THERMOREGULATION IN A LACERTID LIZARD: THE RELATIVE CONTRIBUTIONS OF DISTINCT BEHAVIORAL MECHANISMS[1]

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Abstract. The lacertid lizard *Podarcis hispanica atrata* maintained remarkably constant body temperatures (T_b) throughout its daily activity period in early autumn, despite significant variability in available operative temperatures (T_e). Lizard T_bs were substantially closer to the species' selected temperature range (the target T_bs for thermoregulation, estimated by the central 80% of the temperatures selected in a laboratory photothermal gradient) than were a random sample of T_es, indicating that this population thermoregulates both accurately and effectively. We compared observed behaviors and T_bs to the predictions of two hypotheses. The "no thermoregulation" null hypothesis predicted that lizard activity and microsite use would be unaffected by thermal constraints. The "only thermoregulation" hypothesis predicted that lizards would be active only at those times and in those places where T_es fell within the selected temperature range. To evaluate the contributions of various behavioral adjustments (activity times, use of microhabitats and sun–shade patches, basking, and shuttling) to temperature regulation, we combined results from direct behavioral observations with information on the T_es available at different times of day and in different microsites (combinations of structural microhabitats and sun–shade patches). Lizard activity patterns did not match the predictions of either hypothesis, but the observed pattern of activity produced T_bs that were, on average, 1.0°C closer to the selected temperature range than were T_bs predicted by the "no thermoregulation" hypothesis. The lizards' use of microsites (combinations of structural microhabitats and sun–shade patches) was more similar to predictions of the "no thermoregulation" hypothesis than to those of the "only thermoregulation" hypothesis. Nevertheless, the lizards' use of specific microsites produced T_bs that were, on average, 1.9°C closer to the selected temperature range than were randomly available T_es. The relative contributions of different behavioral mechanisms varied with time of day. In the early morning, low movement rates, selection of sunny microsites, and most notably, adoption of a basking posture contributed to temperature regulation. In the late morning and early afternoon, no thermoregulatory behaviors were necessary, as indicated by randomly positioned models that achieved mean T_es within the selected temperature range. At midday, frequent movements between sunny and shaded microsites probably reduced heat loads on lizards, preventing T_bs from exceeding the selected temperature range. In the late afternoon, nonrandom use of microsites and basking behavior appeared to contribute equally to the elevation of T_bs above randomly sampled T_es.

Key words: activity times; basking; behavioral thermoregulation; body temperatures; diel variation; Lacertidae; microsite selection; operative temperatures; Podarcis hispanica.

INTRODUCTION

Temperature regulation, a central paradigm of biophysical and physiological ecology (Bartholomew 1964, Gates 1980), is of paramount importance to most aspects of reptilian ecology and behavior (Huey 1982). Regulation allows some reptiles to maintain a high and relatively constant body temperature, T_b (Avery 1982, Huey 1982), which may produce optimal organismal performance in the field (Huey and Stevenson 1979).

Most reptiles regulate T_b behaviorally, although physiological adjustments may also be important (Bartholomew 1982).

Two conceptual and technological breakthroughs now allow reptile ecologists to define and test explicit hypotheses about behavioral temperature regulation under field conditions. First, the formulation of appropriate null hypotheses of "no thermoregulation" enables the unequivocal demonstration of temperature regulation, and the elucidation of its underlying mechanisms (Heath 1964, Huey et al. 1977, Grant and Dunham 1988, Adolph 1990, Hertz 1992, Díaz 1994).

Second, the use of complex biophysical measurements and equations or "physical models" of animals allows the measurement of operative temperatures (T_e), which predict the equilibrium T_bs of nonthermoregulating animals (Bakken 1992). Estimates of available T_es are necessary for the construction of null hypotheses about temperature regulation (Bakken 1992, Hertz 1992).

A comprehensive understanding of behavioral temperature regulation in the field requires knowledge of at least four features of a population's behavior and ecology (Hertz et al. 1993). First, the selected temperature range (T_{sel}) identifies the target T_b that ectotherms attempt to achieve in the absence of environmental constraints on temperature regulation. Second, the distribution of available T_es predicts the T_b distribution in a population of reptiles that does not regulate T_b (Bakken 1992). Third, various behavioral mechanisms can alter rates of heat exchange and produce T_bs that differ from a random sample of T_es. Finally, the field-active T_bs of a population represent the final product of either temperature regulation or thermal conformation. Recent work has established a comprehensive protocol for analyzing thermoregulation by comparing data on T_{sel}, the T_es available to field-active animals, and the resultant T_bs (Hertz et al. 1993). This approach allows us to determine the accuracy (the degree to which T_bs correspond to T_{sel}) and effectiveness (the degree to which T_bs are closer to T_{sel} than are T_es) of temperature regulation. However, it does not identify the behavioral mechanisms that produce a regulated T_b.

A large literature has established that the primary mechanisms of behavioral temperature regulation include the restriction of activity times, the selection of thermally appropriate microhabitats, and postural adjustments that alter rates of heat exchange (Huey et al. 1977, Hertz and Huey 1981, Huey 1982, Van Damme et al. 1989, Castilla and Bauwens 1991a). Under field conditions, reptiles often use these behaviors simultaneously, but few researchers have attempted to estimate their relative contributions to a regulated T_b (Porter et al. 1973, Muth 1977). In a theoretical analysis, Stevenson (1985b) ranked the effects of three behavioral mechanisms. He predicted that restricting activity time would have the greatest impact on an ectotherm's T_b, and postural adjustments would have the least.

In this paper, we extend these new analytical approaches to evaluate the relative contributions of several behavioral mechanisms to temperature regulation in a population of the lacertid lizard *Podarcis hispanica atrata*. Examination of diel variations in T_e and T_b demonstrate that these lizards regulate T_b with high accuracy and effectiveness. To understand the basis of temperature regulation in this population, we combine information on levels of lizard activity and microhabitat use with data on temporal and spatial variations in the availability of sun–shade patches and T_e. First, we determine whether or not lizards restrict activity to those times and places where T_e is within T_{sel}. Such behavior

might imply that the availability of favorable T_es is the sole determinant of activity times and microhabitat selection, a suggestion that our observational data do not support. Second, we use T_e data to predict the thermal consequences of the behaviors we observed, and compare these predictions to the T_bs we actually recorded. This procedure allows us to estimate directly the relative contributions of activity times and microhabitat selection to temperature regulation. We also indirectly assess the relative contributions of basking behavior, postural adjustments, and shuttling movements.

MATERIALS AND METHODS

Study site and species

Podarcis hispanica atrata is a small (adult snout–vent length: 52–74 mm; adult body mass: 4–10 g) lacertid lizard with a geographic distribution limited to the Columbretes Archipelago, a group of small islets (total area ≈20 ha) of volcanic origin situated in the Mediterranean, ≈50 km off the coast of Castellón (province of Castellón, Spain). *P. h. atrata* is a heliothermic, ground-dwelling, and saxicolous lizard that actively searches for arthropod prey. Details on several aspects of its ecology are given by Castilla and Bauwens (1991a, b).

We conducted our study on Columbrete Grande, the largest (13 ha) of the Columbretes islands (39°54' N, 0°41' E). Vegetation on the island includes patches of grasses, herbs (*Lobularia maritima, Lavatera mauritanica, Malva parviflora*), and low (maximum height 1 m) perennial shrubs (*Suaeda vera*). The foliage of *Suaeda* is generally dense near a bush's center, but sparse at the edges. Trees are absent, except for one introduced individual of *Ficus carica*.

