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EVOLUTIONARY AND ENVIRONMENTAL EFFECTS ON THERMOREGULATION AMONG COMPLEX LIZARD COMMUNITIES

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

SHAWN SCOTT SARTORIUS
Norman, Oklahoma
2002

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EVOLUTIONARY AND ENVIRONMENTAL EFFECTS ON THERMOREGULATION AMONG COMPLEX LIZARD COMMUNITIES

A Dissertation APPROVED for the
DEPARTMENT OF ZOOLOGY

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Preface

The first chapter of this dissertation has been formatted for the journal Ecology, the second for the journal Oecologia, and the third for the journal Biological Conservation.

Chapter I

Historical and Environmental Effects on Thermoregulation in an Arizona Lizard Community

Abstract

A community of ten sympatric lizard species was studied in a mountain canyon in southern Arizona to determine the effect of phylogeny on habitat use and thermoregulation. Habitat use, body temperatures (T_b) and operative environmental temperatures (T_e) were recorded in the field, as well as the selected temperature range (T_{sel}) for active lizards in the laboratory. T_e varied significantly with elevation, time of day, macrohabitat, and microhabitat with most of the variation occurring at the microhabitat level, indicating a small spatial scale of thermal heterogeneity at the study site. At most times of day and in most macrohabitats, T_e bracketed T_{sel} for the species indicating that maintenance of T_b within T_{sel} was possible during most daylight hours. Randomization analyses of matrices of phylogenetic similarity, habitat use and microsite temperature overlaps showed significant correlations between phylogenetic similarity, habitat use, and field active T_bs. There was no correlation between phylogenetic similarity and T_{sel}. Indices of thermoregulation calculated for each species revealed that although these lizards thermoregulated effectively, there was no correlation between the matrix of phylogenetic similarity and similarity matrices for accuracy or effectiveness of thermoregulation. Pseudocommunity analyses showed no partitioning of thermal resources, indeed species tended to use similar thermal resources despite disparate habitat use. The significant effect of phylogeny on microhabitat use, and field T_b but not on T_{sel} suggests that microhabitat selection may override thermoregulation, possibly due to tradeoffs between thermoregulation, foraging, predator avoidance or reproduction.

Introduction

Body temperature (T_b) is an important physiological and ecological parameter for many ectotherms because of its wide-ranging effects on rates of biochemical and physiological processes. When an organism regulates T_b, it receives the benefit of partial release from constraints that environmental temperature regimes place on its physiology, at the cost of energy required for thermoregulation, exposure to predation, or loss of time for reproduction or foraging (Huey 1974). These costs and benefits must be balanced and vary among species depending on the ecology and physiology of each species. Many physiological and ecological traits that determine the necessity for thermoregulatory accuracy and precision may be rooted deeply in phylogenetic hierarchies and thus may be under strict evolutionary constraints, resulting in a high level of conservatism in temperature preferences and thermoregulatory strategies (Magnusson et al. 1985). Alternatively, if these parameters are not conservative, temperature preference and thermoregulation should be tailored to the habitats and microhabitats that each species uses, and past evolutionary history should have little effect on current thermoregulatory tactics.

Body temperature has a direct effect on nearly all physiological performance measures including locomotion (Waldschmidt and Tracy 1983, Stevenson et al. 1985, Huey and Bennett 1987, Huey and Kingsolver 1989, Huey et al. 1989), digestion (Dorcas et al. 1997), metabolism (Brett 1971, Grant 1990, Christian and Weavers 1994), and growth (Avery 1984, Bronikowski et al. 2001). These physiological effects of temperature lead to effects on behavior (Bennett 1980, Hertz et al. 1982) and ecology (Grant and Dunham 1988, Grant 1990, Huey 1991). A thorough understanding of an organism's responses to environmental temperatures is therefore required in order to understand many aspects of its biology, including foraging mode, habitat use, geographical distribution, and interactions with other species.

