DIEL VARIATION IN PREFERRED BODY TEMPERATURES OF THE MOORISH GECKO *TARENTOLA MAURITANICA* DURING SUMMER

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We studied diel variation in preferred body temperatures (T_p) of adult and subadult geckos (*Tarentola mauritanica*) in a laboratory thermogradient. Overall T_p averaged 31.6°C and is significantly higher that the activity body temperatures recorded in the field. We did not detect differences in T_p between adult and subadult lizards. T_p varied according to a diel cycle. There was a gradual increase in T_p during the afternoon-early evening period, leading to peak values just before the beginning of the night-time activity period. During the subsequent hours, T_ps decrease again.

INTRODUCTION

Lizards are well known for their capacity to precisely regulate body temperature through the exploitation of environmental heat sources by means of behavioural adjustments (review in Huey, 1982). Nevertheless, some forms have only restricted access to heat during routine activities. Geckos provide a striking example. Most species of geckos restrict surface activity and foraging to the night, when ambient temperatures are low and opportunities for behavioural regulation are severely limited (Porter & Gates, 1969). Hence, it is not surprising that most nocturnal geckos exhibit lower and more variable activity body temperatures than sympatric diurnal lizards (Stebbins, 1961; Licht, Dawson, & Shoemaker, 1966a; Heatwole, 1976; Werner, 1976; Werner & Whittaker, 1978; Pianka & Huey, 1978; Avery, 1982; Pianka, 1986; Huey, Niewiarowski, Kaufmann & Herron, 1989). However, differences in activity body temperatures between diurnal and nocturnal lizards might reflect dissimilarities in thermal preferences, instead of being a direct consequence of differences in environmental constraints. In other words, the mere observation of lower and more variable body temperatures in nocturnal lizards does not provide information on the proximal mechanisms - environmental constraints and/or thermal preferences -that induce this difference (Huey, 1982). One way to overcome this problem is to assess thermal preferences, and use them as an independent yardstick for the evaluation of differences in activity body temperatures (Van Damme, Bauwens & Verheyen, 1986, 1987; Hertz, Huey & Stevenson, 1993).

The preferred (or selected [Pough & Gans, 1982]) body temperatures of ectotherms, measured in a laboratory thermogradient, indicate the range of body temperatures that lizards will maintain in the absence of abiotic and biotic restrictions (Licht *et al.*, 1966a; Van Damme *et al.*, 1986). They estimate the preference zone of body temperatures maintained by behavioural thermoregulation, and reflect a behavioural choice (Huey, 1982). However, the preferred temperature cannot be considered as a fixed characteristic for a given species, because it has been shown to be subject to considerable intraspecific variation (Huey, 1982).

Here we present results of a preliminary study of the preferred body temperatures of the gecko *Tarentola mauritanica*. This is a medium-sized gecko (adult snout-vent length: 47.4 - 75.1 mm) found over most of the Mediterranean areas of Europe. It is very often associated with human habitations, and restricts foraging to the night, although in some parts of its range individuals may be seen basking in sunshine during early morning or late afternoon. Our objectives were to (1) determine preferred body temperatures and critical thermal minimum and maximum temperatures; (2) examine differences in thermal preferences between age classes; and (3) explore the extent of diel variations in thermal preferences. In a forthcoming study, we will use this information to evaluate proximal causes of variations in activity body temperatures.

MATERIALS AND METHODS

Five adult and five subadult (= immature) geckos were caught during July 1992 near Candeleda (40°05' N - 05°10' W; prov. Avila; Spain; altitude = 400 m). Lizards were transported to the laboratory, where they were kept for one week in large terraria on a 15L : 9D natural photoperiod. Water and food (mealworms) was available *ad libitum*. Lizards were marked individually with colour codes on the body.

The five adult lizards were then transferred to a thermal gradient. This was a rectangular terrarium (100 x 50 x 50 cm) with a 250 W ceramic heat bulb suspended above one end, and a cooling system with ice in the other. Light was provided during the day by a fluorescent tube suspended above the centre of the terrarium.