We delimited a study site (40 × 40 m) in a relatively flat area with typical vegetation and four microhabitat types: (1) rock (isolated rocks with diameter ≥25 cm, piles of stones, and remnants of cement walls); (2) the centers of *Suaeda vera* bushes (ground cover >50%); (3) the edges of *Suaeda vera* bushes (transition between shrubs and grass or soil, ground covered by bush <50%); and (4) open microhabitats (patches of soil, low herbs, or grasses). The site provides a fine-grained mosaic of microhabitats and sun–shade patches, among which lizards can readily move. We estimated the relative abundance of each microhabitat by sampling at 1-m intervals along five parallel transect lines that crossed the entire study plot.

In this report, we describe data collected over two consecutive days (3–4 October 1993) when weather conditions were similar (uniform moderate wind, continuous sunshine until 1600, some cloud afterwards). This short sampling period eliminates seasonal effects as a source of variation in the data. Moreover, *P. h. atrata* is so abundant (≈800 lizards/ha; Castilla and Bauwens 1991b) that sufficient data can be collected within a short period of time.

Sampling the thermal environment

We measured operative temperatures (T_e) and the relative frequencies of sunlit and shaded microsites, using hollow, electroformed copper lizard models with low heat capacity and rapid response time (Hertz 1992). Because the copper models have roughly the same size, shape, and radiative properties as a live lizard, they equilibrate to the temperature of an animal that does not behaviorally or physiologically regulate its body temperature (Bakken 1992). All models were identical in structure, constructed in a perching posture with four feet, the posterior half of the venter, and most of the tail in contact with the substrate. Each model had the tip of a Type T thermocouple probe built into its central cavity. Models were painted either gray or brown, but the difference in color had no effect on equilibrium temperatures (Hertz 1992).

Because these operative temperature thermometers were modeled on male *Anolis* lizards (Hertz 1992), we compared the models' responses to changing heat loads to those of living *P. h. atrata*. Two pairs of models and restrained live lizards were tested side by side at room temperature ($\approx 23°–26°C$). A 400-W high-pressure metal halide lamp (Philips HPI-T AGRO 400) provided radiant heat from above, and a constant flow of air from a room fan provided convective cooling. We varied the heat load on each model and lizard pair by adjusting the lamp height from 115 cm to 40 cm. For each of five heat loads, we continuously monitored the temperatures of models (T_e) and lizards (T_b, cloacal) until both reached equilibrium. Although models heat much faster than lizards, they successfully mimic the thermal responses of restrained live lizards under simulated field conditions. In both tests, differences in the equilibrium temperatures of models and lizards, which ranged from 23° to 37°C, were ≤0.2°.

We used 44 copper lizard models to sample T_es and the frequency of sun–shade patches at the microhabitats available to lizards in the field. We sampled rock microhabitats with 16 models attached to four rocks with a dab of silicone cement; models were evenly distributed on the top and east-, south-, and west-facing sides of rocks. We sampled bush center microhabitats with four models, each placed at the center of a *Suaeda* bush. Operative temperatures in bush edge microhabitats were estimated with 12 models under four *Suaeda* bushes; we positioned models under the edge of the canopy to the east, south, and west of each bush's center. We sampled open microhabitats with four models on the ground between living *Lobularia* herbs, four on the stems of dead *Lobularia* plants, and four on bare ground.

We sampled all models at 45-min intervals on two consecutive days from 0730 until 1830 (15 time periods), obtaining a total of 1320 readings of T_e. Because our sampling schedule bracketed the hours when lizards were active, we obtained data on the available T_es before lizards emerged in the morning and after they retreated for the night. At each sampling, we recorded time of day, temperature of the model, the microhabitat where it was positioned, and its exposure to sunlight (full sun, partially shaded, fully shaded). Hereafter, we use the term "microsite" to distinguish among the 12 combinations of microhabitat type (rock, bush center, bush edge, open) and exposure to sun (full sun, partially shaded, fully shaded).

Lizard behaviors and body temperatures

On the first sampling day, we recorded the microsite use and behavior of every adult lizard seen ($N = 521$). We walked across the study area between 0730 and 1830, using a constant sampling effort throughout the lizards' period of activity. Upon sighting a lizard, we recorded time of day, its microsite when first sighted, and its posture and movement: basking (dorsoventrally flattened, body perpendicular to sun), immobile, walking, or unknown. For each basking lizard, we also noted the compass direction toward which its back was oriented. We note that our definition of basking includes a postural component, unlike the definition used in some studies of other lizards (i.e., perching in sun; see, e.g., Díaz 1991, Hertz 1992).

On the second day of sampling, again using a constant effort throughout the day, we captured 193 adult lizards with a baited noose (Castilla et al. 1994). We were especially careful to sample lizards from all microhabitats. Immediately after capture, we measured cloacal body temperature (T_b) to the nearest 0.1°C with a quick-reading Miller–Weber thermometer, and noted time of day and the microsite occupied.

We collected additional data on the movement patterns of adult lizards under comparable weather conditions in late September and early October 1994. We followed focal animals for 10-min periods, recording time of day and the length of time spent in a particular microsite. From these data, we calculated the lizards' mean residence time in microsites as well as the rate at which lizards moved from one type of microsite to another.

Data analyses and hypothesis testing

Following Hertz et al. (1993), we evaluated the thermal suitability of microsites and the accuracy and effectiveness of temperature regulation, with reference to the target T_bs that thermoregulating lizards attempt to achieve. This reference, the selected temperature range (T_{sel}), was estimated by the central 80% of temperatures selected by adult *P. h. atrata* in a laboratory photothermal gradient (31.9°–36.8°C; Castilla and Bauwens 1991*a*). The selected temperature range was used as an estimator of the "set-point temperature range" by Hertz et al. (1993). We used two indices to determine how well a T_b or T_e distribution conformed to T_{sel} (see Hertz et al. 1993 for details). First, we determined the percentage of T_b or T_e readings that fell within T_{sel}.

Second, we calculated the absolute value of each deviation of T_b or T_e from T_{sel} (d_b and d_e, respectively). When T_b or T_e is within T_{sel}, the corresponding d_b or d_e equals 0. Mean d_b estimates the accuracy of temperature regulation, and mean d_e estimates the thermal suitability of a microhabitat. We evaluated the effectiveness of temperature regulation, using the formula $E = 1 - (d_b/d_e)$, where E indexes the extent to which T_bs are closer, on average, to the selected temperature range than are T_es.

A null hypothesis ("no thermoregulation") asserts that times of activity and microsite selection are independent of T_e and opportunities to regulate T_b. This model predicts that lizards should exhibit a constant level of activity throughout the day, and should occupy microsites in proportion to their availabilities, irrespective of their thermal properties. Because our copper models did not sample the four microhabitats in proportion to their availability, we weighted data from the models using data from the microhabitat survey. For each microhabitat type, the weighting coefficient was p_j/m_j, where p_j is the proportion of available microhabitats of type j, and m_j is the proportion of models positioned in microhabits of type j. The weighted frequencies of models in sunny or shaded patches in the four microhabitats predict the frequencies with which randomly positioned lizards would occupy such microsites (Hertz 1992). Similarly, the weighted T_e distribution predicts the equilibrium T_b distribution of randomly positioned lizards that do not regulate T_b. We used this T_e distribution (i.e., weighted for microhabitat availability) as a baseline estimate in all further analyses.