Preferred body temperatures (the target temperature that an organism attempts to maintain in the absence of external constraints) are thought to be correlated with optimal temperatures for whole-organism performance (Huey 1982; Huey and Kingsolver 1989). Because a wide variety of physiological functions must be optimized within a single organism, a complex set of tradeoffs between physiological functions may result. Two conflicting views of the evolution of preferred T_b are that: 1) temperature preferences are evolutionarily conservative and show little variation within species and among closely related clades (Huey 1982; Rosen 1991) and 2) thermal preferences are evolutionarily plastic such that selective pressures will modify thermal performance to optimize performance levels for activity under local conditions (Hertz et al. 1983). Predictions stemming from the first view ("phylogenetic inertia") include the likelihood that closely related taxa that share a common thermal milieu will have similar preferred T_bs and similar thermal ecology. Closely related taxa that inhabit dissimilar thermal environments must either use dissimilar thermoregulatory mechanisms or employ the same mechanisms to a greater or lesser degree to maintain T_b within their preferred range, or they must be tolerant of sub-optimal T_b. Predictions stemming from the second view ("physiological adaptation") suggest that ectotherms will maintain their T_b within an optimal range by changing what that optimal range is. Under this scenario, closely related taxa inhabiting dissimilar thermal environments may employ similar thermoregulating mechanisms to a similar degree and still maintain T_b within an optimal range because the optimal range has shifted. In addition preferred T_bs of distantly related species in similar thermal environments should converge over time.

Although temperature is not in the strict sense a resource, in that it is not depletable as it is exploited by organisms, space is a resource, and the spatial correlation of temperature and habitat in a heterogeneous landscape makes temperature a potential proxy resource, or the mechanism by which space may be partitioned among species. Individuals may occupy areas of desirable temperature and prevent other individuals from occupying that same space either directly by interference or passively by depleting other resources like food, mates, or retreat sites. Just as morphological adaptation to certain microhabitat types may serve to decrease competitive interactions between closely related species (Pianka 1973, 1975, Vitt et al. 1981, Losos et al. 1997, Vitt et al. 1997, Vitt et al. 2000), the unique thermal physiology of each species may adapt it to a particular thermal regime. This thermal niche may then serve as a niche axis upon which niche partitioning may occur (Pianka 2000). Ectothermic vertebrates often utilize their habitats' thermal opportunities non-randomly (Grant and Dunham 1988, Bauwens et al. 1996, Sartorius et al. 1999, Wills and Beaupre 2000). Therefore, habitat temperatures can be viewed as a resource, much like more traditional resources often considered in ecological studies (Magnuson et al. 1979, Tracy and Christian 1986, Hertz 1992). Thermal niches of organisms may change due to selection on physiological traits to minimize competition between individuals of sympatric species in much the same way that optimal foraging theory predicts evolution of foraging strategies among interacting species (Pyke et al. 1977, Magnuson et al. 1979). Consideration of temperature as a resource allows the possibility that organisms actively compete for thermally optimal habitats, and that over evolutionary time this competition will lead to interspecific partitioning of thermal resources.

If sympatric animals partition resources based on temperature, then there should be detectable differences in at least one of three measures. 1) selected temperature range (T_{sel}), 2) field-active T_b, 3) a measure of the effectiveness of thermoregulation showing the amount that the field active T_b distribution is shifted away from the operative environmental temperature (T_e) distribution toward the T_{sel} distribution (see below for further description of thermoregulatory parameters). A difference in T_{sel} indicates an intrinsic difference in temperatures that animals attempt to maintain in the absence of environmental constraints. This difference may or may not be reflected in field active T_b distributions. A difference in field active T_b indicates that a difference exists between the temperatures that the species utilize under field conditions. This may be due to different temperature preferences but also may be due to one or more of the species sacrificing optimal T_b in favor of some other fitness benefit such as enhanced success in foraging, reproduction, or predator avoidance. The index of thermoregulatory effectiveness (E) (Hertz et al. 1993) combines T_{sel}, T_b, and T_e to allow the investigator to determine the extent to which the animal takes advantage of the thermal opportunities available in the habitat (see formula below). A high level of thermoregulatory effectiveness means that the distribution of T_b is closer to T_{sel} than is the distribution of T_e.

Numerous studies exist addressing temperature relations of ectothermic vertebrate species either in sympatry (Huey and Pianka 1977, Hertz 1992, Vitt et al. 2000, Grbac and Bauwens 2001), or a combination of sympatric and allopatric populations (Schoener and Gorman 1968, Pianka 1969, Huey and Webster 1976, Magnuson et al. 1979, Adolph 1990). These studies have concentrated on field body temperature comparisons often with no measures of environmental temperatures or of preferred temperatures. Thermoregulatory interactions of a complex lizard community have never been subjected to a phylogenetic analysis, nor has the potential for thermal niche partitioning ever been explored for a community of lizards simultaneously in the same location.

