 1992), T_p of each species was lower than that found in our study. Several experimental factors may affect T_p but one plausible cause may be differences in observation time. Dial and Grismer (1992) collected their data on *C. mitratus* and *E. macularius* during an unspecified season. Thus, they may have emphasized morning hours when, according to our findings, T_p is relatively low. Angilletta and Werner (in press) recorded T_p of *O. marmorata* and *O. reticulata* over 24 h, including scotophase when T_p is somewhat lower (although such variation was not significant in that study). Greer (1989) assembled data on T_p for five other species of gecko collected during photophase and scotophase. Among comparable studies, T_p s during photophase generally exceeded T_p s during scotophase. Overall, our T_p s for the four species accord with previous data and hence the T_p for the fifth, *H. turcicus*, should be dependable.

Diel Variation

Our study revealed that geckos exhibit diel variation in T_p during photophase. Preferred body temperature increased significantly from morning to evening (Fig. 2; Table 3). Gil et al. (1994) noted a similar increase in T_p during photophase in the gecko *Tarentola mauritanica*. However, other studies report no diel variation in T_p s, including three of the species examined here. Autumn and DeNardo (1995) found no difference between T_p measured during day and night in *E. macularius*. A previous study of *O. marmorata* and *O. reticulata* (Angilletta and Werner, 1998) found no significant differences in T_p s within and between photophase and scotophase. While we also found no diel variation in the T_p of *O. reticulata*, the T_p of *E. macularius* and *O. marmorata* increased from morning to evening (Table 3). Why would similar studies of T_p produce inconsistent results? One possibility is that diel variation was present in both studies, but the differences were not recognized due to low statistical power. This is a likely scenario in the case of Angilletta and Werner (1998) who used smaller sample sizes and made more measures on each individual, both of which decrease the power of ANOVA. However, diel cycles of thermoregulation can undergo seasonal changes in amplitude, sometimes even disappearing altogether (reviewed by Underwood, 1992). Indeed, studies of other species of reptiles have provided contradictory evidence concerning the existence of diel rhythms (Underwood, 1992).

The function of an increase in T_p during photophase may be directly related to the thermoregulatory behavior of geckos in

nature. In the field, some nocturnal species of geckos actively thermoregulate throughout the day (Greer, 1989; Werner and Whitaker, 1978; Werner, personal observation). Most diurnal lizards exhibit higher T_p s during photophase than during scotophase. Diurnal lizards bask to raise their body temperatures before the onset of activity (Cowles and Bogert, 1944; Huey, 1982). Underwood (1992) suggested that an increase in T_p may stimulate the thermoregulatory behaviors that result in increased daytime T_b s relative to nighttime T_b s observed in diurnal lizards, and this may be true for geckos as well.

While most activities of geckos occur at night, high daytime T_b s would aid in digestion, maintenance, growth, and other physiological processes that are temperature dependent. It is not known whether diel variation in T_p observed in lizards is due to the existence of circadian rhythms or thermoregulatory behavior is driven by some environmental cue, such as photoperiod. In either case, our data indicate that higher field T_b s observed in geckos during photophase are at least partially the result of temperature selection.

Variation with Age

Ontogenetic changes in physiology and behavior are quite common among ectotherms and have been widely studied (e.g., Werner et al., 1998). Behaviors such as habitat selection (Congdon et al., 1992; Higgins and Ezcurra, 1996; Reinert, 1993; Werner et al., 1983), foraging behavior (Arnold, 1993; Huey and Pianka, 1981; Rose, 1976; Sempeksi and Gaudin, 1996), and sociality (Rand, 1965; Watkins, 1995) change with ontogeny, and these shifts have consequences for the availability of thermal microclimates (Higgins and Ezcurra, 1996; Huey, 1991; Magnuson et al., 1979) and thermoregulatory behavior (Huey and Slatkin, 1976). Field body temperatures of reproductive females are often higher than those of nonreproductive individuals (Peterson et al., 1993; Werner, 1990b). Laboratory studies confirm that reproductive condition can cause changes in T_p (Peterson et al., 1993). We know less about the temperature preferences and

the constraints on thermoregulation that are associated with age, as variation in T_p with age has received little attention to date. However, given the high frequency of ontogenetic change in behavior and physiology, it would be surprising if differences in thermoregulatory behavior were not common.

