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Patterns of Thermoregulation in *Podarcis hispanica* (Lacertilia: Lacertidae)

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The family Lacertidae exhibits a broad range of thermoregulatory abilities /Brattstrom, 1965; Curry-Lindahl, 1979/; some species have relatively low activity temperatures /Avery, 1982/, whereas others in the family are very thermophilic /Bowker, 1984; Huey et al., 1977/. Podarcis hispanica is found in the western Iberian Peninsula /Arnold and Burton, 1978/, a region of moderate annual climate. Frequently associated with man, it often inhabits cracks in the walls of buildings and fences. It is one of the few lacertids which remain active throughout the year, and it has extended daily activity periods as well /Busack, 1978; Mellado, 1983/. Cloacal temperatures of animals in the field indicate relatively low preferred body temperatures /Busack, 1978/, and a wide range of individual variation /Mellado, 1983/. In addition, P. hispanica exhibits extremely high tail regeneration frequencies, perhaps an indicator of high predation rates /Jaksic and Busack, 1984; Vitt, 1983/. Thus P. hispanica appears to be relatively atypical for the family and affords the opportunity to examine thermoregulation of a group which has an unusually close association with man, which exhibits long daily / seasonal activity times, and which has very high tail loss rates. Continuously recording body temperature /$\underline{T}_b$/ has proved useful in understanding short term patterns of thermoregulation /Bowker and Johnson, 1980/ and has provided some useful ways of making interspecific comparisons of temperature control /Bowker, 1984/. The purpose of this study is to examine the precision of thermoregulation of the lizard Podarcis hispanica using these techniques.

MATERIALS AND METHODS

GENERAL HABITAT INFORMATION. Podarcis hispanica were collected in Coimbra, Portugal from April 1984 through June 1984. All lizards were noosed on walls and buildings in the city of Coimbra near the south bank of the Mondego River. Usually a lizard was used in a thermoregulation experiment on the day of capture; some, however, were not tested until two or three days later. These were maintained in aquaria and dipteran larvae and water were provided ad libitum.

THERMOREGULATION. A typical thermoregulation study consisted of placing a lizard in an enclosure with a heat source, allowing the animal to move about to regulate $\underline{T}_b$, and continously recording its cloacal temperature. The temperature enclosure, constructed after the basic design of DeWitt /1967/, was a circular aluminium enclosure, 1 m in diameter, with a wall 30 cm high and the floor covered with sand. The enclosure was set up in the laboratory and an infrared lamp was used as the heat source. The lamp was suspended over the center of the box and provided a thermal gradient. Temperature of the substrate ranged from approximately 25°C at the edge to greater than 50°C in the center of the enclosure. An animal was placed in the enclosure and allowed to thermoregulate for approximately 2 hours. All experiments were conducted during the times of day when the lizards are active in nature.

Body temperature was measured using a calibrated YSI tissue implantation thermistor /YSI 511/ connected to an Apple II Plus computer with AI 13 analog/digital interface. The thermistor was inserted 1-2 cm into the cloaca of the lizard, and the wire taped to the base of the tail. The animals could move freely in the enclosure and seemed undisturbed by the thermistor wire. Cloacal temperatures were monitored for approximately two hour intervals as the animal moved about the enclosure, and the temperatures were recorded /to the nearest 0.1°C/ at 15 second intervals by the computer. After a period of adjustment in the enclosure, approximately 100 consecutive temperatures were recorded for each animal /temperatures read to the nearest 0.1°C/.

RESULTS

Nineteen thermoregulation experiments were conducted for Podarcis hispanica and the results of seventeen are presented here. Two experiments were excluded because the animals were disturbed during the course of the experiment and clearly behaved abnormally. Typically an animal regulated T_b by shuttling between warm and cool areas in the enclosure and this movement resulted in sinelike fluctuations of T_b with time. Recording the temperatures at 15 second intervals provides information on short term regulation of T_b /Bowker and Johnson, 1980/. First, individual mean body temperatures /$\overline{T}_b$'s/ were calculated by averaging the temperatures for a particular animal, and the standard deviation of this mean gives a measure of how carefully that individual regulated T_b /= individual precision/. These individual standard deviations were then averaged to produce a mean SD of the individual means /= Pooled SD/, providing an overall measure of thermoregulatory precision for the species /Tab. 1/. The value of 1.94°C indicates that the individuals were relatively imprecise thermoregulators /see Bowker, 1984 for comparison/.