The objective of this study is to analyze thermoregulation among sympatric lizard species in a community context. I treat T_e as a resource that can be partitioned among species much like more traditional resources such as food and space. The hypothesis that lizards have adapted their thermal physiology to the thermal conditions of their habitat is tested statistically by comparing measures of thermoregulation to phylogenetic relationships of the species. The related question of whether or not closely related species divide thermal resources to reduce competition, or conversely, whether closely related species share thermoregulatory characteristics, is also examined.

Materials and Methods

Field Sites and species

Lizards in this study are derived from two ancient lineages: Iguania and Scleroglossa. Six species fall within the Phrynosomatidae of the Iguania (Frost and Etheridge 1989). The two species *Sceloporus clarki* and *S. magister* are arboreal, preferring larger trees in xero-riparian areas as well as boulder and cliff habitats. *S. undulatus* is partially arboreal but is also found on boulders, stones and on the ground. *Urosaurus ornatus* is a small arboreal species inhabiting most structural components of the habitat studied including small shrubs, large trees, boulders, and cliff faces. Two species of "sand lizard" were also studied. *Callisaurus draconoides* is a desert species that is at its upper elevational limit at the two low elevation sites in this study. *Cophosaurus texanus* typically inhabits moderate elevations in Arizona from 1000m to 1500m. Both of these species are strictly terrestrial, only using small stones as lookout points and almost never climbing.

Four species of *Cnemidophorus* occurred at that site: *C. burti*, *C. sonorae*, *C. uniparens*, and *C. tigris*. *Cnemidophorus* is a member of the Teiidae within the Scleroglossa. The species of *Cnemidophorus* species are all primarily terrestrial.

Four study areas located on the northwest versant of the Santa Catalina Mountains in Pinal County, Arizona, USA were studied during summer 1999. The sites were distributed linearly in the drainage of Peppersauce Canyon, a tributary of the San Pedro River at elevations of 1097 m, 1219 m, 1417 m, 1509 m. This canyon is dry year-round except during flash flooding events after rainstorms. The canyon is characterized by steep, rocky slopes and a flat, sandy arroyo bottom. Each site contained approximately 2 km of wash bottom and adjacent canyon slopes with 2 km to 4 km separating adjacent sites. Tree and shrub canopy coverage increased with elevation between the four sites. Vegetation typical of the Sonoran Desert including saguaro cactus (*Carnegia gigantia*), creosote bush (*Larrea tridentata*), and foothills paloverde (*Cercidium microphylum*) were abundant at the lowest site, indicating that it is situated at the upper elevational limit of the Arizona Upland Subdivision of the Sonoran Desert (Brown and Lowe, 1974). At the 1219 m site, desert plants were less abundant and canopy coverage increased. In the canyon bottom adjacent to the wash canopy coverage was continuous for long stretches and the canyon slopes were sparsely vegetated. The 1417 m site was ecotonal between desert grassland and oak/juniper woodland with extensive canopy coverage on north facing slopes and sparse bunch grasses on the south facing slopes. The highest site at 1509 m was solidly in oak woodland with the most canopy coverage. Again, canopy coverage was greatest on the wetter north facing slopes. These sites provided a gradient not only in elevation but also in vegetation stature with tree height and density increasing with elevation.

Lizard Sampling

Lizards were sampled 11 May to 5 June and 15 July to 1 August in 1999. In the first sampling period, two people spent six days at each of the four sites. In the second sampling period, two people spent six days at the two low elevation sites and 3 days at the high elevation sites. Lizards were sampled for a total of 84 person-days, 48 person-days at the two low elevation sites and 36 person-days at the two high elevation sites. We surveyed haphazard transects through all available habitats during all hours of diurnal lizard activity (~0700 to ~1900 hrs). We sampled all time intervals approximately equally and divided search time between canyon bottom and slopes approximately 2:1. When a lizard was located it was identified to species, and the habitat (north slope, south slope, canyon bottom), microhabitat (branch, trunk, sand, soil, grass, rock, stone, litter, gravel, other) where the lizard was first seen, and time of day were recorded on micro-cassette recorders. When possible, lizards were collected immediately using a noose, by hand, or with pneumatic (BB) rifle, and T_b was measured to the nearest 0.1C using a Miller and Weber® rapid-register cloacal thermometer. Lizards were held by a hind foot during temperature measurement to minimize heat transfer between lizard and investigator. Lizards collected by lethal methods were preserved in a 10% formalin solution, individually tagged and deposited in the Sam Noble Oklahoma Museum of Natural History at the University of Oklahoma in Norman, Oklahoma, USA.