The substratum consisted of a 4 cm layer of sand. Fifteen floor-tiles (15 x 15 cm) were placed at regular intervals over the total length of the terrarium, with one side tilted 5 cm above the surface. The tiles provided both shelter and opportunities for thermoregulation by thigmothermy. Surface temperature in the gradient ranged from 19.3 to 68.7 °C. No food was provided, but water was available in small dishes. Lizards were given two days to habituate to the experimental conditions. During the next two days, we recorded the body temperatures of the lizards during two five hour periods: 1630 - 2030 hr, which corresponds to the warmest period of the day in the field, and 2230 - 0230 hr, which is the period of maximal lizard activity in nature (Gil, 1992). Each individual lizard was taken out of the gradient at hourly intervals, and we measured its cloacal (=body) temperature, to the nearest 0.1° C, with a thermocouple connected to an electronic thermometer (Digitron). We only took measurements for lizards that were undisturbed prior to capture. This procedure was then repeated for the group of five subadult lizards.

As we repeatedly sampled body temperatures of each individual lizard, we analysed these data by a two-way ANOVA with repeated measurements. Some lizards were disturbed prior to capture, so that on each experimental day some hourly body temperature records were missing for some individuals. Although the ANOVA designs allow for missing data, we retained for analysis the average body temperature recorded during the two days for each individual, time period and hour as this is the ideal situation for this method. The ANOVA was designed with two "within" factors (period [day or night] and hour) and one "between" factor (age class [adult or subadult]). This allows testing of differences in preferred temperatures between age classes, periods and hours, and of the in-teraction effect between these factors. We also used the Greenhouse-Geisser epsilon (G-G) and Hunyh-Feldt epsilon (H-F) correction (Keppel, 1991) because the sphericity assumption will rarely be satisfied in a repeated measurement study as the correlation between responses close together in time will tend to be greater than the correlation between responses far apart in time.

RESULTS

Preferred temperatures (T_p) of *Tarentola mauritanica* are normally distributed (Kolmogorov-Smirnov test: $DN = 0.03$, $P = 0.99$), so parametric analyses are appropriate. Overall, T_p averages 31.56°C (SE = 0.17, $n = 151$); the interquartile range (the range including the central 50% of the temperature measurements, a non- parametric statistic of variance) equals 2.55°C. The preferred temperatures are considerably higher than the activity body temperatures measured in the field during the same period and study area ($\bar{x}$ = 24.8 °C, SE = 0.51, $n = 30$ [Gil, 1992]; $t = 14.1$, $P < 0.001$).

The results of the two-way ANOVA are summarized in Table 1. There are no significant differences between lizard age-classes, time periods (day or night), or hours. However, the interaction effect of period by hour is highly significant (Table 1). T_ps increase gradually during the course of the day period, whereas they decrease during the night (Fig. 1). During each of the two periods, significant hourly variation in T_p were detected (one-way ANOVA with repeated measurements; day: $F = 3.71$, df = 4, 36, $P < 0.02$; night: $F = 3.20$, df = 4, 36, $P < 0.05$).

Variance in preferred temperatures did not differ between the day and night periods, or among hours within each of the two periods (Bartlett's test for homogeneity of variances, $P > 0.05$ in all cases).

	df	SS	MS	F	P	G-G	H-F
Age-class	1	4.22	4.22	0.44	0.52		
Subject	8	76.31	9.53				
Period	1	3.74	3.74	1.46	0.26	0.26	0.26
Period*Age-class	1	0.85	0.85	0.33	0.57	0.57	0.57
Period*Subject	8	20.51	2.56				
Hour	4	3.71	0.29	0.95	0.44	0.40	0.43
Hour*Age-class	4	2.06	0.51	0.52	0.71	0.60	0.67
Hour*Subject	32	31.23	0.97				
Period*Hour	4	24.82	6.20	5.11	0.00	0.06	0.00
Period*Hour*Age-class	4	2.94	0.73	0.60	0.66	0.61	0.66
Period*Hour*Subject	32	38.84	1.21				