Table 1. Average thermoregulation characteristics for Podarcis hispanica.

	$\overline{X}$	SD	N
Body Temperature	33.8	1.22	17
Pooled SD	1.94	0.49	17

The individual $\overline{T}_b$'s were then averaged to produce a grand mean for the species and the standard deviation of this mean gives an indication of the amount of variation among individuals /Tab. 1/. The low $\overline{T}_b$ /33.8°C/ indicates that P. hispanica is thermophobic and the large standard deviation /1.22/ indicates considerable individual variability.

DISCUSSION

Avery /1982/ includes the Lacertidae within the group of lizards which "seem to fit the paradigm of dependence on diurnal basking for precise or fairly precise thermoregulation". The data presented here clearly support that contention for P. hispanica. They regulated T_b in the laboratory temperature gradient by shuttling frequently between the warm and cool areas of the enclosure. These movements resulted in sinelike fluctuations of T_b with time and produced thermoregulation patterns similar to those of other species which actively control T_b by shuttling /Bowker, 1984/. Individuals selected a relatively low range of temperatures indicating that their preferred temperatures are low; this corresponds with the findings of Busack /1978/ and Mellado /1983/ for animals in the field.

The SD of the individual T_b can be used as a measure of the thermoregulatory precision /Bowker, 1984/, although Huey /1983/ discusses some problems with this technique. Individual P. hispanica exhibited large SDs, an indication of imprecise thermoregulation. These were the least pre ise thermoregulators of more than 24 species from North America, Africa and Europe examined to date in this laboratory. This is consistent with their lifestyle. They are active throughout the day and throughout the year even during times when environmental conditions preclude achieving a high T_b. Thus they apparently sacrifice a degree of thermal control for longer activity times.

There was fairly large variation among individuals in the choice of T_b, /Tab. 1/ indicating that the absolute temperature range was relatively unimportant, however, individuals were quite consistent in the amount of variation they allowed /SD/. Thus although perhaps the temperature "set points" /sensu Berk and Heath, 1975/ differed among individuals, the absolute variability individuals were willing to tolerate was quite similar.

What are the costs/benefits of a low body temperature and imprecise thermoregulation? The lizards shuttled frequently in the laboratory experiments and, even though the thermal gradient offered a wide range of temperatures possibilities, they regulated T_b imprecisely and selected relatively low T_b's. There are some advantages to having a low preferred temperature. Certainly the energy costs will be lower /Bennett and Dawson, 1976/ and this will allow the animal the opportunity to be active at times when the environmental heat sources would not be sufficient for the animal to be active for many hours during the day. Thus lowering the activity temperature can expand the foraging times, but presumably would reduce efficiency. There are clear disadvantages to shuttling frequently, for any movement in nature should increase the probability of predation and be costly in terms of energy. In this regard, P. hispanica shows remarkably high incidence of tail break/regeneration /Jaksic and Busack, 1984; our population averaged 81.7% with regenerated tails/ and this is frequently used as an indicator of predation intensity /Vitt, 1983/ although Jaksic and Busack /1984/ dispute this.

A suite of conditions relating to the lifestyle of the lizard seem to influence the thermoregulation of the species. First, the habitat of the species seems to be extremely important. Those which do not thermoregulate tend either to live in generally moderate climates or in places/times where they are unable to control T_b /Huey, 1982/. Second, the foraging mode /Pianka, 1966; Schoener, 1971/ of the species seems to be significant. Species categorized as "widely foraging" or "wait and ambush" seem to have different thermoregulatory patterns /Bowker, 1984/. Third, the length of the daily active time also seems to have bearing on thermoregulation. Some species are active for brief periods daily whereas others are active throughout the day. Fourth, the seasonal patterns of activity also seem to be significant to understanding the lizards temperature physiology. Some species are active only during parts of the year /e.g. summer, or spring and fall, or during rainy sesons/ whereas others are active all year. Podarcis hispanica is interesting because it appears to be an extreme member of the family: it is found in moderate temperature climates, utilizes both widely foraging and wait and ambush modes, is broadly active during the day, and is found throughout the year on appropriate days. Although it does thermoregulate, it has a low, imprecisely regulated body temperature both in the laboratory and in the field.

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