Although habitat structure varied considerably between sites, I perceived little or no difference in our ability to detect lizards; all sites provided ample visual access to all microhabitats. Several species of lizard occurred at one or more of the sites in very low numbers or were nocturnal. The banded gecko (*Coleonyx variegatus*) is nocturnal and was not sampled; the gila monster (*Heloderma suspectum*), great plains skink (*Eumeces obsoletus*), lesser earless lizard (*Holbrookia maculata*), regal horned lizard (*Phrynosoma solare*), leopard lizard (*Crotaphytus wislizeni*), and madrean alligator lizard (*Elgaria kingi*) were found in very small numbers (1 to 4 individuals) within the study sites, or nearby off-site, and were considered rare or peripheral occurrences in the canyon and were not included in the community analyses.

Operative Temperature Sampling

Operative environmental temperatures (T_e) were measured simultaneously with lizard sampling. I used Tidbit® temperature data loggers (Onset Computer Inc.) to approximate lizard T_e. These miniature data loggers are self-contained in a shell of epoxy resin and record equilibrium temperatures similar to small copper lizard models traditionally used in studies of lizard operative temperatures (Vitt and Sartorius 1999; Shine and Kearney 2001). I established a 210 m transect at a 90° angle to the direction of flow down the canyon and centered on the center of the canyon bottom. Along this transect I placed 21 data loggers at 10 m intervals so that one data logger was in the center of the canyon bottom with 100 m of transect radiating out and up the canyon slopes on each side. At the 1097 m site the canyon bottom became wider than 200 m so the transect was divided into two with 10 data loggers placed on each side of the canyon, 4 data loggers running 40 m up the slope and 6 running 60 meters into the wash. This transect was moved within each site a random distance up or down the canyon each day so that within each 24-hr sampling period a new set of microsites was sampled. Temperatures were recorded at 1 hr intervals for 28 days between 11 May and 1 August, 1999.

In order to eliminate confounding effects of temporal and spatial T_e variation during the study, I calculated a single T_e value for each lizard T_b measurement. Hourly means were calculated over two-day intervals corresponding to times of data collection at each individual sub-site. Each lizard T_b measurement was assigned a corresponding T_e, the mean over the hour in which the capture occurred. This technique allowed me to evaluate thermoregulation based only on T_e that the lizards could actually exploit, i.e., those that occurred within the range of an individual's daily movements, and during the time that the individual was active. And eliminated variation resulting from changes in seasonal weather patterns, or elevation. This procedure resulted in a single T_e measure for each field T_b measure and a unique T_e distribution for each lizard species that corresponds to the times and places that lizards were encountered. Thermoregulatory calculations in which T_e is measured over a long period of time or over a large area, do not offer the fine resolution that is required to accurately examine behavioral thermoregulation.

Selected Body Temperature Measurement

T_{sel} was measured in a laboratory thermal gradient at the University of Oklahoma in the summer of 2001. The thermal gradient consisted of a circular aluminum disk 1.5 m in diameter with two aluminum hot plates attached to the undersurface of one side. This created a temperature gradient running across the disk ranging from 60° C to 16° C. Lighting was provided by two 1.2-m full-spectrum fluorescent tubes placed directly over the gradient, running parallel to the direction of temperature change. Lizard subjects had a thermocouple inserted into the cloaca and affixed with adhesive tape. Lizard temperature was recorded at 5 min intervals by a Model 50 electronic data logger (Electronic Controls Design Inc., Milwaukie, Oregon, USA).