It is noteworthy that in the cases where T_p of different age classes has been examined, younger individuals prefer higher body temperatures than older ones. For example, Lang (1981) found that the T_p of hatchling New Guinean crocodiles (33.4–33.9 C) was higher than that of young juveniles (31.8–32.2 C). Furthermore, both hatchlings and young juveniles had T_p s 2 C higher than field T_b s of older juveniles and adults. A similar observation was made by Perez-Quintero (1994). Body temperatures of field-active skinks, *Chalcides chalcides*, averaged 33.0 C for juveniles, 29.0 C for sub-adults, and 28.8 C for adults. We found no significant differences in the T_p s of juveniles and adults of either *E. macularius* or *O. marmorata*. However, considering the small number of juveniles examined here, it is possible that further investigation will reveal ontogenetic differences in the T_p s of geckos. Consequently, studies that examine field T_b , T_p , and the thermal sensitivity of physiological performance of individuals of known age would be a valuable contribution to our understanding of ontogenetic changes in thermoregulatory behavior.

Acknowledgments.—We thank the Western Australian Museum, particularly K. Aplin, J. Dell, and L. Smith for hospitality and advice; Y. Martin, A. Roberts, and especially N. Werner for help in collecting; P. Withers and Y. Martin for animal housing and care, respectively, in Australia; A. Bauer and J. Vindum for vital help in bridging Perth and Philadelphia; G. Perry for providing *Hemidactylus* and R. Tremper for providing adults of *Eublepharis*. Many thanks to J. Saunders for financial and logistical support, and partial personal support of Y. L. Werner (Research Award DC-00510 if NIDCD). A. E. Dunham advised us on the design of the thermal gradient. Portions of this manuscript were written while Y. L. Werner was a guest at the Institute of Zoology, Technical University, Munich (Garching), under the auspices of the Sonderforschungsbereich 204 (Gehoer); and later in the Department of Zoology, National Museum, Prague. He thanks G. A. Manley and J. Moravec of the Technical University and the National Museum,

respectively, as well as both institutions for hospitable environments and manifold support. A. Alberts, K. Christian, R. S. Winters, and an anonymous reviewer made valuable comments on the manuscript. 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

