Influence of Heat Transmission Mode on Heating Rates and on the Selection of Patches for Heating in a Mediterranean Lizard

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ABSTRACT

Heliothermy (heat gain by radiation) has been given a prominent role in basking lizards. However, thigmothermy (heat gain by conduction) could be relevant for heating in small lizards. To ascertain the importance of the different heat transmission modes to the thermoregulatory processes, we conducted an experimental study where we analyzed the role of heat transmission modes on heating rates and on the selection of sites for heating in the Mediterranean lizard *Acanthodactylus erythrurus* (Lacertidae). The study was conducted under laboratory conditions, where two situations of different operative temperatures (38° and 50°C) were simulated in a terrarium. In a first experiment, individuals were allowed to heat up during 2 min at both temperatures and under both heat transmission modes. In a second experiment, individuals were allowed to select between patches differing in the main transmission mode, at both temperatures, to heat up. Experiences were conducted with live, nontethered lizards with a starting body temperature of 27°C. Temperature had a significant effect on the heating rate, with heat gain per unit of time being faster at the higher operative temperature (50°C). The effect of the mode of heat transmission on the heating rate was also significant: at 50°C, heating rate was greater when the main heat transmission mode was conduction from the substrate (thigmothermy) than when heating was mainly due to heat gain by radiation (heliothermy); at 38°C, heating rates did not significantly differ between transmission modes. At 38°C, selection of the site for heating was not significantly different from that expected by chance. However, at 50°C, the heating site offering the slowest heating rate (heliothermic patch) was selected. These results show that heating rates vary not only with environmental temperature but also with different predominant heat transmission modes. Lizards are able to identify and exploit this heterogeneity, selecting the source of heat gain (radiation) that minimizes the risk of overheating when temperature is high.

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Introduction

The body temperature of lizards depends on both the magnitude of temperature variation in the environment and the lizards' ability to regulate heat exchange with the environment. For most small diurnal lizards living in the temperate zone, the source of heat is primarily radiant energy. Lizards are influenced by radiant energy in two ways. They may be heated directly by the sun's rays (radiation), or they may obtain heat from perches or patches previously warmed by radiant energy (conduction; Heatwole and Taylor 1987). Lizards depending primarily on radiation to attain the preferred body temperature are known as "heliotherms," while those that depend primarily on conduction are known as "thigmotherms" (Pough and Gans 1982; Heatwole and Taylor 1987). Heliothermy is generally restricted to shortwave solar radiation. Lizards gaining heat from longwave thermal radiation emitted by rocks or other types of substrates are usually considered thigmothermic. These two contrasting ways of heat gain should not be seen as exclusive thermoregulation modes. As is well known in classic literature on thermoregulation (Huey 1982; Heatwole and Taylor 1987), a lizard's equilibrium temperature is determined by many heat sources and sinks (radiation, conduction, convection, evaporation) all contributing simultaneously, although the relative importance of the two main avenues of heat gain (radiation and conduction from substrate) varies among species.

Actually, there is no agreement about the role of the heat transmission mode on heat gain of lizards. While heliothermy has been given a prominent role in basking lizards (Díaz 1991; Carrascal et al. 1992; Rivera-Vélez and Lewis 1994; Martín et al. 1995), both strategies have been observed in some agamids, geckos, amphisbaenians, and many snakes (e.g., Bustard 1967; Sullivan 1981; Lowe 1982; Tanaka 1986; Martín et al. 1990; Autumn and De Nardo 1995; López et al. 1998). Heat transfer by conduction between an animal and its environment has frequently been considered to be negligible to the energy balances of lizards (Norris 1967; Porter and Gates 1969; Porter et

al. 1973; Porter and James 1979). However, the substrate heats the air layer immediately in contact with it, and a thin, warm layer of air surrounding the organism is produced (boundary layer; Bakken 1989). For small lizards, this warm air, together with direct heat transmission from the substrate, could be important for heating, thus giving relevance to the role of thigmothermy. This seems to be the case for *Cordylus macropholis* because its body temperature is not regulated by exposure to solar radiation (Bauwens et al. 1999).

