

Body temperature regulation in the amphisbaenian *Trogonophis wiegmanni*

Pilar López, Emilio Civantos, and José Martín

Abstract: We studied the thermal ecology of the amphisbaenian *Trogonophis wiegmanni* at the Chafarinas Islands (North Africa). We aimed to evaluate the extent of thermoregulation in this fossorial amphisbaenian by analyzing the relationships between environmental available operative (T_e) and body (T_b) temperatures of active individuals found under stones. Amphisbaenians are typical thigmotherms that obtain heat through contact with soil and, thus, T_b was closely correlated to T_e under stones. However, the comparison of T_b with T_e s available in the study area indicated that T_b deviated less from the set-point range of preferred temperatures than would result from a random response, which is indicative of behavioral temperature regulation. Measurements of T_e under rocks selected by *T. wiegmanni* deviated significantly less from the range of preferred temperatures than T_e beneath available rocks. This suggests that amphisbaenians occupied rocks with or when thermal properties were suitable for maintaining their preferred T_b . We found a bimodal pattern of T_b during the day, with amphisbaenians being active at higher T_b during the afternoon than in the morning. This did not reflect changes in the thermal environment, but was presumably a voluntary selection pattern, as indicated by similar results obtained in thermal gradients in a previous study. Also, juveniles had higher T_b than adults, but this might be a biophysical effect of differences in body size and heating rates. We conclude that amphisbaenians seem capable of regulating body temperature to an extent that comparable with epigeal diurnal lizards.

Résumé : Nous avons étudié l'écologie thermique de l'amphisbénien *Trogonophis wiegmanni* dans les îles Chafarinas (Afrique du Nord). Notre objectif était d'évaluer l'importance de la thermorégulation chez cet amphisbénien fouisseur, par l'analyse des relations entre les températures de fonctionnement disponibles dans l'environnement (T_e) et la température du corps (T_b), chez des individus actifs trouvés sous les pierres. Les amphisbénien sont des organismes thigmothermes typiques qui captent la chaleur du sol par contact et, de ce fait, T_b s'est révélée en corrélation étroite avec T_e sous les pierres. Cependant, la comparaison de T_b aux températures T_e disponibles dans l'environnement indique que T_b s'éloigne moins de l'étendue des valeurs de référence des températures préférées que si elle était déterminée de façon aléatoire, ce qui indique un contrôle comportemental de la température. Les températures T_e sous les pierres choisies par *T. wiegmanni* s'éloignent moins de l'étendue des températures préférées que les températures T_e sous les pierres disponibles. Cela semble indiquer que les amphisbénien choisissent les pierres avec des propriétés thermiques qui permettent le maintien de leur température T_b préférée. Nous avons constaté que la température T_b suit une courbe bimodale durant le jour; les amphisbénien sont plus actifs à des températures T_b plus élevées l'après-midi que le matin. Cela ne reflète pas des changements dans l'environnement thermique, mais relève probablement d'un pattern de sélection volontaire, si on en juge par les résultats semblables obtenus le long de gradients thermiques au cours d'une étude antérieure. De plus, les températures T_b des juvéniles sont plus élevées que celles des adultes, mais il peut s'agir là d'un effet biophysique relié à des différences dans la taille du corps ou les taux de réchauffement. Les amphisbénien semblent donc capables de contrôler la température de leur corps autant que le font les lézards épigées diurnes.

[Traduit par la Rédaction]

Introduction

In ectotherm animals, such as reptiles, the attainment and regulation of an optimal body temperature range is essential, to maximize numerous physiological and ecological processes

(Huey 1982). Careful behavioral thermoregulation increases the time that reptiles spend at physiologically favorable body temperatures (Grant and Dunham 1988; Bauwens et al. 1996). Recent studies have established a comprehensive protocol for analyzing thermoregulation in reptiles by comparing data on selected temperatures, the operative temperatures available to field-active animals, and the resultant field body temperatures (Hertz 1992; Hertz et al. 1993, 1999), and by evaluating the contribution of behavioral mechanisms to temperature regulation (Bauwens et al. 1996). However, most studies of reptilian thermal biology are based primarily on easily watched epigeal taxa, such as lizards and snakes (Avery 1982; Huey 1982). In contrast, the thermal ecology of fossorial reptiles is poorly known, because observations under natural conditions are difficult (but see Papenfuss 1982; Martín et al. 1990; Gil et al. 1993; López et al. 1998) and because evalu-

Received 21 February 2001. Accepted 29 October 2001.
Published on the NRC Research Press Web site at
<http://cjz.nrc.ca> 17 January 2002.