- ANGILLETTA, M. J., AND Y. L. WERNER. 1998. Australian geckos do not display diel variation in thermoregulatory behavior. *Copeia* 1998:736–742.
- ARNOLD, S. J. 1993. Foraging theory and prey size—predator-size relations in snakes. Pp. 87–116. In R. A. Seigel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, New York, U.S.A.
- AUTUMN, K., AND D. F. DENARDO. 1995. Behavioral thermoregulation increases growth rate in a nocturnal lizard. *Journal of Herpetology* 29:157–162.
- AUTUMN, K., R. B. WEINSTEIN, AND R. J. FULL. 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiological Zoology* 67:238–262.
- EVERY, R. A. 1982. Field studies of body temperatures and thermoregulation. Pp. 93–166. In C. Gans and F. H. Pough (Eds.), *Biology of the Reptilia*, Vol. 12. Academic Press, New York, New York, U.S.A.
- BEAUPRE, S. J. 1995. Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. *Ecology* 76:1655–1665.
- BEAUPRE, S. J., A. E. DUNHAM, AND K. L. OVERALL. 1993a. Metabolism of a desert lizard: the effects of mass, sex, population of origin, temperature, time of day, and feeding on oxygen consumption of *Sceloporus merriami*. *Physiological Zoology* 66:128–147.
- . 1993b. The effects of consumption rate and temperature on apparent digestibility coefficient and passage time in canyon lizards (*Sceloporus merriami*) from two populations. *Functional Ecology* 7:273–280.
- BENNETT, A. F. 1980. The thermal dependence of lizard behaviour. *Animal Behaviour* 28:752–762.
- . 1990. Thermal dependence of locomotor capacity. *American Journal of Physiology* 250:R253–R258.
- BENNETT, A. F., AND W. R. DAWSON. 1976. Metabolism. Pp. 127–224. In C. Gans and W. R. Dawson (Eds.), *Biology of the Reptilia*, Vol. 5. Academic Press, New York, New York, U.S.A.
- BUSTARD, H. R. 1968. Temperature dependent activity in the Australian gecko *Diplodactylus vittatus*. *Copeia* 1968:606–612.
- 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.
- . 1996. Thermoregulation by the spotted tree monitor, *Varanus scalaris*, in the seasonal tropics of Australia. *Journal of Thermal Biology* 21:67–73.
- CHRISTIAN, K. A., AND C. R. TRACY. 1981. The effect of the thermal environment on the ability of hatching Galapagos land iguanas to avoid predation during dispersal. *Oecologia* (Berlin) 49:218–223.
- CHRISTIAN, K. A., 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.
- . 1985. Inter- and intra-individual variation in body temperatures of the Galapagos land iguana (*Conolophus pallidus*). *Journal of Thermal Biology* 10:47–50.
- CHRISTIAN, K. A., AND B. W. WEAVERS. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological Monographs* 66:139–157.
- COGGER, H. G. 1992. *Reptiles & Amphibians of Australia*, 5th ed. Cornell University Press, Ithaca, New York, U.S.A.
- CONGDON, J. D., S. W. GOTTE, AND R. W. MCDIARMID. 1992. Ontogenetic changes in habitat use by juvenile turtles, *Chelydra serpentina* and *Chrysemys picta*. *Canadian Field-Naturalist* 106:241–248.
- COWLES, R. B., AND C. M. BOGERT. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum Natural History* 83:265–296.
- DIAL, B. E., AND L. L. GRISMER. 1992. A phylogenetic analysis of physiological-ecological character evolution in the lizard genus *Coleonyx* and its implications for historical biogeographic reconstruction. *Systematic Biology* 41:178–195.
- DORCAS, M. E., C. R. PETERSON, AND M. E. T. FLINT. 1997. The thermal biology of digestion in rubber boas (*Charina bottae*): physiology, behavior, and environmental constraints. *Physiological Zoology* 70:292–300.
- GANS, C., AND F. H. POUGH. 1982. Physiological ecology: its debt to reptilian studies, its value to students of reptiles. Pp. 1–13. In C. Gans (Ed.), *Biology of the Reptilia*, Vol. 12. Academic Press, New York, New York, U.S.A.
- GIL, M. J., F. GUERRERO, AND V. PEREZ-MELLADO. 1994. Diel variation in preferred body temperatures of the Moorish gecko *Tarentola mauritanica* during summer. *Herpetological Journal* 4:56–59.
- GOODE, M. J., AND D. DUVALL. 1989. Body temperature and defensive behaviour of free-ranging prairie rattlesnakes, *Crotalus viridis viridis*. *Animal Behaviour* 38:360–362.
- GRANT, B. W. 1990. Trade-offs in activity and physiological performance for thermoregulating desert lizards, *Sceloporus merriami*. *Ecology* 71:2323–2333.
- GRANT, B. W., AND A. E. DUNHAM. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69:167–176.
- . 1990. Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. *Ecology* 71:1765–1776.
- GREENWALD, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974:141–148.