The aim of this study is to ascertain the importance of different heat transmission modes for thermoregulatory processes. The interaction between operative temperature and heat transmission modes might offer a mosaic of patches with different heat flux properties that lizards could evaluate and exploit. The influence of heat transmission mode on the thermoregulatory process was explored with an experimental approach under laboratory conditions in *Acanthodactylus erythrurus* (Lacertidae), a lizard species of sparsely vegetated habitats that avoids the hottest patches in the home range to prolong the time spent within its preferred thermal range without being forced to shuttle continuously between sun and shade. This allows the lizards to ambush prey while motionless in the sun (Ulmasov et al. 1992; Belliure et al. 1996; Schwarzkopf 1998). We specifically address the following questions: (1) Does heating rate change under different heat transmission modes (radiation/conduction)? (2) Are the effects of heat transmission modes on heating rates consistent over the natural range of operative temperatures? (3) Are individuals able to exploit the availability of heating rates offered by patches with different heat transmission modes through active selection of sites for heating up?

Material and Methods

The Species

Acanthodactylus erythrurus is a small lizard (snout-vent length up to 82 mm, <10 g) that belongs to an advanced clade of Eurosaharan species from xeric climatic zones (Salvador 1981). The species inhabits open sandy areas with sparsely distributed vegetation, where shadow patches are mainly provided by vegetation and clouds. Lizards encounter and have to choose among a diversity of heating sites that differ in equilibrium temperatures and also in the dominant source of heat flux (e.g., in deep shade mainly via conduction or in full sun mainly via shortwave solar radiation). The species shows a preferred body temperature between 36° and 37°C (Bauwens et al. 1995; Belliure et al. 1996) and a relatively low heating rate when compared with other shuttling heliotherms (Belliure et al. 1996). It frequently spends long periods of time motionless in the sun or near a vegetation patch waiting for prey (Belliure et al. 1996).

Considering the characteristics of *A. erythrurus* described above, we predict that (i) when temperatures are uniformly too hot, lizards should select the site giving the slowest rate of heating so as to prolong the time lizards can stay motionless

in the sun and (ii) when operative temperatures are within the preferred range and there is no risk of overheating, lizards should choose the site giving the fastest rate of heating so as to attain the preferred body temperature in the shortest time possible.

Study Area

In June 1993, 13 lizards were captured at the Integral Reserve of La Punta, a sand dune area of ca. 25 ha located within the Natural Park of L'Albufera (Valencia, East of Spain, 37°40′N, 0°30′E). Only male adult lizards were considered for the study to avoid influencing the reproductive status of females at this time of the year. Mean snout-vent length of individuals was 62.8 mm (SD = 4.02, $n = 13$).

The study was conducted at El Ventorrillo field station (Navacerrada, Madrid). After capture, lizards were allowed to acclimatize for 1 wk under a 12L : 12D cycle. Incandescent illumination allowed thermoregulation (range of temperatures: 25°–55°C). Food (crickets and mealworms) and water were supplied ad lib. Duration of captivity was 25 d, manipulation of individuals was not traumatic, and at the end of the study lizards were released to the area of capture.

Experimental Design

We used a 100 × 50 × 40-cm (l × w × h) terrarium with a wooden base covered with sand to simulate the nature of the ground in the area of capture and of the typical habitat for the species (Salvador 1981). The same terrarium was used for measurement of the heating rates under different modes of heat transmission and for the experiment on selection of heating sites (see Fig. 1). In this study, we define "heating site" as a place where lizards stop to warm up through any kind of heat source (radiation or conduction).

Two different modes of heat transmission were experimentally simulated in this terrarium: direct solar radiation and conduction from substrate. Direct solar radiation (hereafter, "heliothermic patch") was simulated with a 100-W incandescent lightbulb of 900 lm, providing both heat and light. Heat conduction from the substrate (hereafter, "thigmothermic patch") was simulated with an electric heater placed in direct contact with the wood base of the terrarium, in combination with an 18-W fluorescent lightbulb of 800 lm, providing less heat by radiation but similar light intensity. Therefore, the luminous flux (i.e., the visible energy emitted into a given solid angle by a light source per unit of time) was similar in both patches, although the radiant energy emitted by the two lightbulbs was considerably different. All tests were conducted between 1000 and 1700 hours.