P. López,¹ E. Civantos,² and J. Martín. Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (Consejo Superior de Investigaciones Científicas), José Gutiérrez Abascal 2, 28006 Madrid, Spain.

¹Corresponding author (e-mail: Pilar.Lopez@mncn.csic.es).

²Present address: Department of Engineering and Natural Sciences, University of Växjö, S-351 95 Växjö, Sweden.

ating the extent of thermoregulation in fossorial ectotherms is difficult.

Epigeal lizards are able to maintain their body temperature within relatively narrow ranges through behavioral means, by modifying basking frequency, activity times, and microhabitat use (Huey 1982; Waldschmidt and Tracy 1983; Adolph 1990). However, behavioral thermoregulation may sometimes be too costly in terms of time and energy expended (Huey and Slatkin 1976) and, in such cases, some epigeal lizards can become relative thermoconformers (Hertz and Huey 1981). Thus, the relatively low field body temperatures that characterize most fossorial reptiles (Avery 1982), including amphisbaenians (Gatten and McClung 1981; Papenfuss 1982; Abe 1984; Martín et al. 1990; Hailey and Elliot 1995; Al-Johany 1999), have been considered as a convergent adaptation to the limitations of the underground environment. Nevertheless, recent studies of the amphisbaenian *Blanus cinereus* have shown that, although its field body temperatures are relatively low and strongly dependent on substrate temperatures (Martín et al. 1990), it seems able to maintain its preferred temperature by moving vertically between cooler areas deep below the surface and warmer areas nearer the surface, and by actively selecting rocks of different thicknesses at different times of day (López et al. 1998). These studies, however, examined the thermal biology of a single species inhabiting Mediterranean temperate habitats in which diel as well as seasonal substrate temperature cycles may constrain amphisbaenians from thermoregulating optimally and prevent them from achieving optimal temperatures (López et al. 1998). To know whether fossorial reptiles have the ability to thermoregulate or whether they are thermoconformers, it is necessary to analyze the thermal biology in relation not only to the field body temperatures but also to the thermal environment of taxonomically diverse species inhabiting warmer climates where underground thermal restrictions may be unimportant. Under such conditions, amphisbaenians may not only achieve higher field body temperatures (e.g., Al-Johany 1999) but, also, thermoregulation may be more effective, allowing amphisbaenians to maintain their preferred body temperatures in the field for longer with low thermoregulatory costs.

We present the results of a field study designed to examine the relationship between available underground thermal environment and the thermal biology of the amphisbaenian *Trogonophis wiegmanni*, a fossorial reptile that is the only representative of subfamily Trogonophidae in North Africa (Bons and Geniez 1996). It is a Mograbin endemic with a range in the Mediterranean biome that extends from southwest Morocco to northeast Tunisia. Its elongate limbless body, reduced vision, and compact skull are morphological adaptations for burrowing (Gans 1974, 1978) and, thus, it lives buried in the soil in areas with sandy soils or an abundance of leaf litter. It is usually found under rocks or dead wood, especially in the wetter seasons, but, in summer, is usually found buried deep in the ground (Bons and Geniez 1996). Little research has been carried out on this species, but some data have been published on body temperature preferences in a laboratory thermal gradient (Gatten and McClung 1981), aerobic- and anaerobic-activity metabolism (Kamel and Gatten 1983), and the reproductive cycle (Bons and Saint Girons 1963). In this paper, we specifically examine the thermal biology of *T. wiegmanni*, by presenting field

body temperatures and patterns of presence under stones at the Chafarinas Islands (North Africa). Our aim was to evaluate the extent of thermoregulation in this amphisbaenian by analyzing the relationships between body and environmental available operative temperatures.