- GREER, A. E. 1989. *The Biology and Evolution of Australian Lizards*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- HERTZ, P. E., R. B. HUEY, AND E. NEVO. 1982. Fight versus flight: body temperature influences defensive responses of lizards. *Animal Behaviour* 30: 676–679.
- HERTZ, P. E., R. B. HUEY, AND R. D. STEVENSON. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* 142:796–818.
- HIGGINS, L. E., AND E. EZCURRA. 1996. A mathematical simulation of thermoregulatory behavior in an orb-weaving spider. *Functional Ecology* 10:322–327.
- HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25–74. *In* C. Gans and F. H. Pough (Eds.), *Biology of the Reptilia*, Vol. 12. Academic Press, New York, New York, U.S.A.
- . 1991. Physiological consequences of habitat selection. *American Naturalist* 137:S91–S115.
- HUEY, R. B., 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? *Physiological Zoology* 62:488–504.
- HUEY, R. B., AND E. R. PIANKA. 1981. Ecological consequences of foraging mode. *Ecology* 62:991–999.
- HUEY, R. B., AND M. SLATKIN. 1976. Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51:363–384.
- LANG, J. W. 1981. Thermal preferences of hatchling New Guinea crocodiles: effects of feeding and ontogeny. *Journal of Thermal Biology* 6:73–78.
- LICHT, P., W. R. DAWSON, V. H. SHOEMAKER, AND A. R. MAIN. 1966. Observations on the thermal relations of Western Australian lizards. *Copeia* 1966: 97–110.
- MAGNUSON, J. J., L. B. CROWDER, AND P. A. MEDVICK. 1979. Temperature as an ecological resource. *American Zoologist* 19:331–343.
- MINTON, S. A., JR. 1966. A contribution to the herpetology of West Pakistan. *Bulletin of the American Museum of Natural History* 134:27–184.
- NIEWIAROWSKI, P. H., AND S. R. WALDSCHMIDT. 1992. Variation in metabolic rates of a lizard: use of SMR in ecological contexts. *Functional Ecology* 6:15–22.
- PEREZ-QUINTERO, J. C. 1994. Thermal ecology in a salt-marsh population of *Chalcides chalcides*. *Resúmenes, Herpetología, III Congreso Luso-Español & VII Congreso Español*, Badajoz, 19–23 September:84.
- PETERSON, C. R. 1987. Daily variation in the body temperatures of free-ranging garter snakes, *Thamnophis elegans*. *Ecology* 68:160–169.
- PETERSON, C. R., A. R. GIBSON, AND M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. Pp. 241–314. *In* R. A. Seigel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, New York, U.S.A.
- POTVIN, C., M. J. LECHOWICZ, AND S. TARDIF. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71:1389–1400.
- RAND, A. S. 1965. The adaptive significance of territoriality in iguanid lizards. Pp. 106–115. *In* W. W. Milstead (Ed.), *Lizard Ecology*. University of Missouri Press, Columbia, Missouri, U.S.A.
- REINERT, H. K. 1993. Habitat selection in snakes, Pp. 201–240. *In* R. A. Seigel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, New York, U.S.A.
- REYNOLDS, W. W., AND M. E. CASTERLIN. 1979. Behavioral thermoregulation and the “final preferendum” paradigm. *American Zoologist* 19:211–224.
- ROSE, B. R. 1976. Habitat and prey selection of *Sceloporus occidentalis* and *Sceloporus graciosus*. *Ecology* 57:531–541.
- SCRIBNER, S. J., AND P. J. WEATHERHEAD. 1995. Locomotion and antipredator behavior in three species of semi-aquatic snakes. *Canadian Journal of Zoology* 73:321–329.
- SELGER, K. W. 1986. Life history of a successful colonizer: the Mediterranean gecko, *Hemidactylus turcicus*, in southern Texas. *Copeia* 1986:956–962.
- SEMPECKI, P., AND P. GAUDIN. 1996. Size-related shift in feeding strategy and prey-size selection in young grayling (*Thymallus thymallus*). *Canadian Journal of Zoology* 74:1597–1603.
- SIEVERT, L. M., AND V. H. HUTCHISON. 1988. Light versus heat: thermoregulatory behavior in a nocturnal lizard (*Gekko gekko*). *Herpetologica* 44:266–273.
- STATSOFT. 1995. *Statistica for Windows*. Vol. 1: General Conventions & Statistics I. StatSoft, Inc., Tulsa, Oklahoma, U.S.A.
- STORR, G. M., L. A. SMITH, AND R. E. JOHNSTONE. 1990. *Lizards of Western Australia III. Geckos & Pygopodids*. Western Australian Museum, Perth, Australia.
- TYLE, T., AND P. STEPHENS. 1993. Maintenance and breeding of the Central American banded gecko (*Coleonyx mitratus*). *Vivarium* 5:18–19.
- UNDERWOOD, H. 1992. Endogenous rhythms. Pp. 229–297. *In* C. Gans and D. Crews (Eds.), *Biology of the Reptilia*, Vol. 18. University of Chicago Press, Chicago, Illinois, U.S.A.
- 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. *Functional Ecology* 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*. *Physiological Zoology* 59:376–383.
- WATKINS, G. G. 1995. *Sexual Dimorphism and Social Behavior in the Tropicurid Lizard Microlophus occipitalis*. Ph.D. Dissertation, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.
- WERNER, E. E., J. F. GILLIAM, D. J. HALL, AND G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.