An alternative hypothesis ("only thermoregulation") proposes that lizards restrict activity to times and places that are thermally suitable, which we define as microsites where T_e is within T_{sel} (i.e., where $d_e = 0$). This hypothesis predicts that lizard activity should be proportional to the availability of thermally suitable microsites. To verify this prediction, we tested for an expected positive correlation between the number of active lizards observed per sampling period and the percentage of T_e measurements falling within T_{sel}. We also tested for an expected negative correlation between the number of active lizards observed and the mean d_e per sampling period. The "only thermoregulation" hypothesis also predicts that, within each sampling period, lizards should be randomly distributed among thermally suitable microsites because no other constraints influence microsite selection. The relative frequencies of microsite types at which T_e is within T_{sel} predict the spatial distribution of lizards that are randomly positioned among such microsites.

We used a modification of the index proposed by Grant and Dunham (1988) to estimate the similarity, within each sampling period, of lizard microsite use and the microsite use predicted by each hypothesis:

$$S = \sqrt{2} - \sqrt{\Sigma[o_i - e_i]^2},$$

in which S is the similarity of the two distributions, o_i is the proportion of lizards observed in microsite type i, and e_i is the proportion of lizards expected in that microsite. The index varies from 0 to $\sqrt{2}$, with higher values indicating greater similarity of the two distributions.

We estimated the thermal consequences of the observed activity patterns by calculating the distribution of T_es that we would have measured, had the number of copper models sampled within each period been proportional to the number of lizards we actually observed. We calculated this distribution by weighting the measured T_e values by the number of lizards seen in the different sampling periods. For each sampling period, the weighting coefficient was p_j/m_j, where p_j is the proportion of lizards observed during period j, and m_j is the proportion of models sampled during period j. The resulting distribution (T_{ea}; operative temperatures weighted for activity levels) predicts the T_bs that lizards would achieve during their daily activity, in the absence of other thermoregulatory mechanisms. To evaluate the effect of the observed activity pattern on temperature regulation, we calculated the deviations of the T_{ea} values from T_{sel} (d_{ea}), and compared mean d_{ea} to the mean of the random d_e values.

Within each sampling period, we assessed the thermal consequences of the observed microsite use by weighting the measured T_e values by the frequencies with which lizards actually used different microsites. The weighting coefficient for each microsite type was p_j/m_j, where p_j is the proportion of lizards seen in microsites of type j, and m_j is the proportion of models positioned in microsites of type j. The resulting distribution (T_{em}; operative temperatures weighted for microsite use) predicts the T_bs that lizards would achieve at the microsites they actually occupy, if they did not use other behavioral or physiological mechanisms to regulate T_b. To evaluate the contribution of the observed microsite selection to temperature regulation, we calculated the deviations of the T_{em} values from T_{sel} (d_{em}), and compared them to the random d_e values. We assessed the contribution of microsite use to temperature regulation within sampling periods and for the overall data set by comparing mean d_{em} to mean d_e. In graphical representations, we compared T_{em} to both random T_es and observed T_bs in each sampling period. We note that our data allowed us to compare the means of these variables, but not their variances. The lizard models had much higher heating and cooling rates than live lizards, and approached equilibrium temperatures faster. Thus, the variance of the (weighted) T_e records probably overestimated the variance in heat loads actually experienced by lizards.

We used the WEIGHT procedure of SPSS/PC+ V5.0 to weight the operative temperature data. This algorithm allows fractional values as weights, so that the
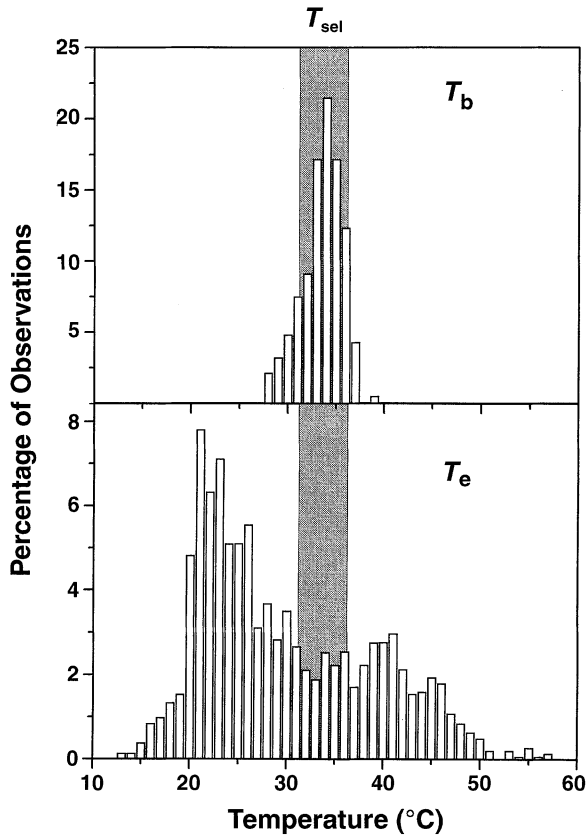
FIG. 1. Distributions of body temperature (T_b) in a population of *Podarcis hispanica atrata* and available operative temperature (T_e) during early autumn. The shaded area identifies the selected temperature range (T_{sel}).

original sample size can be maintained. Hence, the resulting weighted distributions can be used for statistical testing. We employed standard statistical methods (correlation coefficients, ANOVA, chi-square tests) to identify relationships or differences among variables, using a probability of $P \leq 0.05$ as a standard criterion of statistical significance. Whenever necessary, we transformed data logarithmically to homogenize variances before testing.

RESULTS

Overall body temperatures and operative temperatures

The mean T_b of *P. h. atrata* in early autumn (33.9 $\pm$ 2.1°C, $\bar{X} \pm 1$ SD; $N = 193$) was considerably higher than the mean T_e (weighted for microhabitat availability; 30.3 $\pm$ 8.9°; $N = 1320$). Moreover, the T_b distribution was much narrower than the T_e distribution (Fig. 1). Lizards maintained T_b close to T_{sel} (77% of T_bs within T_{sel}; mean $d_b = 0.3$°). By contrast, most T_es were far from T_{sel} (16% of T_es within T_{sel}; mean $d_e = 6.3$°). Thus, *P. h. atrata* regulates T_b with high effectiveness ($E = 0.95$).

Some T_e measurements fell within this species' T_{sel}

during all 45-min sampling periods except the first and the last (Fig. 2B). Thus, field-active lizards could potentially achieve temperatures within the selected range during most hours. Nevertheless, <20% of T_e measurements fell within the selected temperature range in the vast majority of sampling periods (Fig. 2B; 0–29% of T_es within T_{sel}; range of mean $d_e = 3.2$°–11.7°). These data indicate that only a small fraction of the microsites available offer ideal thermal conditions to these lizards. Despite these constraints, lizard T_bs were highly accurate during all sampling periods (Fig. 2A; 23–95% of T_bs within T_{sel}; range of mean $d_b = 0.0$°–1.6°). Thus, lizards regulated T_b effectively throughout the day (range of E values = 0.71–0.99). These results confirm previous observations of apparent temperature regulation by *P. h. atrata* (Castilla and Bauwens 1991a). The following sections examine the contributions of various behavioral mechanisms to temperature regulation.