Methods

Study area

We conducted the field work at the Chafarinas Islands (Spain). The archipelago of the Chafarinas is located in the southern–western area of the Mediterranean Sea (35°11′00″N, 2°25′35″W), 2.5 nautical miles to the north of the Moroccan coast (Ras el Ma, Morocco) and 27 miles to the east of the Spanish city of Melilla. It consists of three islands: Congreso, Isabel II (the only one inhabited), and Rey Francisco. Congreso is the westernmost, largest (25.6 ha), and highest (137 m asl) of the islands and Isabel II (15.1 ha; 35 m asl), located between Congreso (at 1 km) and Rey Francisco (at 175 m), is the most eastern, smallest (13.9 ha), and lowest (31 m asl). The islands present a dry, warm, Mediterranean climate very influenced by dominant winds from the east and west. The vegetation is conditioned by the aridity of the climate (an average annual precipitation of 300 mm), the higher soil salinity, and the guano accumulation from numerous seabird colonies. The current vegetation is dominated by plants adapted to the salinity and drought, such as species of *Atriplex*, *Suaeda*, and *Salsola*. In general, the soils of the islands are little developed and immature. They are characterized by a thin layer rich in organic matter, where the vegetation settles, that is underlain almost directly by the original volcanic rock (andesite or basalt).

Field body temperatures

The study area was visited regularly during March and occasionally from May to June 2000. We followed 73 different random routes (approx. 100 m/h) covering all the habitats available in the islands. The transects were walked at known times for a total of 19 days in March and 11 days in May–June during the day between 07:00 and 18:00 (GMT), searching for amphisbaenians by lifting all stones found. Amphisbaenians were typically found active under stones. Body (= cloacal) temperatures (T_b) were recorded (to the nearest 0.1°C) within 10 s after lifting the stones, using a digital thermometer. The small size of the thermometer (3 mm at the tip) allowed us to insert it into the cloaca of every specimen. To prevent alterations in T_b during readings, specimens were kept on the substrate by means of a wooden stick. We also recorded date, time of day, age (adults versus juveniles), sex of adults, snout–vent length (adults, 142 ± 2 mm (mean \pm SE); juveniles, 93 ± 4 mm), and body mass (adults, 5.7 ± 0.2 g; juveniles, 1.8 ± 0.2 g). The frequency of appearance of specimens under stones in relation to search effort was recorded. The number of observations was divided by the number of routes followed in that hour during the sample period.

Environmental operative temperatures

In many studies, the thermal environment has been measured using copper models resembling the study animal (Bakken 1992). However, in a study of fossorial ectotherms, the main

mechanism of heat transfer for a model buried in the soil is conduction, and there are no effects of the absorption of solar and thermal radiation by the surface of the model (López et al. 1998). The thermal environment beneath a rock approaches blackbody condition (Kearney and Predavec 2000). Thus, soil temperature is generally a sufficient parameter to estimate the steady-state body temperature of an animal resting at a particular point underground. We used an electronic digital thermometer (range = -10 to 110°C , resolution = 0.1°C) to record the environmental available operative temperatures (T_{es}) at the study site. T_e was recorded at the exact capture site of each amphibiaenian (T_{es}) immediately after capture, with the probe of the thermometer (3 mm at the tip) slightly buried in the soil under the rock. Air temperature (T_a) was also recorded, with the shaded thermometer at 5 cm above the ground. Additionally, to estimate the availability of temperatures in the study area during the same sample period, operative temperatures (T_{ea}) in the soil under randomly chosen rocks of different thicknesses were recorded, again with the probe of the thermometer slightly buried in the soil. To explore spatial and temporal variability, measurements were taken under different stones and in different times throughout the day (between 07:00 and 18:00 GMT).

Evaluating the extent of thermoregulation

To test whether amphibiaenians regulate T_b , we compared T_e with T_b of amphibiaenians. We used indices proposed by Hertz et al. (1993) to test whether T_b s of amphibiaenians deviate less from their preferred (selected) temperature range (T_{sel}) than do T_e values. The value of the T_{sel} range (21.7 – 23.4°C) was taken from an experiment that measured T_b s selected by *T. wiegmanni* in a laboratory thermal gradient (Gatten and McClung 1981). Thereafter, we calculated \bar{d}_b , computed as the mean of the absolute values of the deviations of T_b from T_{sel} , which measures the accuracy of temperature regulation. We also calculated \bar{d}_{ea} and \bar{d}_{es} , computed as the mean of the absolute values of the deviations of T_{ea} or T_{es} , respectively, from T_{sel} , which measure the quality of the thermal environment for amphibiaenians. If $\bar{d}_b \geq \bar{d}_{ea}$, then amphibiaenians are not regulating T_b (see Hertz 1992; Hertz et al. 1993, 1999).