Lizards were collected from the same field sites in early June 2001 by hand and noose. Lizards were transported to the University of Oklahoma and placed in terraria separated according to species, body size, and in some cases sex to avoid aggressive interactions. Lizards were allowed to freely thermoregulate during daylight hours (0600 hrs to 2100 hrs) between 30°C (the room background temperature) and 60°C under incandescent spot lamps. At night the spot lamps were turned off and temperatures stabilized at the 30° C background temperature. During photophase, additional background lighting was supplied by full spectrum fluorescent tubes to simulate illumination conditions in the field. Lizards were fed in the 24 hrs prior to temperature measurement. No lizards were placed in the gradient without at least 7 days under these acclimation conditions. My acclimation regime was designed to approximate the thermal regime that these lizards experience during the summer months at the Peppersauce site. This regime is more realistic than acclimating animals to a constant temperature, as is often done in laboratory studies. I compared laboratory gradient T_bs to the T_bs of animals active in nature where their thermal history is unknown. I therefore compromised a full knowledge of the thermal history of the animals involved in the gradient study in order to achieve a more realistic assessment of the T_{sel} with which to compare field-acclimated animals.

Lizards were placed in the thermal gradient 30 min. after the beginning of photophase and allowed to explore the thermal gradient for 1 hour before temperature recording began. Temperatures were recorded continuously at an interval of 5 min. for 10 hours. Following Hertz et. al. (1993), I use the inter-quartile range (central 50%) of the temperatures selected in the gradient as my estimate of T_{sel}.

Indices of thermoregulation

Following the methods of Hertz et. al. (1993) as outlined by Christian and Weavers (1996), I calculated three indices of thermoregulation to evaluate: 1) habitat thermal quality, 2) accuracy of thermoregulation, and 3) effectiveness of thermoregulation for each species. The first index, habitat thermal quality (d_e) is the average of the deviation of T_e from T_{sel} for each species. This index can range from 0, meaning all T_e are within T_{sel}, to infinity; a lower value indicates higher thermal quality of the habitat. The index d_b is the average deviation of T_b from T_{sel}. This index can vary from 0, perfect maintenance of T_b within T_{sel}, to infinity. Higher d_b values indicate lower thermoregulatory accuracy. The effectiveness of thermoregulation (E) is calculated using the following formula:

$$E = 1 - (d_b/d_e)$$

E varies from a high of 1, indicating perfect maintenance of T_b within T_{sel}, to negative infinity. Negative values indicate avoidance of T_e within T_{sel}, i.e. lizards are using T_e within T_{sel} less than would be expected if they were sampling the thermal environment randomly. The E index is a measure of the lizard's ability to take advantage of available thermal opportunities while it goes about its daily routine. E

may also be used as a crude measure of the cost of thermoregulation if it is accepted that within an environment, the cost of thermoregulation increases as effectiveness increases. A lizard having a higher E value than other sympatric species may be investing more resources in thermoregulation than species with low E values. An additional index of the effectiveness of thermroegulation developed by Blouin-Demers and Weatherhead (2001), the difference between d_e and d_b, is reported as well. This index may be a better estimate of the effectiveness of thermoregulation because it is not undefined if de is zero, and it is not a ratio, making it more amenable to statistical testing.

Statistical methods

To evaluate potential for temperature to be used as a resource in community ecology studies I conducted pseudocommunity analyses (Winemiller and Pianka 1990) on the field T_b and habitat use data for the lizard assemblage at Peppersauce Canyon following Vitt and Zani (1996). This analysis calculates interspecific niche overlaps creating a matrix of overlap values calculated from the geometric mean of the proportional utilization coefficients and electivities for each species' use of each resource category. The overlap matrix provides data on similarity between species pairs. To test the hypothesis that species overlap values are randomly distributed, two separate bootstrap analyses were performed using the MacScramble software package (Winemiller and Pianka 1990). In the first analysis, all values in the resource utilization matrix were randomized 1000 times (scrambled zeros) and new sets of overlaps calculated. Thus, niche breadths and number of resources were retained and guild structure (if any) was eliminated. In the second analysis, all values in the resource utilization matrix except zero entries were randomized 1000 times with respect to position for each species (conserved zeros) and new sets of overlaps calculated, thus retaining niche breadths, number of resource states, and zero structure. Mean overlaps were then compared at each nearest neighbor rank following Inger and Colwell (1977). The real community was considered different (structured) if pseudocommunity overlaps fell above or below real community overlaps 95% of the time. Real community overlaps that are lower than scrambled zero overlaps indicate niche partitioning within the real community. Real community overlaps that exceed conserved zero overlaps indicate that guild structure exists among the community members. For a complete explanation of pseudocommunity analysis see Winemiller and Pianka (1990).