Times of activity

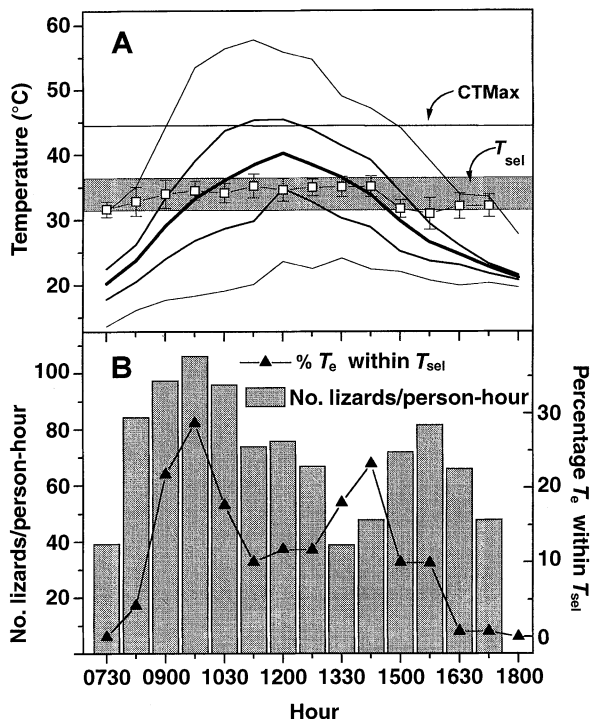Because the "no thermoregulation" hypothesis assumes that lizard activity is independent of thermal

FIG. 2. (A) Summary statistics of diel variation in distributions of body temperatures (T_b; open squares; mean ± 1 SD) and operative temperatures (T_e; curves from bottom to top: minumum, first quartile, mean, third quartile, and maximum temperatures recorded during 45-min intervals). The shaded area identifies the selected temperature range (T_{sel}); the horizontal line identifies the critical thermal maximum temperature (CTMax). (B) Diel variation in the number of lizards observed per person-hour (vertical bars) and in the percentage of T_e readings that fall within T_{sel} (triangles).

TABLE 1. Summary statistics of operative temperatures (mean ± 1 SE; sample size in parentheses) for copper models positioned in different microhabitat types and exposed to full sun, partial sun, or shade.

	T_e (°C), by microhabitat			
Exposure	Bush center	Rock	Bush edge	Open
Sun	34.7 (1)	34.9 ± 0.5 (113)	44.6 ± 1.6 (29)	41.3 ± 0.6 (87)
Partial shade	28.2 ± 0.5 (90)	30.6 ± 0.4 (271)	31.4 ± 0.6 (229)	31.6 ± 0.6 (193)
Shade	22.4 ± 0.7 (13)	21.7 ± 0.5 (44)	21.1 ± 0.4 (54)	20.7 ± 0.5 (32)

conditions, it predicts a uniform level of activity (i.e., a constant number of lizards observed) from dawn until dusk. In fact, lizards exhibited a bimodal pattern of daily activity, with a morning peak between 0900 and 1100 and an afternoon peak between 1500 and 1700 (Fig. 2B). This pattern clearly deviates from the prediction of the "no thermoregulation" model ($\chi^2 = 161.8$, df = 14, $P < 0.001$).

The observed activity pattern also fails to match the predictions of the "only thermoregulation" hypothesis: the number of lizards observed per sampling period was neither positively correlated with the percentage of T_e readings within T_{sel} ($r = 0.441$, df = 12, $P > 0.10$), nor negatively correlated with the mean d_e per sampling period ($r = -0.337$, df = 12, $P > 0.30$). Although the morning peak in activity corresponded to a time of favorable T_e, morning emergence occurred before any T_e measurements fell within T_{sel}. Moreover, the afternoon retreat occurred long after most T_e readings fell below T_{sel}. Thus, diel variation in the number of active lizards observed is not well predicted by diel variations in available T_e.

We evaluated the thermal consequences of the observed activity pattern by weighting our T_e measurements by the number of lizards seen in each sampling period, and calculating the deviations of those T_{ea}s from T_{sel}. Overall, mean d_{ea} was 1.0°C lower than mean d_e (mean $d_{ea} = 5.3 \pm 4.4°$, $\bar{X} \pm 1$ SD; mean $d_e = 6.3 \pm 4.3°$; $t = 6.25$, df = 2638, $P < 0.001$). Hence, the T_es experienced by active *P. h. atrata* are, on average, 1.0° closer to T_{sel} than those encountered by a hypothetical lizard population with a uniform level of activity throughout the day.

Availability and selection of microsites

In this section, we first describe the combined effects of microhabitat type, exposure to sun, and time of day on T_e. We then examine microsite availability and the lizards' use of microsites in relation to the predictions of the two hypotheses. Finally, we consider the thermal consequences of the observed microsite use.

Thermal properties of microsites.—Variation in T_e was influenced by a significant interaction effect between microhabitat type and exposure to sun (Table 1; two-way ANOVA: $F_{6, 102} = 3.97$, $P = 0.001$; to avoid pseudoreplication, we performed the analysis on the

mean values of $\log_{10} T_e$ calculated for each combination of individual model and exposure to sun category). The influence of full sun is substantially greater in bush edge and open microhabitats (Table 1), reflecting the interactive effect of the two factors. Thus, the analysis of microhabitat use by lizards must include reference to the distribution of sun, filtered sun, and shade in the four microhabitat types.

Bush center was the least variable of the microhabitats with respect to diel variation as well as within-period variability of T_e (Fig. 3). It was also the coolest, with the vast majority (84.2%) of T_e readings falling below and relatively few (2.5%) falling above T_{sel}. Only from 1000 to 1500 did any bush center T_es fall within T_{sel}. Most models in bush center were partially shaded by vegetation. This habitat offers thermally favorable microsites only during midday sampling periods.

Rock microhabitats provided slightly more variable and somewhat warmer thermal conditions. Operative temperatures were above T_{sel} in 16.5% of the readings, but only rarely reached the lizards' critical thermal maximum temperature (CTMax; Fig. 3). A considerable fraction of T_e readings (26.0%) were within T_{sel}. In fact, in each sampling period between 0900 and 1600, >20% of the models on rocks achieved T_es within T_{sel}, including many that were in full sun.

Bush edge and open microhabitats provided extremely variable T_es within and among sampling periods. These microhabitats were also the hottest, with T_e rising quickly in the morning (Fig. 3). During the middle of the day (1030–1415), a large fraction of T_es (53.5% in bush edge and 74.3% in open) exceeded T_{sel}, with many readings (30.0% in bush edge and 27.5% in open) above the CTMax. In both microhabitats, T_es only rarely fell within T_{sel}, with the majority of these readings recorded in mid-morning and mid-afternoon. Models in the open microhabitat were exposed to full sun more often than those in bush edge; in both microhabitats, most models in full sun had T_e readings well above T_{sel}.