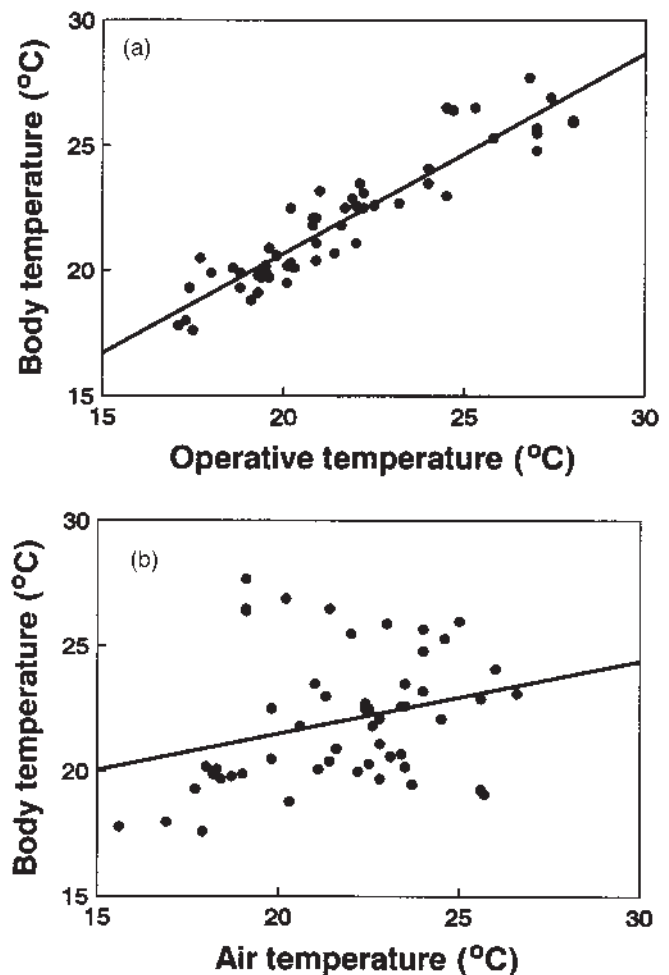
Given the large size of the area surveyed and the high density of amphibiaenians, and because we avoided walking routes taken previously, the probability of sampling the same individual more than once was very low. We therefore treated all measurements as independent. We used Pearson's correlation and partial correlations to evaluate relationships between temperatures, and we compared means with one-way analysis of variance (ANOVA) or with analysis of covariance (ANCOVA), to exclude the effect of covariation of T_b with T_{es} (Sokal and Rohlf 1995). Data were log-transformed to ensure normality. Tests of homogeneity of variances (Hartley's F_{max} test) showed that, in all cases, variances were not significantly heterogeneous.

Results

Field body temperatures and patterns of presence under stones

The average field T_b of amphibiaenians captured under stones ranged between 17.6 and 27.6°C (mean \pm SE = $22.0 \pm$

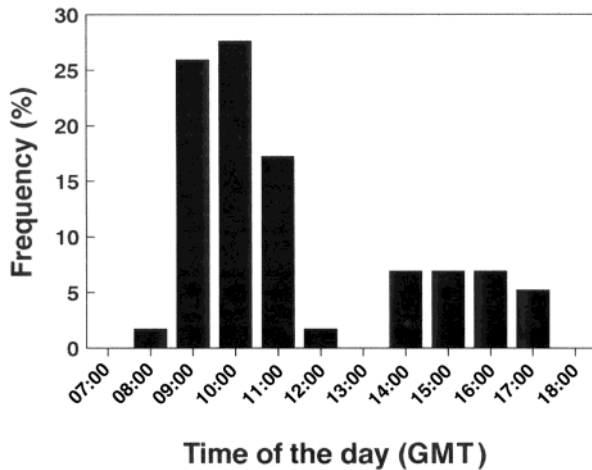
Fig. 1. Relationship between field body temperature of *T. wiegmanni* found under rocks ($N = 55$) and (a) the environmental available operative temperatures under rocks selected by amphibiaenians and (b) the air temperature at 5 cm above the rocks. The regression lines for each relationship are shown.



