Behavioral Thermoregulation Increases Growth Rate in a Nocturnal Lizard

KELLAR AUTUMN1,2 AND DALE F. DE NARDO2

1Museum of Vertebrate Zoology and 2Department of Integrative Biology, University of California, Berkeley, Berkeley, California 94720, USA

ABSTRACT.—We tested the hypothesis that thermoregulation increases growth rate in nocturnal lizards. Leopard geckos (Eublepharis macularius) maintained from hatching at 25 C grew at a rate of 0.11 g/day, while geckos allowed to thermoregulate at preferred body temperatures (30 C for 13.5 h per day) grew 1.5 times as fast (0.16 g/day). Long-term thermal treatment had a significant reverse acclimation effect on preferred body temperature (Tp): Tp was 1.2 C lower in thermoregulatory individuals than in those kept at 25 C. Feeding and time of day also had significant but minor effects on Tp. Despite their nocturnal ecology, leopard geckos seem to be typical among lizards in requiring a diurnal heat source for maximal growth. This result provides a physiological explanation for the observation that some nocturnal lizards thermoregulate in burrows during the day, and may have implications for the biogeography of nocturnal ectotherms.

Nocturnality and diurnality form one of the few dichotomous niche parameters. Lizards are ancestrally diurnal and the majority of lizard species, genera, and families have remained diurnal. While nocturnality has arisen independently several times, the Gekkonoidea contains most nocturnal lizard species. Unique adaptations may have arisen that permit lizards, and particularly geckos, to be nocturnal. Because of a limited opportunity for thermoregulation at night, nocturnality requires activity at lower temperatures than does diurnality (Huey et al., 1989; Autumn et al., 1994). Optimality theory predicts the coadaptation of (physiological) thermal optima and activity temperatures (Huey and Slatkin, 1976; Huey and Bennett, 1987; Hailey and Davies, 1988; Huey and Kingsolver, 1989; Huey et al., 1989). In the best of all worlds, nocturnal lizards would achieve maximum performance capacity at their activity temperatures. However, the thermal optima for sprinting and sustained locomotion are much higher than the body temperatures (Tb) nocturnal lizards experience at night (Huey et al., 1989; Autumn et al., 1994). Nocturnality may impose a thermal handicap that constrains performance to submaximal levels (Autumn et al., 1994). This controversial finding implies that it is not possible to predict the evolution of physiology from ecology alone.

Nocturnal lizards may actively thermoregulate during the day (Bustard, 1967; Werner and Whitaker, 1978; Huey et al., 1989; Autumn et al., 1994). Using radiotelemetry, Autumn et al. (1994) found that a nocturnal gecko had a daily thermal cycle typical of a diurnal lizard: high Tb during the day and low Tp at night. It has long been known that nocturnal lizards choose higher body temperatures in a laboratory thermal gradient than they experience during field activity (Licht et al., 1966; Huey, 1982; Arad et al., 1989). The preferred body temperature, in theory, could reflect physiological requirements (Cowles and Bogert, 1944; Licht et al., 1966; Huey and Bennett, 1987; Huey and Kingsolver, 1989). Digestion, reproduction, and growth in lizards require the products of rate processes that may be sufficiently rapid at temperatures generally available only during the day (30–45 C; Cowles and Bogert, 1944; Dawson 1975; Andrews, 1982; Avery, 1984; Stevenson et al., 1985; Hailey and Davies, 1987; Troyer, 1987). In this study, we test the hypothesis that nocturnal lizards require diurnal temperatures for maximal growth rates. If so, while nocturnal lizards forage at night, they could be dependent on diurnal heat sources while in burrows. This requirement might represent an evolutionary constraint that limits the geographic distribution of nocturnal species.