Experimental measurements of heating rates and observations of patch selection for heating were obtained under two different environmental temperatures: 38° and 50°C. These
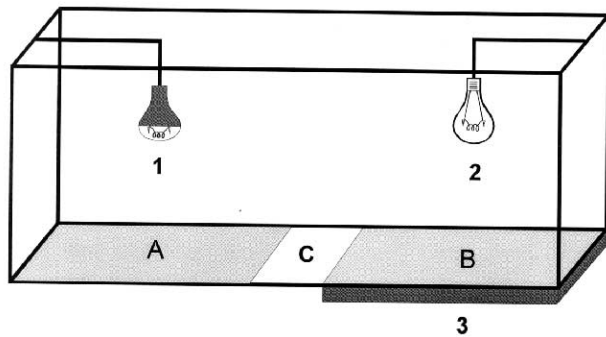
Figure 1. Diagram of the test cage (100 × 50 × 40 cm) used to determine heating rates and selection of sites for heating up. *A*, Heliothermic patch where light and heat gain are obtained by radiation from an incandescent lightbulb of 100-W and 900 lm (*1*). *B*, Thigmothermic patch where light is obtained by a fluorescent lightbulb of 18-W and 800 lm (*2*) and heat gain is obtained from an electric heater placed in direct contact with the wood base of the terrarium (*3*). *C*, Neutral zone.

temperatures represent the natural range of variation of summer morning environmental temperatures in full sun (between 0730 and 1000 hours GMT: 38.2°C, SD = 1.4, *n* = 13 different days) to summer midday temperatures (between 1050 and 1200 hours GMT: 47.6°C, SD = 5.1, *n* = 12; operative temperatures measured with hollow copper cylinders). In the heliothermic patch, operative temperatures were reached by varying the height of a 100-W lightbulb over the terrarium because heat radiation is proportional to the inverse of the distance between light/heat source and the surface. The operative temperature of 38°C was reached by suspending the lightbulb 40 cm above the ground of the terrarium. The 50°C operative temperature was reached by suspending the lightbulb 20 cm above the ground of the terrarium. In the thigmothermic patch, both temperatures were reached by controlling the power of the heater, maintaining the 18-W lightbulb at 20 cm (at 38°C) or 40 cm (50°C) above the ground of the terrarium.

Operative temperatures (i.e., the temperature of a physical model representing all potential components of the energy balance; see Tracy 1982) were measured with an electronic digital thermometer (precision of 0.1°C) using 50-mm hollow copper cylinders that were placed on the sand. These copper models were closed at both ends except for a small fissure allowing introduction of the thermometer's probe. Belliure et al. (1996) corroborated that these copper models provided reasonably close approximations of actual lizard temperatures because the mean values at equilibrium of lizard body temperatures (T_b) and model temperatures (T_e) were highly correlated ($r^2 > 0.99$), satisfying the criterion for T_e determinations in Bakken et al. (1985). The resulting regression equation had slopes and intercepts that did not differ from 1 and 0, respectively (seven replicates for each freshly dead lizard; $T_b = -0.71 + 1.01 \times T_e$). This procedure

allows measuring of the approximate temperatures attained by lizards at the relevant microsites and times (Bakken and Gates 1975; Grant and Dunham 1988; Bakken 1992; Hertz 1992).

Body temperature of individuals immediately before the trials was around 27°C. Cloacal temperatures were measured with a Miller-Weber quick-reading mercury thermometer (±0.1°C). Measurements of heating rates and patch selection did not take place until operative temperatures were at equilibrium (simulated conditions were switched on 1–2 h before data recording), and we checked during the trials that operative temperatures in the heliothermic and thigmothermic patches did not differ from the intended temperatures of 38° and 50°C by more than 0.5°C.

Heating Rates with Different Heat Sources

Individuals were heated under both modes of heat transmission at both operative temperatures to explore the influence of heat sources and temperature on heat flux processes. Previous to each test, lizards had enough time and opportunity to learn their novel thermal environments (i.e., they were released on several occasions in the experimental arena during a pilot study to check that the procedures worked and did not stress lizards). Lizards were placed in the middle of the spot characterized by an operative temperature and a transmission mode without tethering them, and they were allowed to heat up during 2 min. In that time, individuals did not move from the center of the spot.

Average initial cloacal temperature of lizards before all the trials was 27.1°C (SD = 0.48, *n* = 52). After the initial cloacal temperature of the experimental lizard was measured, it was placed in the middle of the desired patch in the terrarium (see Fig. 1) and, after 2 min, its cloacal temperature (T_b) was recorded again. From these two measures, the heating rate in degrees Celsius per minute was calculated as (final T_b − initial T_b)/2 min. Because heating rate in degrees Celsius per minute is virtually identical to the slope in the exponential relation between body temperature and time (Díaz et al. 1996), this measure can be considered a good approximation to the process of heat gain in small lizards. Two assays for each operative temperature and mode of heat transmission were made for each individual (both measures of heating rate were averaged). Measurements were made of alternating modes of heat transmission and operative temperatures. Only one lizard was measured at a time, and no more than two trials per lizard were obtained per day.