0.3°C ; $N = 55$). Associated operative temperature under these stones (T_{es}) varied from 17.1 to 27.7°C ($21.5 \pm 0.4^{\circ}\text{C}$) and T_a varied from 15.6 to 26.5°C ($21.6 \pm 0.3^{\circ}\text{C}$). The correlation between T_b and T_{es} was highly significant (Pearson's correlation, $r = 0.93$, $F_{[1,53]} = 349.97$, $P < 0.0001$) (Fig. 1a), whereas the correlation between T_b and T_a was weaker but still significant ($r = 0.30$, $F_{[1,53]} = 5.05$, $P = 0.03$; Fig. 1b). However, partial correlations showed that T_b was more strongly influenced by T_{es} ($r = 0.93$) than by T_a ($r = 0.16$) ($P < 0.001$ in a t test for correlation coefficients). Differences between T_b and T_{es} ranged from -2.2°C to $+2.8^{\circ}\text{C}$ (mean \pm SE = $0.4 \pm 0.1^{\circ}\text{C}$). No significant correlation was found between T_b and the difference between T_b and T_{es} ($r = -0.18$, $F_{[1,53]} = 1.85$, $P = 0.18$).

Amphibiaenians showed a bimodal pattern of presence under stones (Fig. 2). Thus, the percentage of individuals observed under stones, corrected for search effort, was maximum at mid-morning (about 71% of observations were made between 09:00 and 13:00 GMT), with another peak at mid-afternoon (26% of observations were made between 14:00 and 17:00 GMT).

Fig. 2. Percentage of individual *T. wiegmanni* found under rocks ($N = 55$) for each hourly period between 07:00–18:00 GMT (corrected for search effort, see Methods).



Daily and intraspecific variation of body temperatures

There was a significant hourly variation in T_b of amphisbaenians. When all observations were grouped into two time periods, amphisbaenians showed significantly lower T_b in the morning (08:00–13:00 GMT, $21.6 \pm 0.4^\circ\text{C}$) than in the afternoon (13:00–17:00 GMT, $23.2 \pm 0.6^\circ\text{C}$), even after excluding the effect of covariation of T_b with T_{es} (ANCOVA, $F_{[1,51]} = 7.46$, $P = 0.009$).

With respect to intraspecific differences between sexes and between age-classes, adult amphisbaenians (mean \pm SE = $21.8 \pm 0.4^\circ\text{C}$) had significantly lower T_b than juveniles ($22.9 \pm 0.8^\circ\text{C}$), even after excluding the effect of covariation of T_b with T_{es} (ANCOVA, $F_{[1,51]} = 10.28$, $P = 0.002$), whereas adult males ($21.7 \pm 0.5^\circ\text{C}$) and females ($21.8 \pm 0.6^\circ\text{C}$) did not significantly differ in T_b after excluding the effect of T_{es} (ANCOVA, $F_{[1,40]} = 1.17$, $P = 0.29$).

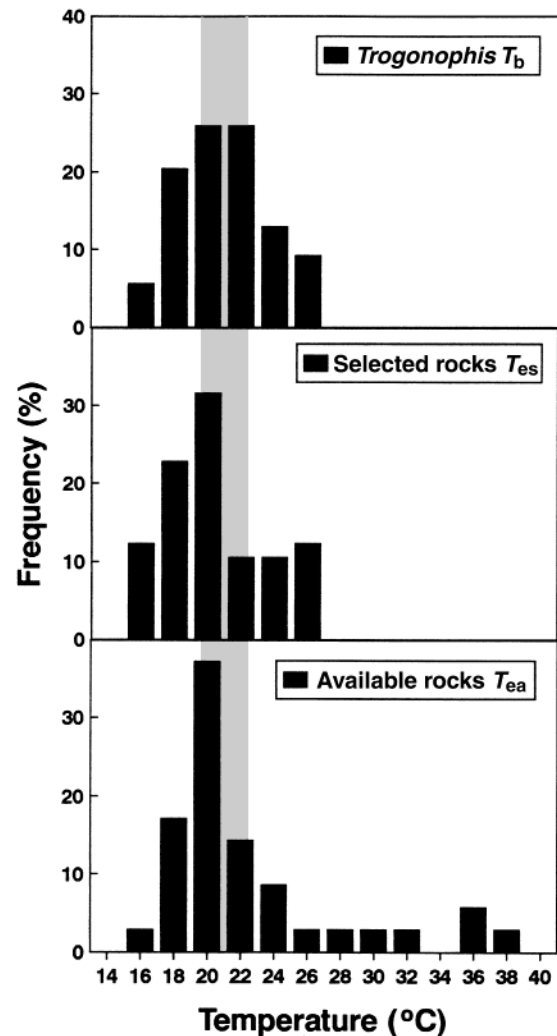
Available temperatures and quality of the thermal environment