- WERNER, Y. L. 1983. Optimal temperatures for inner-ear performance in gekkonoid lizards. *Journal of Experimental Zoology* 195:319–352.
- . 1989. Experimental implications of habitat-dependent thermal regimes of ectothermic animals. *European Journal of Physiology* 413:R36.
- . 1990a. Habitat-dependent thermal regimes of two Hawaiian geckos (Reptilia: Gekkonidae). *Journal of Thermal Biology* 15:281–290.
- . 1990b. Do gravid females of oviparous gekkonoid lizards maintain elevated body temperatures? *Hemidactylus frenatus* and *Lepidodactylus lugubris* on Oahu. *Amphibia-Reptilia* 11:200–204.
- WERNER, Y. L., N. CARILLO DE ESPINOZA, R. B. HUEY, D. ROTHENSTEIN, A. W. SALAS, AND F. VIDELA. 1996. Observations on body temperatures of some neotropical desert geckos (Reptilia: Sauria: Gekkoninae). *Cuadernos de Herpetologia* 10:62–67.
- WERNER, Y. L., L. G. MONTGOMERY, S. D. SAFFORD, P. G. IGIC, AND J. C. SAUNDERS. 1998. How body size affects middle-ear structure and function and auditory sensitivity in gekkonoid lizards. *Journal of Experimental Biology* 201:487–502.
- WERNER, Y. L., AND A. H. WHITAKER. 1978. Observations and comments on the body temperatures of some New Zealand reptiles. *New Zealand Journal of Zoology* 5:375–393.

Accepted: 24 April 1998

Associate Editor: Allison Alberts

Herpetologica, 55(2), 1999, 222–234
© 1999 by The Herpetologists' League, Inc.

COMPARISONS OF TEMPORAL DISPLAY STRUCTURE ACROSS CONTEXTS AND POPULATIONS IN MALE *ANOLIS CAROLINENSIS*: SIGNAL STABILITY OR LABILITY?

MATTHEW B. LOVERN, THOMAS A. JENSSEN, KIMBERLY S. ORRELL, AND TRAVIS TUCHAK¹

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

ABSTRACT: We examined the relative stability versus lability of temporal display structure in males of the lizard *Anolis carolinensis*. We videotaped headbobbing displays across field and laboratory environments, social contexts, and populations for males from Georgia, Florida, and Hawaii, and subsequently generated display-action-pattern (DAP) graphs of these displays for statistical comparison. *Anolis carolinensis* is known to be a recent (circa 1950) colonizer of Hawaii, and displays from this population could therefore be altered through founder effects, genetic drift, and/or a tropical environment unlike that encountered over the rest of the species' range. Therefore, we expected to find lability in temporal display structure between Hawaiian and mainland populations. In contrast, we found that males from each population used the same three, highly stereotyped temporal display structures (i.e., display types, labeled A, B, and C) in their display repertoires, and that all three of these types were used across all measured recording environments and social contexts. Furthermore, intra-display structure was not affected by recording environment or social context, but within the relatively small total variance, a significant population effect was found for a majority of intra-display units.

Key words: Sauria; *Anolis carolinensis*; Communication; Display; Intraspecific variation

COMMUNICATION signals, both their physical structure and their functional expression, are shaped by numerous and potentially antagonistic selection pressures resulting from features of the biotic and abiotic environments (e.g., Endler, 1992; Fleishman, 1992; Hailman, 1977; Ryan

and Rand, 1990). Yet, despite diverse selection pressures, communication signals frequently share some commonly recognized features. Structurally, these signals tend to be species-typical with pronounced stereotypy (Barlow, 1968) in both invertebrates (e.g., Bentley and Hoy, 1972; Lloyd, 1975) and vertebrates (e.g., Hauser, 1996; Jenssen, 1977, 1978; Marler and Peters, 1977; Ryan and Rand, 1993a,b; Tin-

¹ PRESENT ADDRESS: Department of Zoology, Arizona State University, Tempe, AZ 85287, USA.