Selection of Heating Sites

For the selection of heating sites, both spots with different modes of heat transmission were separated by a "neutral" zone (20 × 50 cm; see Fig. 1) in the experimental terrarium. This neutral zone had an operative temperature 10°–15°C lower than

the heating sites. The trials for the selection of heating sites were performed after the pilot study and the measurements of the heating rates. Therefore, we assume that all lizards had experience with the experimental terrarium.

The focal lizard, with an initial body temperature around 27°C, was left in the neutral zone of the experimental terrarium. A kind of initial exploratory behavior was shown, with lizards going from one end to the other of the terrarium with very short stops of less than 5 s. After some time (1–20 s), the individual moved to one of the patches and adopted basking postures. Only the first stay on one of the two patches that lasted longer than 30 s was considered as site selection for heating. If the lizard did not select a site within the first 60 s of stay in the terrarium, that assay was discarded and a new one was tried on a different day after at least 5 h of time.

Five assays were made with each individual lizard at both experimental operative temperatures and after at least 5 h of time. In the design, we randomized the order in which lizards were exposed to both temperatures. Results of the five assays under each operative temperature were expressed as percentage of choices in which the heliothermic patch was selected for heating. The null hypothesis of a nonselective behavior is represented by selection of the heliothermic patch on 50% of the assays.

Data Analyses

Two-way ANOVAs for repeated measures were used to analyze the effect of heat transmission mode and the operative temperature on the heating rates. Percentage of selection for the heliothermic patch against the null hypothesis of 50% was tested with t-tests comparing the observed and expected percentages at both experimentally manipulated operative temperatures. The t-tests are appropriate because we work with percentage of selection (i.e., percentage of choices out of the five assays in which the heliothermic patch was selected) for each individual lizard in order to avoid pseudoreplication and not with the whole sample of 65 choices for 13 lizards at each experimental temperature. We have used the sequential Bonferroni adjustment (Rice 1989; Chandler 1995) with an experiment-wide error rate of 0.05 in each of the two groups of analyses. Results remained significant after the Bonferroni correction.

Results

Heating Rates with Different Sources of Heat

Heating rates at operative temperatures of 38° and 50°C under both heat transmission regimes are shown in Figure 2. Lizards heated faster at the patches with higher operative temperatures ($F = 94.78$, df $= 1, 12$, $P \ll 0.001$). The effect of the mode of heat transmission was also significant ($F = 50.82$, df $= 1, 12$, $P \ll 0.001$), with heat gain being slower under radiation (he-
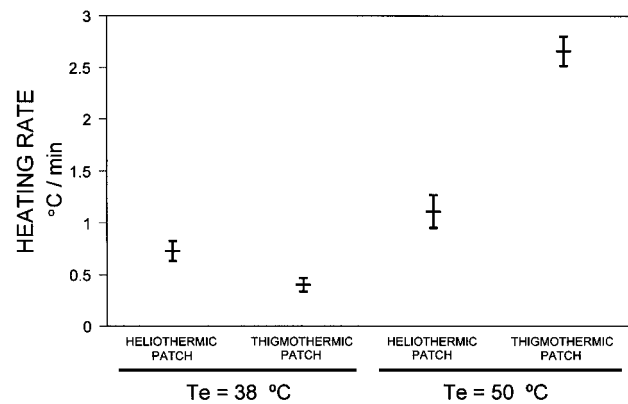

Figure 2. Heating rates at operative temperatures of 38° and 50°C under both heat transmission regimes: radiation-heliothermic patch and conduction-thigmothermic patch. All data are given as the mean ± SE ($n = 13$).

liothermic patch). However, there was no uniform change of heating rate between heat transmission modes under both operative temperatures (interaction term: $F = 69.42$, df $= 1, 12$, $P \ll 0.001$). At 50°C, the heating rate was higher in the thigmothermic patch (Tukey a posteriori honest significant difference test: $P = 0.0002$), while at 38°C, the heating rate was slightly, but not significantly, higher in the heliothermic patch ($P = 0.223$).

Therefore, operative temperature and mode of heat transmission interact to produce different patterns of heat gain in this species, the effect of operative temperature being more striking when heating is through conduction.