MATERIAL AND METHODS

Animals and Husbandry.—Eublepharis macularius (leopard gecko) is a strictly nocturnal, terrestrial, lizard found in southern Iraq and throughout western Pakistan (Minton, 1966). Leopard geckos are found at altitudes up to 3200 m (Minton, 1966). Adults range in size from approximately 100 to 160 mm, snout-vent length. We obtained 24 captive-born, female, hatchling leopard geckos from the Institute for Reptile Reproduction, Hayward, CA. Animals were housed individually in clear plastic rodent cages (25 x 48 x 20 cm). Cages contained no added substrate, but PVC pipe segments at both ends of the cage provided shelter for the lizards.
During the growth experiment, we provided the lizards with 5–6 wk old crickets 3 times per wk in numbers sufficient to assure that all crickets were not eaten before the next feeding. At the time of feeding, we recorded the number of crickets eaten during the last period, removed the uneaten crickets, and added new crickets to the cage as described above. For statistical analysis, food consumption was the number of crickets eaten per week. Once per week, crickets were dusted with vitamin-mineral and calcium gluconate powder before introduction into the gecko cages. Crickets were maintained on an ad lib. diet of Purina Monkey Chow and water. The geckos were provided water via cage misting twice per week. In order to determine the effect of feeding in the preferred body temperature experiment, we alternately fed the geckos ad libitum and starved them for one week.

Growth.—Lizards were housed in an environmentally controlled room with a 14L:10D photoperiod at 24.5 ± 1.0 C. A control group of 12 randomly selected geckos was maintained in cages as described above, with no supplemental heat source. The 12 remaining geckos comprised the thermoregulatory treatment group. The cages were arranged on a rack in four rows of six cages. The control group occupied the top and bottom rows, while the treatment group occupied the middle two rows. The treatment group was provided with a 7.5 cm wide strip of Flexwatt (Flexwatt USA) heating element under one end of each cage. The Flexwatt was on a 13.5 h on, 10.5 h off cycle to coincide with the onset of light to the access to heat. This delay simulated the situation in a burrow where thermal inertia would delay heating following sunrise. The Flexwatt heated the cage floor immediately above it to 35 C. We recorded gecko mass weekly and food intake three times per week as described above. The experiment was terminated after 140 d when the geckos had reached sexual maturity.

Preferred Body Temperature.—At the completion of the growth experiment (see above), we determined the preferred body temperature \( T_p \) of *E. macularius* by placing each lizard in an enclosure which measured 10 × 85 cm. A thermal gradient was created within the enclosure using a modified strip of Flexwatt layered under a stainless steel sheet along the bottom. We modified the Flexwatt to produce a gradual thermal gradient by removing an increasing number of the horizontal heating elements along the length of the strip. The stainless steel sheet provided sufficient conductivity to smooth the gradient between operating heating elements. The gradient was approximately linear and ranged from 18–50 C. This sub-surface thermal gradient mimicked a burrow by providing a thermal choice independent of light intensity. \( T_p \) was measured in all individuals. We placed geckos individually in each of two lanes in the enclosure the night before measurement and captured them by hand once at midday and once at 1 to 3 h following darkness. We recorded cloacal temperature immediately (in less than 15 sec) after capture using a calibrated thermometer accurate to ±0.1 C (Miller & Weber; calibration determined using a Fluke 25 thermocouple module). We measured all animals after normal feeding and then again after a one week starvation period.

Statistics.—For the growth experiment we used a multivariate repeated measures analysis of variance (ANOVAR) to determine the effect of thermoregulatory treatment on growth rate. This technique accounts for non-independence among repeated measures of individuals over time (Potvin et al., 1990). We defined growth rate as the absolute change in log body mass per time, for each sampling period. The assumptions of parametric statistics require log transformation of the mass data (Niewiarowski and Roosenburg, 1993). The multivariate ANOVAR model used thermoregulatory treatment, time, and subject (nested within treatment) as main effects. The model included the interactions, time × treatment, and time × subject (group). The subject (group) and time × subject (group) terms account for repeated measurements of individuals over time. We used Greenhouse-Geiser and Huynh-Feldt epsilon factors to adjust the significance of the effects of time and time × treatment. In a second analysis (univariate repeated measures analysis of covariance; ANCOVAR) we investigated the effect of thermoregulatory treatment on consumption. The univariate ANCOVAR model used treatment, time, and subject (group) as main effects, and mass as a covariate. Because the two analyses are not independent, we emphasized the first in our conclusions, and used the second for primarily descriptive purposes. For the \( T_p \) experiment we used analysis of variance (ANOVA) to determine the effect of acclimation treatment, time of day, and digestive state (starved versus fed) on \( T_p \). We used paired comparisons to determine the significance of contrasts among means. Insignificant factors or interactions were not deleted from the models. In order to validate the assumptions of the models, we checked plots of mass residuals versus covariates and fitted Y-values for patterns, and determined the symmetry of the mass residuals about zero. For all statistical analyses we used the computer program SuperANOVA v.1.11 (Abacus) on a Macintosh II.
THERMOREGULATION SPEEDS GROWTH IN A GECKO