I tested hypotheses of phylogenetic effects on lizard thermoregulation using a phylogenetic similarity matrix calculated from the branching diagram presented in figure 1. This tree is a composite based on studies by Estes et al. (1988), Frost and Etheridge (1989), and Weins and Reeder (1997). Species relationships within *Cnemidophorus* are poorly understood; however, species groups are well defined based on karyotype data (Lowe et al. 1970). Two species groups within *Cnemidophorus* are represented in this study: *Cnemidophorus tigris* is in the tigris group, and *C. burti*, *C. sonorae*, and *C. uniparens* are in the sexlineatus group. *C. uniparens* and *C. sonorae* are parthenogenetic (triploid) species of hybrid origin. Due to the difficulty of accurately representing reticulate evolution in a phylogenetic analysis, the relationships between the three sexlineatus-group species are here represented as a polytomy (Fig. 1). Branch lengths were standardized at 1 in all cases. I compared matrices of thermal and habitat niche overlaps produced in the pseudocommunity analyses to the phylogenetic distance matrix using Mantel's randomization test. In this test all elements of one matrix are randomized and the correlation between the two matrices is calculated, this procedure was repeated 9999 times. The number of randomized correlation coefficients equal to or greater than the observed correlation coefficient forms the basis for the statistical test. Pseudocommunity analyses were performed using MacScramble (Winemiller and Pianka 1990) and Mantel's tests were performed using NTSYSpc 2.02I.

Results

Operative temperatures

Diurnal operative temperatures (T_e) varied from of 7.7° to 75.3° C. I used the general linear model feature (GLM) of SAS to analyze the T_e data. My model classed T_e by season (early/late), locality (1097 m, 1219 m, 1417 m, and 1509 m) hour (0700 hrs to 1700 hrs), macrohabitat (north slope, south slope, canyon bottom), and microhabitat (branch, grass, gravel, litter, bedrock, sand, soil, stone, trunk). This model incorporates likely sources of variation in data that are relevant to lizards and allowed me to determine which variables accounted for significant variation in operative temperatures while all other variables were accounted for. The variables tested accounted for significant variation in the data set (overall GLM $F_{24,6185} = 262.74$, $P < 0.0001$). In addition, each of the grouping variables accounted for a significant portion of the variation explained in the model (Table 1). Most variation in T_e occurred at the microhabitat level, the scale most relevant to lizard thermoregulatory decisions (Fig. 2). In the representative figure presented, lizards have the option of choosing T_e from 32°C to 53°C at midday by moving from one microhabitat to another within the same habitat. Macrohabitat was also a significant contributor to T_e variation with about 8°C difference in mean T_e between wash and slope habitats at midday (Fig. 2). Significant variation between sites also existed (Fig. 2), but sites were far enough apart to make this variation irrelevant to the minute by minute thermoregulatory decisions made by individual animals.

Selected temperature range

Species' median T_b in the thermal gradient varied from a low of 35.3°C for *Urosaurus ornatus* to a high of 37.7°C for both *Callisaurus draconoides* and *Cnemidophorus burti* (Table 2). Temperature preferences (means of individual lizard median T_b) differed between species (ANOVA, $F_{9,41} = 2.409$, $p = 0.0269$). A comparison of all pairwise differences revealed that 14 of the 45 possible comparisons were significantly different (Fisher's PLSD). Species differed in thermoregulatory precision based on comparisons of individual lizard standard deviations (ANOVA, $F_{9,41} = 2.731$, $p = 0.0136$). Pairwise comparisons (Fisher's PLSD) indicated that 9 of 45 possible comparisons were significantly different. A Mantel's test comparing a matrix of median T_{sel} similarity with a matrix of phylogenetic similarity was not significant ($p = 0.4755$); more closely related species were not more likely choose similar temperatures than would be expected at random.