Microsite use.—The "no thermoregulation" hypothesis predicts that lizards would use microhabitat types and sun–shade patches in proportion to their availability. The availability of microhabitats is constant throughout the day (15.3% bush center, 25.8% bush edge, 51.2% open, 7.7% rock). However, because exposure to sun changes continuously, the relative avail-
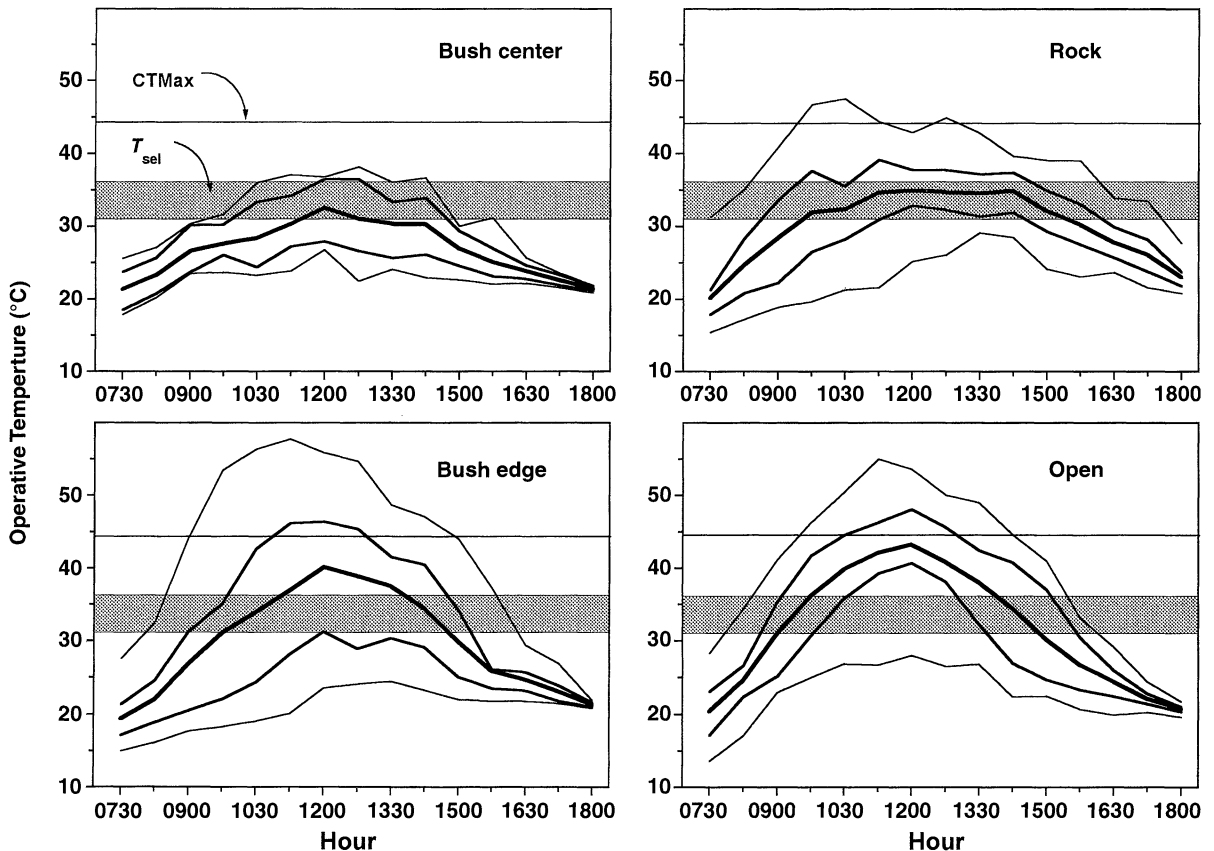
FIG. 3. Summary statistics of diel variation in operative temperatures (T_e) in different microhabitat types. Curves (from bottom to top) indicate the minumum, first quartile, mean, third quartile, and maximum copper model temperatures recorded during 45-min intervals. The shaded area identifies the selected temperature range (T_{sel}); the horizontal line identifies the critical thermal maximum temperature (CTMax).

ability of the 12 microsites varied among sampling periods (Fig. 4).

Lizard microsite use (Obs in Fig. 4) differed significantly from the predictions of the "no thermoregulation" hypothesis (H_N in Fig. 4) in the entire data set ($\chi^2 = 5810.1$, df $= 143$, $P \ll 0.001$). A separate analysis of individual sampling periods showed significant differences in all but one midday period (chi-square tests, sequentially Bonferroni-corrected Ps < 0.05). Similarly, observed microsite use differed also from the predictions of the "only thermoregulation" hypothesis (H_T in Fig. 4) for the whole data set ($\chi^2 = 1382.3$, df $= 143$, $P \ll 0.001$); these differences were significant in all sampling periods (chi-square tests, sequentially Bonferroni-corrected Ps < 0.05).

Our similarity index measures the correspondence of the lizards' use of microsites to that predicted by each hypothesis. During most sampling periods, microsite use was more similar to predictions of the "no thermoregulation" hypothesis than to those of the "only thermoregulation" hypothesis (Fig. 5A). Similarity to predictions of the "no thermoregulation" hypothesis was generally higher during midday periods than in the early morning and late afternoon, and was highest when

mean T_e was either within or above T_{sel} (Fig. 5B). In fact, similarity to predictions of the "no thermoregulation" hypothesis was highly correlated with both mean T_e ($r = 0.847$, df $= 12$, $P < 0.001$) and the standard deviation of T_e ($r = 0.892$, df $= 12$, $P < 0.001$). Thus, lizards occupied microsites more randomly at midday, when T_e was high and a wide range of T_es was available.

A detailed examination of the differences between observed microsite use and that predicted by the "no thermoregulation" hypothesis provides some insights into the pattern of microsite selection (Fig. 4). Lizards used the bush center microhabitat during all sampling periods, roughly in proportion to its availability over the course of a day. However, the number of lizards observed in shaded and partly shaded bush center microsites was greater than expected during midday sampling periods. Lizards used rocks much more often than expected, especially before 1030 and after 1330. Although the number of lizards sampled on shaded or partially shaded rocks was in proportion to availability of these microsites, the numbers observed on rocks in full sun were unexpectedly high.