TABLE 1. Results of the two-way ANOVA with repeated measurements, analysing variation in preferred body temperatures as a function of Period (day or night), Hour, Age-class (adult or subadult), and their interactions. df = degree of freedom; SS = sum of squares; MS = mean square; G-G : Greenhouse-Geisser correction; H-F : Hunyh-Feldt correction.
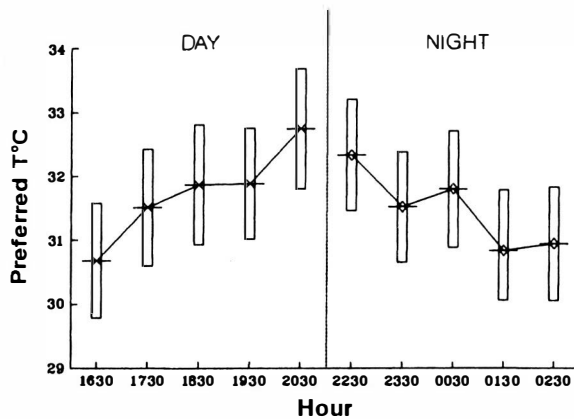
Fig. 1. Average (± 1 SE) preferred body temperatures for adult and subadult *T. mauritanica* at different hourly intervals during the day and night experimental periods.

DISCUSSION

Preferred body temperatures of *Tarentola mauritanica* recorded in a laboratory thermogradient averaged approximately 8 °C higher than the activity body temperatures recorded in nature. This result is consistent with that observed in many other geckos (Licht, Dawson, Shoemaker & Main, 1966b; Dial, 1978; Huey et al., 1989). Given that T_ps are measured in a laboratory environment where abiotic constraints are absent (Licht et al., 1966a; Van Damme et al., 1986), we infer that environmental conditions in nature severely restrain the geckos' abilities to maintain body temperatures near the preferred range. We did not measure the thermal dependence of physiological or whole-animal performance traits, so that we cannot explore to what extent activity or preferred temperatures match the physiologically-optimal temperatures. In other nocturnal geckos, optimal temperatures for sprint speed are substantially higher than field body temperatures (mean difference for four species = 7.1 °C) , and preferred temperatures (mean difference for four species = 3.8 °C) (Huey et al., 1989). Hence, these geckos generally forage at body temperatures that are suboptimal for sprinting (Huey et al., 1989). These authors suggested that the thermal physiology of nocturnal geckos might be coadapted not to the low body temperatures maintained when foraging at night, but rather to the high body temperatures geckos may experience during the day, especially if cold diurnal retreats are unavailable (Heatwole, 1976; Dial, 1978; Huey, 1982).

Our results show significant diel variation in preferred body temperatures, even though ambient conditions in the thermogradient remained constant. Hence, lizards had the opportunity to maintain invariable body temperatures throughout the experimental period. We therefore interpret the observed diel fluctuation as an active shift in behavioural preferences. Diel cycles in T_ps have been observed in several other ectotherms (see review in Sievert and Hutchison, 1988). Together with observations of variation related to age, sex, reproductive condition, and season (e.g., Patterson & Davies, 1978; Beuchat, 1986; Van Damme et al. 1986; Daut & Andrews, 1993), they indicate that preferred temperatures cannot be considered as a fixed trait (Huey, 1982), but that they are subject to considerable intraspecific variation.

Preferred body temperatures of *Tarentola mauritanica* exhibit a gradual increase of approximately 2 °C during the final hours of the day, followed by an equivalent decline during the first five hours of the night. Consistent with the adoption of the highest T_ps during the late afternoon are field observations of overt basking behaviour at that time of the day (Martinez-Rica, 1974).

Two hypotheses may account for the increase in T_p during the final part of the day. First, a preference for relatively low body temperatures during the hot afternoon hours, may induce lizards to choose moderately cool retreat sites, thereby reducing the risk of overheating. Second, the maintenance of fairly high preferred temperatures during the late afternoon, just before the onset of surface activity in the field (Gil, 1992), can be considered as a mechanism to prolong the duration of night-time activity. Due to a scarcity of external heat sources, nocturnal geckos probably have limited opportunities to behaviourally control their body temperatures. Hence, body temperatures of active geckos will decline gradually during the course of the night, until they reach a lower threshold which induces lizards to cease surface activity (Bustard, 1967). At a given cooling rate, the duration of activity should therefore be a function of the body temperature maintained at the initiation of activity, with higher initial temperatures being associated with longer activity periods.

During the night, preferred temperatures are highest in the first few hours after sunset, coinciding with the period of maximum activity in the field (Gil, 1992) when environmental temperatures are still high (Bustard, 1967; Pianka & Pianka, 1976). The availability of external heat sources, and hence opportunities to raise body temperatures, probably decrease during the night. The observed decline of preferred body temperatures during the night might therefore be considered as a mechanism that tends to reduce the time spent in thermoregulatory behaviours.

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