Field body temperature

Field T_b data are summarized in Fig. 3. Species means ranged from 34.3° C for *S. clarki* to 39.7° C for *C. draconoides* (Table 2). Field T_bs were different among species (ANOVA, $F_{9,696} = 45.652$, $p < 0.0001$). And pairwise comparisons (Fisher's PLSD) showed that 26 of 45 possible comparisons were significant, indicating widespread variation in T_b among species. The pseudocommunity analysis of field T_b for the 10 species revealed guild structure, i.e. overlaps in the observed matrix were significantly higher than those of the scrambled zero randomizations for the first five nearest neighbors in niche space (Fig. 4). This result indicates that species tended to use common thermal resources more than expected if temperature use were random. A Mantel's test comparing the matrix of T_b overlaps with the phylogenetic similarity matrix for the species showed a significant correlation ($p = 0.006$). More closely related species were likely to be closer in T_b use than would be expected if T_b use was random. A matrix of inter-specific T_b differences was not correllated with T_{sel} differences (Mantel's test, $p = 0.239$) indicating that variability in laboratory temperature selection was directly translated to field T_b.

Habitat use

Microhabitat use varied among the species with *Callisaurus*, *Cophosaurus* and *Cnemidophorus* species using microhabitats on the ground and *Urosaurus* and *Sceloporus* species usually associated with structural habitat features such as tree trunks and branches, or large rocks and stones (Fig. 5). Pseudocommunity analysis of the microhabitat overlaps revealed a pattern similar to the analysis of the T_b overlaps

(Fig. 4). Observed microhabitat overlaps were significantly higher than scrambled zero overlaps for the first three nearest neighbor ranks indicating guild structure for microhabitat variables. Overlaps for nearest neighbor ranks 6 and 8 were significantly lower than for the conserved zero randomizations indicating some niche partitioning for species in different guilds (Fig. 4). However, interactions at higher ranks are less likely to be ecologically significant than those at lower ranks due to their small overlap values. Plots of standard deviations of overlaps provide further evidence of guild structure (Fig. 4). Guild structure is indicated by a "hump" in observed standard deviations and their degree of difference from scrambled zero overlaps (Winemiller and Pianka 1990). There was a significant correlation between phylogenetic similarity and microhabitat overlaps (Mantel's test, $p = 0.0027$) suggesting that closely related species were more likely to share microhabitats than would be expected if microhabitat use were random.

Indices of thermoregulation

Measures of habitat thermal quality (d_e) varied significantly between species ($F_{9,696} = 2.105$, $P = 0.0271$) (Fig. 6). Similarly, d_b values were significantly different between species ($F_{9,696} = 5.930$, $p < 0.0001$) and d_b values were not correlated with phylogenetic similarity ($p = 0.2062$), there was no phylogenetic effect on the deviation of T_b from T_{sel}. E values varied from 0.615 to 0.867 with a grand mean of 0.759 (± 0.027) (Fig. 7). A Mantel's test comparing the matrix of E similarities with phylogenetic similarities was not significant ($p = 0.193$), indicating that closely related species did not have E indices more similar than would be expected at random. The index de - db varied from 2.86 to 4.73 with a mean of 3.92 (Fig. 7). Correlations of de - db with phylogenetic similarity were not significant (Mantel's test, $p = 0.313$).

Discussion

Operative environmental temperatures and the spatial scale of thermal heterogeneity

Behaviorally thermoregulating lizards rarely seek out and use thermally optimal microsites, rather, they shuttle between microsites with T_e that are too high and too low, rarely reaching equilibrium temperatures (Van Berkum et al. 1986). It is therefore only necessary that T_e "bracket" the target range and that microsites containing both high and low T_e are accessible and positioned close enough together to allow the animal to shuttle between them. It is conceivable that lizards could thermoregulate effectively in a habitat with almost no optimal temperatures if the spatial scale that high and low T_e microsites were positioned was small. Thus, the spatial scale at which thermal heterogeneity occurs may have far-reaching consequences for lizard ecology, including interspecific interactions. For example, species that maintain territories and/or rely on structural components of the habitat will be more dependent on having a relatively small spatial scale of thermal heterogeneity than species that freely move long distances without risk of losing territorial battles or exposing themselves to predation. The field site for this study is best characterized as subtropical thornscrub that grades into open oak woodland at higher elevations. Here, the vegetative canopy is discontinuous and most shrubs and trees occur in small clumps less than 5 m in diameter with 1 to 5 m separating clumps. This patchwork of cool shaded microsites provided by clumps of vegetation with open microsites between clumps creates significant thermal heterogeneity on a scale of one to 5 m. In addition, T_e within a single habitat type varied significantly between microhabitats. Both these factors indicate that lizards needed only move short distances within one macrohabitat to find temperatures that were higher or lower than their optimal range. T_e varied significantly at the scales of habitat and locality. However, the overall variation accounted for at those scales was less than the variation in microhabitats. This means that movements between macrohabitats and localities within the same microhabitat provided less overall temperature change than moving between microhabitats within one macrohabitat in one locality.