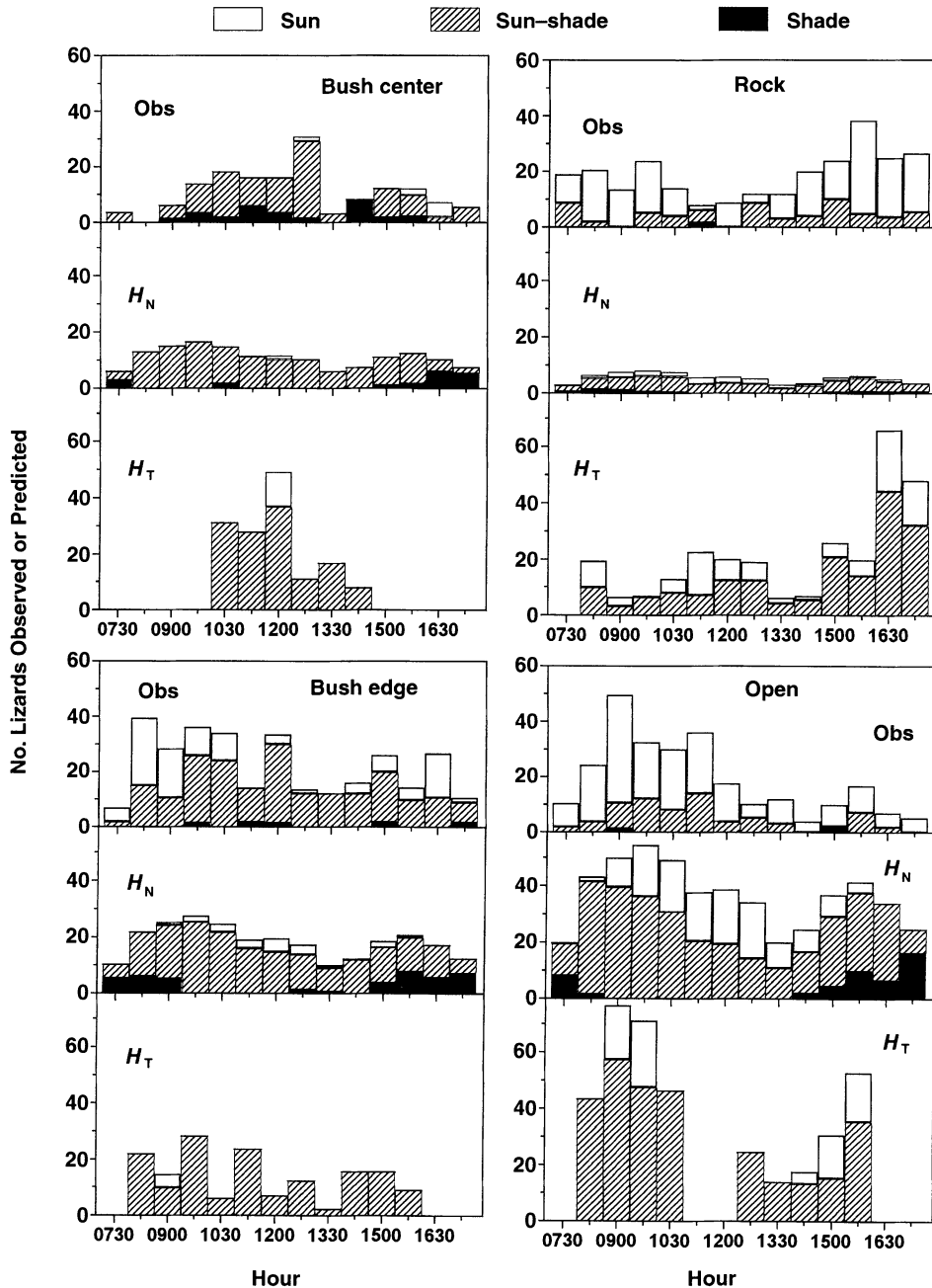Lizards used the sun–shade mosaic within the bush

FIG. 4. Diel variation in observed and predicted use of microsites (combinations of microhabitats and sun–shade exposure). Upper panels show the number of lizards observed per person-hour (Obs); middle panels depict the number per person-hour predicted by the "no thermoregulation" hypothesis (H_N; habitat use proportional to availability); lower panels show the number per person-hour predicted by the "only thermoregulation" hypothesis (H_T; use of microsites where T_e is within T_{sel}).

edge microhabitat nonrandomly. More lizards than expected were seen in full sun before 1115 and after 1500. During the midday hours, patches of sun and shade were used roughly in proportion to their availability. From 1200 until their afternoon retreat, lizards used open microhabitats less frequently than expected. Moreover, lizards occupied open microhabitats nonrandomly: they used partially and fully shaded patches much less fre-

quently than expected, but they used sunlit patches more frequently than expected, especially during the first three and last three sampling periods (Fig. 4).

Thermal consequences of microsite selection.—We examined the thermal consequences of microsite selection by weighting the T_e measurements by the observed microsite use. The resulting T_{em} distribution simulated the operative temperatures experienced by a
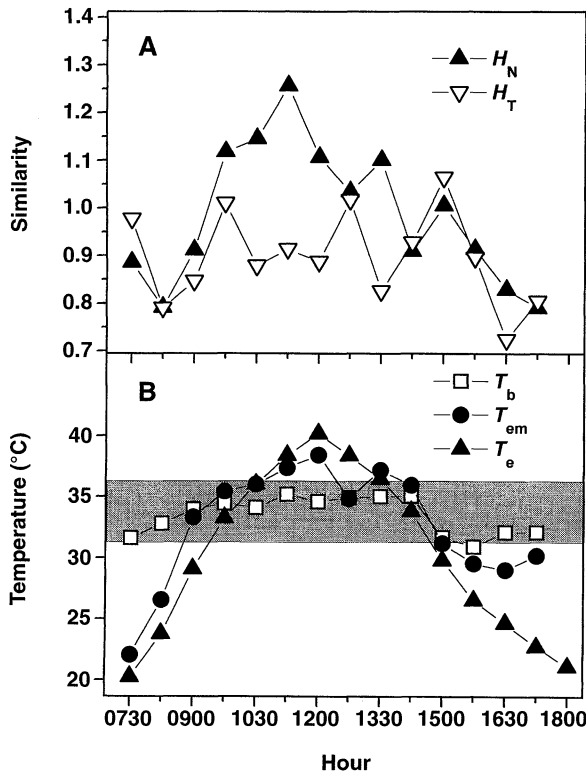
FIG. 5. (A) Diel variation in the similarity between observed microsite use and that predicted by each of two hypotheses: the "no thermoregulation" hypothesis (H_N; habitat use proportional to availability), and the "only thermoregulation" hypothesis (H_T; use of microsites where T_e is within T_{sel}). Higher values indicate greater similarity between observed and predicted distributions. (B) Mean operative temperature (T_e), mean operative temperature weighted for microsite use (T_{em}), and mean body temperatures (T_b) of field-active lizards during different sampling periods. The shaded area identifies the selected temperature range (T_{sel}). The absolute difference between T_{em} and T_e in each sampling period indexes the contribution of observed microsite use to thermoregulation. The absolute difference between T_b and T_{em} in each sampling period indexes the contribution of other adjustments (e.g., basking postures, shuttling) to temperature regulation.

population of models that occupied microsites in proportion to their actual usage by lizards (Fig. 5B). To evaluate the contribution of observed microsite selection to temperature regulation, we compared the deviations of T_{em}s from T_{sel} (d_{em}) to those of the random T_e measurements (d_e). Over the entire day, mean d_{em} was 1.9°C lower than mean d_e (d_{em} = 4.4 ± 4.1°C, $\bar{X}$ ± 1 SD; t = 9.54, df = 2374, $P < 0.001$). Thus, the T_es at the microsites occupied by lizards were, on average, 1.9° closer to T_{sel} than were randomly available T_es.

The thermal consequences of microsite selection varied among sampling periods (Fig. 5B). During 12 of 14 sampling periods, d_{em} was lower than d_e (binomial test, $P = 0.013$). The contribution of microsite selection to thermoregulation, indexed by the differences

between mean d_{em} and mean d_e within sampling periods, was negatively correlated with the similarity of microsite use to predictions of the "no thermoregulation" hypothesis ($r = -0.769$, df = 12, $P < 0.01$). Thus, microsite selection had the greatest influence on temperature regulation during those periods when lizards occupied microsites nonrandomly. In other words, nonrandom microsite use contributed to temperature regulation by this population.

Nonrandom microsite selection generally produced mean T_{em}s within T_{sel} during mid-morning (900–1115) and early afternoon (1245–1545). Nevertheless, the predicted T_{em}s were substantially lower than both T_{sel} and the T_bs actually maintained by lizards during the early morning and, somewhat less so, during the late afternoon. This result implies that lizards also used other mechanisms to regulate T_b at those times of day.