Heating Site Selection

At 38°C of operative temperature, selection of the heliothermic patch for heating occurred 57.1% of the time (SE = 4.62, $n = 13$), while at 50°C of operative temperature, selection of the heliothermic patch occurred 65.7% of the time (SE = 4.88, $n = 13$). Difference from the null hypothesis of a nonselective behavior (50% of occasions in the heliothermic patch) was significant only at 50°C ($t = 3.25$, $P = 0.007$; $n = 13$). At 38°C, selection for the heliothermic patch was not significantly different from the null hypothesis ($t = 1.56$, $P = 0.145$; $n = 13$).

Thus, active selection for the heating site that offered the slowest heating rate occurred under the stressful operative temperature. Selection for the heating site that offered the fastest heating rate (i.e., heliothermy) occurred when the operative temperature was within the selected range, but the trend was not significant.

Discussion

Microhabitat selection in ectotherms is mainly related to the thermal conditions of the habitat (Sexton and Heatwole 1968; Tracy and Christian 1986; Paulissen 1988). Most small lizards devote a lot of time to thermoregulation (Huey and Pianka 1977; Waldschmidt and Tracy 1983; Grant and Dunham 1988), and because of their small size, they are compelled to use behavioral rather than physiological adjustments to regulate body temperature (Bartholomew 1982; Huey 1982; Stevenson 1985; Turner 1987). Given the prominence of behavioral mechanisms in thermoregulation, lizards should integrate information about clues of the thermal environment like operative temperature and light to control heat gain (e.g., Grant and Dunham 1988; Adolph 1990; Castilla and Bauwens 1991; Hertz 1992; Hertz et al. 1994; Bauwens et al. 1996; Díaz 1997). The results of this article show that heating rates change with different heat transmission modes and that lizards are able to exploit the heterogeneity of heating rates offered by patches with different heat transmission modes through active selection. This selection is consistent with a pattern of thermoregulatory behavior tending to high-temperature avoidance in hot environments. *Acanthodactylus erythrurus*, a small species inhabiting hot environments with a pattern of activity that includes long motionless periods of time for basking and prey detection, seems to manage heat gain by the exploitation of the different contributions of both radiation and conduction transmission modes.

Our experimental results in a manipulated thermal environment show that operative temperature has a variable effect on the selection of heat transmission mode and on the magnitude of heating rates. At the nonstressful temperature of 38°C (within the selected range of the species), heating rates did not significantly differ between heliothermic and thigmothermic patches, and lizards did not show any clear pattern of patch selection for heating up. At 50°C, however, *A. erythrurus* selected against the patch where heating rate was higher (thigmothermic patch). The ecological implications of this contrasting pattern is relevant for understanding thermoregulation behavior in small lizards.

Acanthodactylus erythrurus is a small lacertid that prefers open sandy areas with sparsely distributed vegetation (Salvador 1981; Arnold 1987). The movement rate of the species decreases at higher environmental temperature, so at temperatures above 40°–45°C, *A. erythrurus* is a sit-and-wait species (Belliure et al. 1996). At midday hours, xeric, sparsely vegetated environments (sand dunes, degraded shrub lands) usually reach operative temperatures 10°–20°C above the selected range of body temperatures of the species. Under these stressful conditions, prevailing from May to September in the geographic range of the species, the probability of attaining lethal temperatures is very high (given, e.g., that the critical thermal maximum for the species is 46.3°C; Bauwens et al. 1995).

If foraging is mainly performed by being motionless in the

sun and launching rapid and short attacks, the thermal properties of the sites for heating should be known to the animal so as to manage body temperature and, thus, performance. In the habitats where the species occur, temperatures are very often above the critical thermal maximum for the species (46.3°C; Bauwens et al. 1995). Under these circumstances, any opportunity to prolong the time devoted to foraging motionless out of vegetation cover might be important. Another important potential benefit of a lower heating rate in these torrid habitats at midday is the ability to keep body temperature around the preferred level without continuously shuttling between sun and shade, which should make the individual more vulnerable to predators due to the increase in the detection probability.

If several places within the home range of the species have similar operative temperatures but different heat transmission characteristics, lizards could exploit this heterogeneity to reduce heating rate and to prolong the time spent within their preferred thermal range without being forced to shuttle continuously between sun and shade (Belliure et al. 1996). Although the statement about different microhabitats having the same temperatures but different heat transmission characteristics has not been documented, probably because of measurements difficulties under natural conditions, it is a likely possibility in sparsely vegetated habitats providing a striking thermal mosaic. For example, solar radiation and changes in the sun-shade patches related to the relative movement of the sun on the horizon produce a mosaic of patches exposed to the sun for a long time or only recently and patches in deep shade with a heated substrate that was exposed to sun immediately before. Between these two extreme sun-shade changes, a gradient is found considering the amount of sun radiation incident on ground filtered by vegetation.