FIG. 1. Mean body mass over time in captive leopard geckos (Eublepharis macularius) raised from hatching under two thermal conditions. Circles represent means of body mass in geckos allowed to thermoregulate at diurnal temperatures. Squares represent means of body mass in geckos maintained at a constant nocturnal temperature (25°C). Bars represent standard errors. Geckos maintained at 25°C grew at a rate of 0.11 g/day, while geckos allowed to thermoregulate grew 1.5 times as fast (0.16 g/day). Despite their nocturnal ecology, leopard geckos may be typical among lizards in requiring diurnal temperatures for maximal growth rates.

RESULTS

Growth.—Growth rate (ΔMg) in both treatment groups was approximately constant over the duration of the experiment (Fig. 1). Thermoregulatory treatment had a highly significant effect on ΔMg (Table 1). Geckos allowed to thermoregulate grew 1.5 times faster than geckos kept constantly at low temperatures. Since consumption may have an effect on growth (Baupre et al., 1993) we analyzed the factors affecting consumption for primarily descriptive purposes. Mass and time both had a significant effect on consumption (Fig. 2, Table 2). However, once the effect of mass has been accounted for, there was no significant effect of treatment (thermoregulation) on consumption. Combined with our results for growth, this implies that (1) geckos allowed to thermoregulate grew faster, and (2) larger geckos eat more. There was no pattern evident in plots of residuals versus covariates and fitted Y-values, and the residuals were nearly symmetrical about zero. This suggests that our statistical assumptions were valid.

Preferred Body Temperature.—Fed lizards selected body temperatures an average of 0.9°C lower than starved lizards (F = 6.4; df = 1, 81; P = 0.01). This effect was due primarily to a low mean Tp in fed, thermoregulatory group lizards (Table 3). Mean Tp was 1.2°C lower in the thermoregulatory group than in the low temperature group (F = 4.9; df = 1, 81; P = 0.03). Time of day had no significant overall effect on Tp, however Tp was significantly lower in the thermoregulatory group than in the low temperature group at night (Table 4). Also, Tp was significantly lower in fed than starved lizards at night.

Table 1. Analysis of variance of growth rate (ΔMg) in 23 leopard geckos raised from birth under two thermal conditions (treatments). Treatment effects were highly significant, indicating that thermoregulation increased ΔMg. The significance of sources of variation involving repeated measurements over time are adjusted using Greenhouse-Geiser (G-G) and Huynh-Feldt (H-F) epsilon factors.

<table>
<thead>
<tr>
<th>Sources of variation</th>
<th>MS</th>
<th>F</th>
<th>df</th>
<th>P</th>
<th>Corrected P (G-G)</th>
<th>Corrected P (H-F)</th>
<th>Error term</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>0.006</td>
<td>13.15</td>
<td>1</td>
<td>0.0016</td>
<td></td>
<td></td>
<td>Subject (Group)</td>
</tr>
<tr>
<td>Subject (Group)</td>
<td>0.000433</td>
<td>21</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>0.006</td>
<td>9.55</td>
<td>19</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>Time × Subject (Group)</td>
</tr>
<tr>
<td>Time × Treatment</td>
<td>0.000394</td>
<td>0.67</td>
<td>19</td>
<td>0.8</td>
<td>0.7</td>
<td>0.7</td>
<td>Time × Subject (Group)</td>
</tr>
<tr>
<td>Time × Subject (Group)</td>
<td>0.001</td>
<td>399</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Analysis of variance of food consumption in 23 leopard geckos raised from birth under two thermal conditions (treatments). There was no significant effect of treatment on consumption, once the effects of body mass, time, and growth (time x mass) were accounted for. This implies that treatment-induced differences in growth rate (Table 1) were not simply due to differences in consumption.