In a comparison with T_c measured under rocks in the study area during the day, T_b s of amphisbaenians were significantly lower than available T_{ea} s (ANOVA, $F_{[1,78]} = 6.35$, $P = 0.014$) (Fig. 3); however, T_b s of amphisbaenians were not significantly different from T_{es} s, that is, under rocks that were selected by amphisbaenians ($F_{[1,109]} = 1.05$, $P = 0.31$; Fig. 3). Also, \bar{d}_b ($1.5 \pm 0.2^\circ\text{C}$) was significantly smaller than \bar{d}_{ea} ($3.5 \pm 0.9^\circ\text{C}$; $F_{[1,78]} = 8.28$, $P = 0.005$), whereas \bar{d}_b was not significantly different from \bar{d}_{es} ($1.9 \pm 0.2^\circ\text{C}$; $F_{[1,109]} = 2.71$, $P = 0.10$) and \bar{d}_{es} was significantly lower than \bar{d}_{ea} ($F_{[1,81]} = 5.08$, $P = 0.027$). These results indicate that amphisbaenians responded nonrandomly to the thermal environment, so that the deviation of T_b from T_{sel} was reduced by selecting rocks with thermal properties that allowed them to maintain their preferred temperatures.

Discussion

Body temperatures of *T. wiegmanni* showed a strong correlation with environmental temperatures. As might be expected for a species of subterranean habits, body temperatures are

Fig. 3. Distribution of body temperatures (T_b) of *T. wiegmanni* found under rocks ($N = 55$) (upper panel); distribution of available operative temperatures under rocks when they were selected by amphisbaenians (T_{es}) (middle panel); and distribution of available operative temperatures under randomly chosen rocks exposed to the sun at the study site (T_{ea}) ($N = 25$) (lower panel). The shaded area identifies the selected temperature range (T_{sel}).



closely correlated with operative temperatures under stones and, thus, it might initially be considered that *T. wiegmanni* demonstrate a certain degree of thermoconformism (Huey and Slatkin 1976). Amphisbaenians are typical thigmotherms that obtain the heat they need through contact with the soil and by taking advantage of the heat stored in the stones under which they are frequently found. A similar situation was found for the amphisbaenian *B. cinereus* (Martín et al. 1990; López et al. 1998). However, the comparison of body temperatures with available temperatures indicates that *T. wiegmanni* behave nonrandomly with respect to the available thermal environment. This is based on the fact that body temperatures deviated less from the set-point range of preferred temperatures (i.e., $\bar{d}_b < \bar{d}_{ea}$) than they would given a random response, which is indicative of behavioral temperature regulation (Hertz et al. 1993).

Under laboratory conditions, *T. wiegmanni* showed a bi-

modal pattern of temperature selection in a thermal gradient during the day (Gatten and McClung 1981). Interestingly, in our field study, a similar bimodal pattern of body temperatures was also found for *T. wiegmanni*, even after excluding the effect of covariation with substrate temperatures. Thus, amphisbaenians were active at higher body temperatures during the afternoon than in the morning. This may reflect not only changes in the thermal environment but, presumably, also a voluntary selection pattern, as indicated by the results from the laboratory study where there were no thermal restrictions (Gatten and McClung 1981) and by our conclusion that *T. wiegmanni* can behaviorally regulate body temperature. Although reasons for such a pattern remain to be examined, one possible explanation might be related to the selection of elevated body temperatures following feeding (as seen in other epigeal lizards; Tossini et al. 1994), which is aimed at increasing both the digestive rate and its efficiency (Harwood 1979). Thus, amphisbaenians might forage through the soil after heating themselves in the morning, and then come back under stones in the afternoon, selecting higher temperatures to maximize digestion. The bimodal pattern of body temperatures was also found for *B. cinereus* in the field, but it depended on covariation with substrate temperatures (Martín et al. 1990) and was not found in a laboratory gradient (López et al. 1998). This might suggest that, in the more temperate habitat occupied by *B. cinereus*, thermal restrictions prevent amphisbaenians from increasing their body temperatures in the afternoon, whereas in warmer habitats, such as those occupied by other amphisbaenian species, better thermal opportunities may allow higher body temperatures to be achieved (Al-Johany 1999) and a more precise thermoregulation pattern to be maintained. The relatively low preferred body temperatures that characterize most fossorial reptiles (Avery 1982), including amphisbaenians, seem to be a convergent adaptation to the underground environment, because diel and seasonal environmental temperature cycles may prevent a fossorial ectotherm from achieving higher body temperatures even in warm climates. Thus, the selection of relatively low body temperatures could enable fossorial reptiles to maximize the period during which they can maintain body temperatures within an acceptable range (Christian et al. 1983).