Basking and shuttling behavior

The proportion of lizards seen basking was highest in the early morning, declining to near zero between 1115 and 1545 (Fig. 6). The frequency of basking increased again to moderate levels in the late afternoon. The compass orientation of basking lizards tracked the sun through the day, such that their backs were directly exposed to solar radiation (Fig. 6). Slightly less than half (49.6%) of the basking lizards were observed on rock, and most of the remainder were about equally divided between bush edge (24.4%) and open (18.9%) microhabitats.

Among sampling periods, the frequency of basking behavior was negatively correlated with mean T_e ($r = -0.802$, df = 12, $P < 0.001$). In addition, the difference between the T_bs of lizards and the T_{em}s predicted from their choice of microsites was strongly correlated with the frequency of basking ($r = 0.909$, df = 12, $P < 0.001$). These results imply that basking substantially elevates T_b above the levels that could be achieved by microsite selection alone.

Focal animal observations revealed that the rate at which lizards moved from one microsite to another varied through the day (Table 2; ANOVA on $\log_{10}$[number of moves/10 min]: $F_{4,65} = 20.2$, $P < 0.001$). An a posteriori test indicated that lizards moved more often during midday hours than early and late in the day (Table 2). Thus, residence time within a given microsite was greatest during early morning and late afternoon (Table 2; ANOVA on $\log_{10}$ residence time: $F_{4, 192} = 10.8$, $P < 0.001$).

DISCUSSION

Our data clearly indicate that *P. h. atrata* regulates its T_b accurately and effectively in early autumn. We first examine two important assumptions of our approach and their implications for the interpretation of our results. We then consider the thermal constraints imposed by the physical environment and a possible strategy for maintaining T_b within T_{sel}. Finally, we con-

FIG. 6. Percentage of lizards observed basking during different sampling periods, and the compass direction toward which basking lizards oriented their backs.
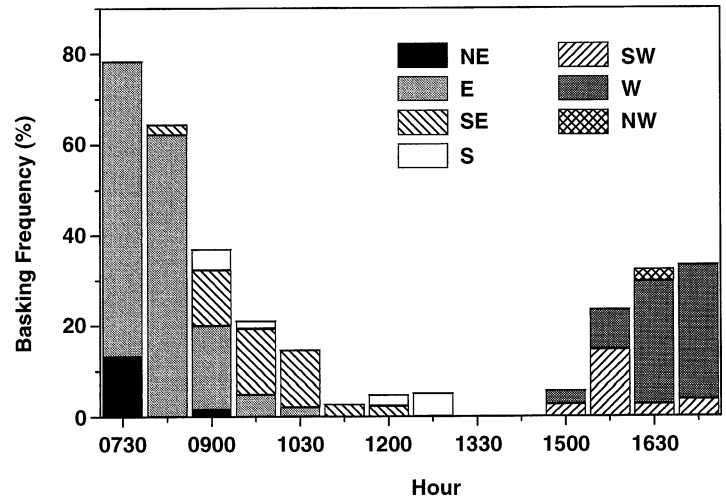
sider the behaviors used by *P. h. atrata* for thermoregulation, and describe the contribution of each.

Assumptions of our approach

We assume that our copper models provided an accurate sampling of T_es in our study site. Although we positioned the models throughout the range of available microhabitats, we may not have sampled the very coolest and warmest microsites used by lizards. Such sampling errors, if they occurred, would produce an underestimate of the variance in T_e during some sampling periods and for the overall data set. Consequently, we may have slightly underestimated mean T_e in the early morning and late afternoon, and overestimated mean T_e during midday hours. As a result, mean T_es may actually have been slightly closer to T_{sel} than our data suggest. These errors would inflate our estimates of d_e, as well as the effectiveness of thermoregulation (E). Furthermore, these errors may have caused us to underestimate the contribution of microsite selection and overestimate the contribution of basking behavior to temperature regulation. We believe that these errors are small, but the only practical way to reduce the likelihood of such sampling errors would be to increase the number of models used to sample T_e.

TABLE 2. Rates of movement between microsites and residence times within microsites for *Podarcis hispanica atrata* at different times of day. Common superscripts within each column identify values that are not significantly different (Newman–Keuls a posteriori test).

Time period	Movements (no./10 min)			Residence time (s)		
	$\bar{x}$	1 SE	n	$\bar{x}$	1 SE	n
0730–0945	1.7[a]	0.9	12	232.9[a]	46.8	22
0945–1200	14.7[b]	3.2	18	42.4[b]	6.3	71
1200–1330	5.8[c]	1.9	8	87.8[b]	16.1	31
1330–1545	10.1[b,c]	3.3	6	68.8[b]	18.1	32
1545–1800	1.1[a]	0.6	26	287.9[a]	36.8	41

Our second assumption is implicit in the use of T_e to calculate the predicted T_bs (i.e., the T_{em}) of lizards that use microsites nonrandomly (Hertz et al. 1993). In calculating the T_{em} distribution, we weighted the random T_es by the observed microsite use, assuming that lizards would achieve thermal equilibrium at the microsites they occupied. Although small lizards have low thermal inertia (Stevenson 1985a), this assumption is unlikely to be met when lizards move frequently among microsites (Tracy and Christian 1986, Hertz et al. 1993). Thus, in our data, lizards may have achieved thermal equilibrium in the early morning and late afternoon when mean residence time in microsites was high, but they were probably not in thermal equilibrium during midday hours when mean residence time was short. A rapidly moving lizard is likely to achieve a T_b that approximates the mean T_e of the microsites through which it moves, rather than equilibrating to the T_e within each microsite (van Berkum et al. 1986). Thus, rapid movement among microsites reduces the variance of the heat loads experienced by lizards and, consequently, the variance of the T_{em}s. such movements, however, are unlikely to affect our estimates of mean T_{em} (Hertz et al. 1993).

Environmental constraints

An extreme strategy of temperature regulation would restrict activity to the times and places where a majority of T_es were within T_{sel}. Our data indicate that *P. h. atrata* does not adopt this strategy in early autumn. The number of lizards observed per sampling period was unrelated to mean T_e, largely because many individuals were active in the early morning and late afternoon. Although lizard activity declined somewhat after a morning peak, large numbers were abroad even during those midday hours when a substantial fraction of T_e readings were above T_{sel}. Apparently, the highest and lowest T_es were neither so extreme nor so common that lizards could not compensate for them with the use of

other thermoregulatory behaviors. Activity periods may be more restricted at other times of year, when heat loads at midday are higher or those in the early morning and late afternoon are lower (Grant and Dunham 1988).

Lizards did not restrict their activity to thermally optimal microsites during any sampling period. In fact, for a substantial portion of the day, the observed microsite use was more similar to the predictions of the "no thermoregulation" hypothesis (i.e., random microsite use) than to the prediction that lizards use only thermally favorable habitat patches (Fig. 5A). The observed pattern of microsite use may have resulted from the relative scarcity of thermally ideal microsites. Moreover, the thermal quality of other microsites was apparently not low enough to prohibit lizard activity. Nevertheless, lizards may have encountered a substantial risk of overheating in the bush edge and open habitats at midday, when $\approx$30% of the T_e observations were above this species' CTMax. However, the available sun–shade mosaic and the proximity of alternative microsites allowed lizards to reduce heat loads by moving relatively short distances. In other words, the thermal constraints imposed by the physical environment in early autumn were probably not very severe.