Our results support the above-mentioned prediction considering the biology of the species because the slow-heating patch (heliothermic patch) was selected under the stressful operative temperature of 50°C. Therefore, the identification and selection of sites for heating according to their heat transmission properties could be seen as a behavioral trait favoring thermoregulation in hot, xeric habitats. The results of this article are consistent with a pattern of thermoregulatory behavior tending to high-temperature avoidance in hot environments (Bradshaw 1986) when lizards tend to be sit-and-waiters.

Small lizards are usually considered shuttling heliotherms because they select brightly illuminated microsites where the radiant energy from sunlight can raise body temperature to a higher level than what is attained in shaded but otherwise comparable microsites (Avery 1982; Crawford et al. 1983). Thigmothermy has been thought not to be a suitable thermoregulatory strategy because, as a result of the sun-shade effect, ground temperature is extremely variable, and lizards do not usually spend a sufficient amount of time on the patches of the thermal mosaic during their daily movements such that body temperatures are equal to ground temperatures (Bar-

tholomew 1982). Nevertheless, thigmothermy seems to play a significant role in microhabitat specialists (Bauwens et al. 1999) or in some small lizard species inhabiting cold or shaded environments (e.g., Tanaka 1986; Carrascal et al. 1992; Martín and Salvador 1993).

This article shows that under certain conditions heat gain can be faster under thigmothermy. The infrared radiation emitted by the substrate heats the thin air layer immediately in contact with it (boundary layer; Bakken 1989). This boundary layer, in addition to the absorption of thermal radiation from the substrate, heats the whole body of the lizard. However, longwave radiation has its main effect on heat gain via irradiation on dorsal parts of the lizard (which comprise less than half of the animal's surface area). Because of the different proportion of an animal's surface area affected by heat, body temperature would tend to equilibrate faster with environmental temperature in the thigmothermic situation than under heliothermy. This effect would be more marked when operative temperature is higher than the preferred one because heating rate is proportional to the magnitude of the difference between the initial body temperature and the operative temperature (see Díaz 1991; Carrascal et al. 1992; and Belliure et al. 1996 for lacertid lizards), and the small size of lizards exerts a considerable constraint on the physiological control of heat gain (Turner 1987). Thus, because of their small body size, the boundary layer and heat conduction from the substrate may have an enormous influence on heating in lacertid lizards (Bakken 1989), greater than that due to direct radiation.

As it is well known in classic literature on thermoregulation (Huey 1982; Heatwole and Taylor 1987), a lizard's equilibrium temperature is determined by many heat sources and sinks (radiation, conduction, convection, evaporation) all contributing simultaneously, although the relative importance of the two main avenues of heat gain (radiation and conduction from substrate) varies among species. These two contrasting ways of heat gain should not be seen as exclusive thermoregulation modes but as a dichotomy simplifying the ways lizards interact with heat sources. Our study demonstrates that a Mediterranean lizard species of xeric environments seems to be able to gauge the rate of heat flux in two basking patches, independent of the operative temperature. As we have previously shown, there are some instances in which this circumstance is possible (recently shadowed or recently exposed to sunlight patches as a consequence of the relative movement of the sun on the horizon), but nevertheless, a lizard will rarely choose between two sites that differ in the primary mode of heat flux but have equal operative temperatures. Therefore, teasing apart these sources of heat flux in the lab seems too artificial to relate back to nature. This decoupling between physiological and behavioral processes and ecological relevance points out the difficulties in bridging the gap between lab and field studies. As thermoregulation through selection of appropriate microhabitats according to operative temperature (Grant and Dunham

1988; Huey 1991; Carrascal et al. 1992; López et al. 1998), modification of basking frequency and duration (Huey 1982; Díaz 1991), and postural modifications (Heath 1964; Muth 1977; Stevenson 1985; Grant and Dunham 1988) has been studied in detail in many occasions, we suggest broadening this research program by designing studies linking field and lab conditions that can assess the ability of lizards to discriminate subtle properties of the thermal environment (e.g., rates of heat flux via specific transmission modes).

Acknowledgments

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