Measurements of operative temperatures indicated that the thermal environment deviated from the range of selected temperatures significantly less under rocks selected by *T. wiegmanni* than it did beneath available rocks (i.e., $\bar{d}_{ea} < \bar{d}_{ea}$). This suggests that amphisbaenians occupied rocks with or when thermal properties were suitable for maintaining their preferred body temperatures. A similar situation has been observed in retreat-site selection of snakes and geckos during long periods of inactivity (Huey et al. 1989; Kearney and Predavec 2000). However, amphisbaenians use the thermal environment under rocks to gain and maintain their temperature during periods of activity and, when thermal conditions are not favorable, they can move to areas deeper in the ground, thus tracking variations of temperature in the substrate that may allow them to be active for longer at preferred temperatures. This was also suggested by the bimodal pattern of *T. wiegmanni* presence under stones, where the periods of minimum presence at midday would coincide with high temperatures in the substrate that could exceed the

amphisbaenians' preferred range. Similarly, in other species of amphisbaenian, it has been suggested that, in the early morning, as substrate temperatures increase, amphisbaenians can increase their body temperature by moving near the surface and under rocks and that later in the day they might move through the soil searching for prey with low thermoregulatory costs (Papenfuss 1982; Martín et al. 1990; López et al. 1998).

Juvenile *T. wiegmanni* had significantly higher body temperatures than adults. Although this might reflect a voluntary selection of warmer substrates, it is more likely to be a biophysical effect of differences in body size. Juveniles with small body mass and high surface-to-volume ratios are subjected to faster heating rates and can reach an equilibrium body temperature in a shorter time than adults. However, this simple physical constraint could affect the thermoregulatory and foraging behavior of juveniles, because long periods of heating under stones would not be needed and more time could be devoted to other activities in deeper layers of the soil, as has been suggested for other lizards (Carrascal et al. 1992). However, juveniles would also cool faster and, thus, should return to the stones to regain temperature more frequently than adults. This points out the need for further studies of thermoregulatory behavior in amphisbaenians that consider body size differences within a species and that provide comparative analyses of temperatures of different species, given the wide range of body sizes present in this and other groups of fossorial lizards.

Given the data from this and other studies, we conclude that, although body temperatures of amphisbaenians are low and highly dependent on available environmental temperatures, they cannot be considered to be thermoconformers, because they seem capable of regulating body temperature to an extent comparable with epigeal diurnal lizards. Further studies on the thermoregulatory behavior of these and other species of amphisbaenians would contribute to understanding the ecological strategies of fossorial reptiles.

Acknowledgements

We thank A. Forsman and two anonymous reviewers for critical comments and L. Sánchez-Mármol for his help in collecting data. The field station of the "Refugio Nacional de Caza de las Islas Chafarinas" provided logistical support. Financial support was provided by a Consejo Superior de Investigaciones Científicas contract to P.L., by Organismo Autónomo de Parques Nacionales (Spain) and GENA S.L. to E.C., and by Dirección General de Enseñanza Superior e Investigación Científica project PB 98-0505 to J.M. and P.L.

References

- Abe, A.S. 1984. Experimental and field record of preferred temperature in the neotropical amphisbaenid *Amphisbaena mertensi* Stauch (Reptilia, Amphisbaenidae). *Comp. Biochem. Physiol.* A, **77**: 251–253.
- Adolph, S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology*, **71**: 315–327.
- Al-Johany, A.M. 1999. The activity and thermal biology of the fossorial reptile, *Diplometopon zarudnyi* (Amphisbaenia: Trogonophiidae) in Central Saudi Arabia. *Asiatic Herpetological*