Alternatively, the thermal properties of microsites are probably not the only determinants of microsite use by lizards. Thermally optimal microsites may be unsuitable for other functions such as foraging, predator avoidance, and social dominance. For example, sunlit rocks were often thermally ideal near midday. Nevertheless, we observed fewer lizards in these microsites than we expected on the basis of their thermal properties. Conversely, many lizards used sunlit bush edge and open microsites near midday, despite the adverse thermal conditions there. We suggest that these observations can be explained, at least in part, by the apparently higher food availability in the open and bush microhabitats (Castilla and Bauwens 1991a). In general, microsite selection inevitably represents a compromise between the need to regulate T_b and requirements for other resources (see Huey 1991).

Mechanisms of behavioral thermoregulation

Our data suggest that *P. h. atrata* uses fairly subtle behavioral or physiological mechanisms to regulate its T_b. Physiological ecologists have traditionally identified three non-exclusive mechanisms of behavioral temperature regulation (Stevenson 1985b): the adjustment of activity times (Hertz 1981, Hertz and Huey 1981, Grant and Dunham 1988, Grant 1990); the selection of microhabitats and sun–shade patches (Huey et al. 1977, Christian et al. 1983, Grant and Dunham 1988, Huey et al. 1989, Adolph 1990, Hertz 1992); and the use of postural adjustments and other behaviors that alter rates of heat exchange (Avery 1976, Muth 1977, Van Damme et al. 1987). We evaluate the contribution of each of these mechanisms in turn.

The observed activity pattern and microsite use clearly differed from those predicted by the "no thermoregulation" hypothesis, suggesting that these behaviors constitute thermoregulatory adjustments (Huey et al. 1977, Adolph 1990, Hertz 1992). However, observations of nonrandom behavior alone do not demonstrate that these behaviors contribute to temperature regulation. Indeed, the lizards' responses to nonrandom distribution of food, predators, or conspecifics could produce similar observations. We therefore extended our analysis by predicting the thermal consequences of the behaviors we observed. We then compared these predictions to the observed T_bs to evaluate the relative contributions of the different behavioral adjustments to a regulated T_b.

Diel variations in levels of activity had only a limited effect on the T_es actually encountered by active lizards. Our analysis suggests that the T_bs predicted from variations in activity level (T_{ea}) were, on average, only 1°C closer to T_{sel} than were the randomly sampled T_es. Thus, the adjustment of activity time made a fairly minor contribution to temperature regulation. This result contradicts Stevenson's (1985b) emphasis on the importance of activity times to temperature regulation. However, the disparity between our result and his prediction may have arisen because we sampled T_es only during daylight hours.

Nonrandom occupation of microsites appeared to have a somewhat larger effect on T_b (mean T_{em} was 1.9° closer to T_{sel} than was mean random T_e). Thermal characteristics of the four microhabitats changed throughout the day because of diel variations in their exposure to sun. Because most microhabitats offered a sun–shade mosaic, lizards could alter the heat loads to which they were exposed, either by changing microhabitats or by shifting among sunny and shady microsites within a single microhabitat. Although lizards occupied microsites nonrandomly overall, their selection of microsites was least random during the early morning and late afternoon, when mean T_e and the variance in T_e were low. Not unexpectedly, the contribution of microsite selection to temperature regulation increased with the lizards' selectivity.

In the late morning and early afternoon (0945–1115 and 1330–1500), lizards that used microsites randomly would generally encounter mean T_es within T_{sel} (Fig. 5B). Hence, at these times of day, lizards could potentially minimize the time and cost required to regulate T_b (Huey 1974, Huey and Slatkin 1976). Consequently, they could safely devote time to activities unrelated to thermoregulation (e.g., foraging, social interactions). The frequent movements among microsites and short residence times within microsites observed during these sampling periods may reflect an absence of strong thermal constraints (see also Díaz 1991, Avery 1993). Alternatively, these movements may reflect obligatory shuttling between microsites with different thermal characteristics. Indeed, because many microsites had

T_es either below or above T_{sel} during these times of day, frequent movement among thermally distinct microsites may constitute a useful thermoregulatory adjustment (Tracy and Christian 1986).

The components of "basking behavior" in these and many other temperate zone lizards include dorsoventral flattening of the body and a body orientation that provides maximal exposure to sun (Heath 1965, Avery 1976). Thus, these behaviors collectively maximize the heating rates of basking lizards. We cannot establish null hypotheses about the effects of basking behavior and shuttling among microsites because our copper models had a single posture and occupied fixed positions in the field. Nevertheless, our results, as well as previous research on diverse lizard species, indicate that basking is most frequent when environmental temperatures are low (e.g., Pearson 1954, Van Damme et al. 1987).

Although we have no null hypothesis for evaluating our data on basking rates, correlative evidence suggests that basking behavior was intentional and had a dramatic effect on lizard T_b, especially in the early morning hours, when T_es were low. During our first and last three sampling periods, when microhabitat selectivity and basking rates were high, the mean residence time at microsites was long, averaging 4–5 min. We believe that the effects of basking behavior are evident in the differences between actual lizard T_bs and those predicted from the lizards' microsite choices alone (T_{em}s in Fig. 5B). Although T_es were similar in the early morning and late afternoon, the relative contributions of basking and nonrandom microsite use to thermoregulation appeared to differ at these times. During early morning, basking seemed to have a much greater effect than microsite selection, whereas their thermal consequences were more similar in the late afternoon.

During midday (1115–1330), random microsite selection would result in mean T_bs above T_{sel} (Fig. 5B). Surprisingly, lizards did not use microsites selectively during these periods, and predicted T_bs were often above T_{sel}. Nevertheless, the T_bs that we observed at these times were quite accurate (i.e., had a low d_b), indicating that lizards experienced heat loads that were lower than those available at the microsites they apparently occupied. The frequent movements among microsites that we observed during these periods cannot explain the discrepancy: these movements would influence the variance, rather than the mean, of the predicted T_b (van Berkum et al. 1986, Hertz et al. 1993). However, an artifact of our sampling procedure may have biased our results. Lizards moving across open or bush edge microhabitats are more conspicuous than those that occupy shaded bush centers. As a result, we may have overestimated the frequency of lizards in warmer microsites and underestimated the frequency of those in cool, shaded microsites. If the censuses were slightly biased in these directions, we may have overestimated the effect of high heat loads in warm habitats.

Thus, our predicted T_bs for these three sampling periods may be somewhat high.

In summary, *P. h. atrata* regulates its T_b by adjusting its times of activity, by using microsites nonrandomly, and by varying its posture and rates of movement. Our data suggest that basking behavior and associated postural adjustments contribute as much to behavioral temperature regulation as do restriction of activity times and nonrandom use of microsites, especially in the early morning. Of course, these behaviors are highly integrated under field conditions. For example, lizards must occupy appropriate microsites for basking, just as they must seek shaded microsites when environmental heat loads are exceptionally high. The relatively limited contributions of activity times and microsite selection to temperature regulation in this population are rather surprising on theoretical grounds (Stevenson 1985b); many prior studies have identified these behavioral mechanisms as major determinants of T_b. Future studies of reptilian temperature regulation should also address the contributions of postural adjustments and shuttling behavior.

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