<table>
<thead>
<tr>
<th>Sources of variation</th>
<th>MS</th>
<th>F</th>
<th>df</th>
<th>P</th>
<th>Error term</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass</td>
<td>214.60</td>
<td>22.49</td>
<td>1</td>
<td>0.0001</td>
<td>Subject (Group)</td>
</tr>
<tr>
<td>Treatment</td>
<td>38.74</td>
<td>4.06</td>
<td>1</td>
<td>0.06</td>
<td>Subject (Group)</td>
</tr>
<tr>
<td>Subject (Group)</td>
<td>9.54</td>
<td></td>
<td>21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>4.44</td>
<td>1.95</td>
<td>20</td>
<td>0.009</td>
<td>Time x Subject (Group)</td>
</tr>
<tr>
<td>Time x Mass</td>
<td>10.44</td>
<td>4.44</td>
<td>20</td>
<td>0.0001</td>
<td>Time x Subject (Group)</td>
</tr>
<tr>
<td>Time x Treatment</td>
<td>2.45</td>
<td>1.05</td>
<td>20</td>
<td>0.4</td>
<td>Time x Subject (Group)</td>
</tr>
<tr>
<td>Time x Subject (Group)</td>
<td>2.35</td>
<td></td>
<td>399</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

DISCUSSION

Growth.—Despite their nocturnal ecology, individuals of Eublepharis macularius were similar to diurnal lizards in increasing growth rate by thermoregulating at typically diurnal temperatures (Fig. 1). Strong evidence exists that digestion rate in ectotherms decreases rapidly with decreasing body temperature (Dawson, 1975; Andrews, 1982; Avery, 1984; Stevenson et al., 1985; Hailey and Davies, 1987; Troyer, 1987). We did not measure digestion in this study, and can only speculate that the thermal sensitivity of digestive processes was partially responsible for the differences in growth rate. Food consumption and size are clearly related and our results suggest that differences in size were responsible for differences in consumption (Fig. 2, Table 2).

Preferred Body Temperature.—$T_p$ in E. macularius is consistent with values for other geckos, and is 5°C lower than the mean $T_p$ for 13 species of diurnal lizards (Huey et al., 1989). $T_p$ measured in this study is 3.8 to 4.1°C higher than the $T_p$ reported for starved E. macularius by Dial and Grismer (1992). There was a slight (1°C) reverse acclimation effect on $T_p$ in E. macularius. This is the opposite of the acclimatory pattern found in Xantusia vigilis (Kaufmann and Bennett, 1989). The reverse acclimation effect on $T_p$ in E. macularius could be a behavioral artifact due to greater locomotor activity in the thermoregulatory group than in the low temperature group when in the thermal gradient. Geckos of the low temperature group tended to remain immobile in the gradient. Possibly, heat was a high-priority resource to geckos raised in the absence of diurnal temperatures. Contrary to expectations (Regal, 1966; Gatten, 1974; Harlow et al., 1976; Waldschmidt et al., 1986; Lilleywhite, 1987; Lutterschmidt and Reinert, 1990; Kanui, 1991), there was no postprandial increase in $T_p$. This pattern is not unique; several studies report the absence of postprandial thermophily in ectothermic reptiles (see Brown and Brooks, 1991). While there were highly significant effects of feeding (Table 3) and thermoregulatory treatment on $T_p$, the differences were quite small (<2°C). $T_p$ appears to be a biologically meaningful and consistent variable in E. macularius, and may represent physiological requirements (Licht et al., 1966; Dawson, 1975). The range of field body temperatures (10–45°C) in lizards is much greater than the range of $T_p$. This implies that thermal physiology is relatively conservative in lizards.