- Research 8: 1–6. [Asiatic Herpetological Research Society, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, U.S.A.]
- Avery, R.A. 1982. Field studies on body temperatures, and thermoregulation. *In* *Biology of the Reptilia*. Vol. 12. *Edited by* C. Gans and F.H. Pough. Academic Press, New York. pp. 93–166.
- Bakken, G.S. 1992. Measurement and application of operative and standard operative temperatures in ecology. *Am. Zool.* **32**: 194–216.
- Bauwens, D., Hertz, P.E., and Castilla, A.M. 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology*, **77**: 1818–1830.
- Bons, J., and Geniez, P. 1996. *Amphibians and reptiles of Morocco*. Asociación Herpetológica Española, Barcelona, Spain.
- Bons, J., and Saint Girons, H. 1963. Ecologie et cycle sexuel des amphibiens du Maroc. *Bull. Soc. Sci. Nat. Phys. Maroc*, **43**: 117–158.
- Carrascal, L.M., López, P., Martín, J., and Salvador, A. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. *Ethology*, **92**: 143–154.
- Christian, K.A., Tracy, C.R., and Porter, W.P. 1983. Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology*, **64**: 463–468.
- Gans, C. 1974. *Biomechanics: an approach to vertebrate biology*. Lippincott, Philadelphia.
- Gans, C. 1978. The characteristics and affinities of the Amphisbaenia. *Trans. Zool. Soc. Lond.* **34**: 347–416.
- Gatten, R.E., and McClung, R.M. 1981. Thermal selection by an amphisbaenian, *Trogonophis wiegmanni*. *J. Therm. Biol.* **6**: 49–51.
- Gil, M.J., Guerrero, F., and Pérez-Mellado, V. 1993. Observations on morphometrics and ecology in *Blanus cinereus* (Reptilia: Amphisbaenia). *J. Herpetol.* **27**: 205–209.
- Grant, B.W., and Dunham, A.E. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, **69**: 167–176.
- Hailey, A., and Elliot, M. 1995. Thermoregulation of the amphisbaenian *Zygaspis quadrifrons*. *J. Herpetol.* **5**: 281–284.
- Harwood, R.H. 1979. The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicarinatus* and *Sceloporus occidentalis*. *Comp. Biochem. Physiol. A*, **63**: 417–433.
- Hertz, P.E. 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology*, **73**: 1405–1407.
- Hertz, P.E., and Huey, R.B. 1981. Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology*, **62**: 515–521.
- Hertz, P.E., Huey, R.B., and Stevenson, R.D. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* **142**: 796–818.
- Hertz, P.E., Huey, R.B., and Stevenson, R.D. 1999. Temperature regulation in free-ranging ectotherms: what are the appropriate questions? *Afr. J. Herpetol.* **48**: 41–48.
- Huey, R.B. 1982. Temperature, physiology and ecology of reptiles. *In* *Biology of the Reptilia*. Vol. 12. *Edited by* C. Gans and F.H. Pough. Academic Press, New York. pp. 25–91.
- Huey, R.B., and Slatkin, M. 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**: 363–384.
- Huey, R.B., Peterson, C.R., Arnold, S.J., and Porter, W.P. 1989. Hot rocks and not-so-hot rocks: retreat site selection by garter snakes and its thermal consequences. *Ecology*, **70**: 931–944.
- Kamel, S., and Gatten, R.E. 1983. Aerobic and anaerobic activity metabolism of limbless and fossorial reptiles. *Physiol. Zool.* **56**: 419–429.
- Kearney, M., and Predavec, M. 2000. Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology*, **81**: 2984–2996.
- López, P., Salvador, A., and Martín, J. 1998. Soil temperatures, rock selection and the thermal ecology of the amphisbaenian reptile *Blanus cinereus*. *Can. J. Zool.* **76**: 673–679.
- Martín, J., López, P., and Salvador, A. 1990. Field body temperatures of the amphisbaenid lizard *Blanus cinereus*. *Amphib.-Reptilia*, **11**: 87–96.
- Papenfuss, T.J. 1982. The ecology and systematics of the amphisbaenian genus *Bipes*. *Occas. Pap. Calif. Acad. Sci.* **136**: 1–42.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry*. 3rd ed. W.H. Freeman and Co., New York.
- Tossini, G., Jones, S., and Avery, R.A. 1994. Effects of feeding on set point temperatures and thermoregulatory behaviour in the lizards *Podarcis muralis* and *Lacerta vivipara*. *Amphib.-Reptilia*, **15**: 257–265.
- Waldschmidt, S., and Tracy, C.R. 1983. Interactions between a lizard and its thermal environment: implications for sprint performance and space utilization in the lizard *Uta stansburiana*. *Ecology*, **64**: 476–484.