Ecophysiological Consequences of Nocturnality.—It is unlikely, during most nights, that these geckos could achieve field body temperatures near their thermal optimum ($T_o$) or $T_p$ for a sig-

Table 3. Preferred body temperature (°C ± SE) in fed and starved leopard geckos raised from birth under two thermal conditions. Superscripts (A and B) denote significant pairwise comparisons of group means (ANOVA; df = 1, 81; P < 0.001 for all 3 comparisons).

<table>
<thead>
<tr>
<th></th>
<th>Thermoregulatory</th>
<th>Low temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fed</td>
<td>28.7 ± 0.392*</td>
<td>30.5 ± 0.286*</td>
</tr>
<tr>
<td>Starved</td>
<td>30.6 ± 0.287*</td>
<td>30.3 ± 0.371*</td>
</tr>
</tbody>
</table>

Table 4. Preferred body temperature (°C ± SE) during laboratory daytime and nighttime in 24 adult leopard geckos raised from birth under two thermal conditions. Superscripts (A and B) denote a significant pairwise comparison of group means (ANOVA; F = 9.5; df = 1, 81; P < 0.01).

<table>
<thead>
<tr>
<th></th>
<th>Thermoregulatory</th>
<th>Low temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day</td>
<td>29.9 ± 0.341*</td>
<td>30.0 ± 0.344*</td>
</tr>
<tr>
<td>Night</td>
<td>29.4 ± 0.433*</td>
<td>30.7 ± 0.320*</td>
</tr>
</tbody>
</table>
significant length of time (Werner, pers. comm.). There are at least two possible consequences of this (which are not mutually exclusive): (1) Nocturnality imposes a thermal handicap that constrains growth to submaximal rates. (2) Diurnal thermoregulation occurs in the burrow which allows $T_b$ to approach $T_a$. The latter possibility has been discussed by Bustard (1967) and others (Huey et al., 1989; Autumn et al., 1994), but few data exist. The heat sum (days·K above a threshold temperature; Skre, 1972) required for a complete lizard life cycle may not be available at night.

If nocturnal lizards require diurnal temperatures for maximal growth (and perhaps for reproductive functions as well), this could explain the decreasing proportion of nocturnal to diurnal species with increasing latitude. At high latitudes, heleothermic species could achieve near optimal $T_b$ for a sufficient length of time to meet the demands of growth and reproduction, while thigmothermic species confined to burrows could not. High latitude nocturnal lizards might have to be long-lived and slow-growing. At low latitudes, nocturnal lizards may have an advantage in utilizing the burrow during the day as a thermally buffered microhabitat that is both a humid refuge and a thermal gradient. Thermoregulation in diurnal heleotherms may be much more ecologically costly (Huey and Slatkin, 1976) due to the precise temporal, spatial, and postural adjustments required to avoid lethal body temperatures (Cowles and Bogert, 1944; Porter et al., 1973; Muth, 1977; Losos, 1987), and the probable increased risk of predation. Much work remains to be done in addressing these questions. Recent advances in modelling growth potentials (Porter, 1989) could be applied to determine the effect of environment (e.g., nocturnality, latitude, temperature) on performance capacity (e.g., growth potential).

Future research should address the role of diurnal thermoregulation in nocturnal lizard ecology. Radiotelemetry will undoubtedly be crucial in the collection of these data. The causal relationships among body temperature, food consumption, digestion, and growth in nocturnal lizards requires further investigation.

Acknowledgments.—We thank Harry Greene, Paul Licht, Yehudah Werner, Doug Price, Linda Pollack, Barbara Shoplock, the staff of the U.C. Berkeley Office of Laboratory Animal Care, and three anonymous reviewers.

LITERATURE CITED


HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles. In C. Gans and F. H. Pough,
K. AUTUMN AND D. F. DE NARDO


Accepted: 1 January 1995.