Field body temperature and thermoregulatory indices

During 84 person-days of sampling I encountered and collected data for a total of 1623 individuals of the 10 lizard species included in the analysis. This lizard fauna is a relatively simple assemblage compared to lizard communities of the Amazon Basin (Vitt and Zani 1996, 1998), dry tropical formations in South America (Vitt 1991, 1995, Vitt and Carvalho 1995), and Australian deserts (Pianka 1973, 1975). However, diversity of lizards at this site is higher than average diversity for desert sites in North America (Pianka 1975). Among the species, median T_b ranged from 34.3 to 39.2°C. Standard deviations within species were low, indicating that each species maintained its T_b within a narrow range throughout its activity (high precision). Likewise, d_b values were quite low (0.59 to 2.48, X = 1.29) indicating that lizards were able to maintain T_b within or close to T_{sel} most of the time (high accuracy). Species' measures of d_e ranged from 4.26 to 6.45 (mean = 5.21). This is slightly lower than the d_e values reported for tropical monitor lizards in Australia (Christian and Weavers 1996), slightly higher than values reported for Caribbean *Anoles* (Hertz et al. 1993), and much lower than d_e values for temperate lacertid lizards extrapolated from Bauwens et al. (1996) and Grbac and Bauwens (2001). The distribution of d_e values at this site during the summer is more similar to those reported for dry tropical habitats than for other temperate habitats. Despite the overall high temperatures in this area, microsites with T_e within or below each species' T_{sel} were available during all daylight hours in each of the habitat types. This indicates that the thornscrub habitat with closely associated sunny and shady patches was an ideal environment for lizards to actively regulate T_b through shuttling behavior. This suggests that mean d_e, as a measure of actual habitat thermal quality, may be misleading in high-insolation habitats. Under these circumstances, the absolute values of the T_es present may not be as important as the juxtaposition of microsites bearing those T_es. The positioning of microsites with high and low T_es in close proximity allows a shuttling lizard to maintain a "running average" of the overall environmental temperatures within its body, even though temperatures in the sun may be too hot and temperatures in the shade too cold for optimal performance (Van Berkum et al. 1986).

Despite relatively low diversity of this lizard assemblage, phylogenetic patterns in the T_b overlap matrix were detected. This could mean that close relatives attempt to maintain T_b at similar temperatures or alternatively that T_b is similar among close relatives due to another variable that co-varies with T_b and phylogeny. If close relatives were choosing to thermoregulate at similar T_b then it would be reasonable to expect that T_{sel} would also correlate with phylogeny. This was not the case; T_{sel} variation had no apparent phylogenetic component nor did T_{sel} correlate with T_b. Several possible explanations exist for this apparent paradox. One explanation is that there simply was not enough total variation in T_{sel} to make the patterns that were present in the laboratory detectable under field conditions. Median T_{sel} varied from a low of 35.2°C to a high of 37.7. This small (though statistically significant) difference in temperature preference between species would be difficult to detect under field conditions when so many confounding variables are present. Another possible explanation is that the laboratory gradient did not effectively approximate preferred temperatures in complex natural environments. Different species may have behaved differently while in the gradient, masking potential phylogenetic patterns. Most species in this study maintained higher T_b in the field than in the gradient, a result that is not surprising given the high T_e in most microsites. However, variability in field T_b was very low (Table 2). Despite high variability in T_e between microhabitats and habitat types, lizard species maintained T_b within a narrow range.

By design, laboratory thermal gradients remove lizards from distractions inherent in natural habitats such as the necessity to forage, avoid predators, maintain territories, and mate. They also provide a wider range of thermal opportunities than are often found in nature. The result is that the lizard chooses its optimal temperature, although in some cases, temperature preference and optimal sprint performance may not be linked (e.g. some nocturnal lizards) (Huey and Bennett 1987). If the optimal temperature is different for different activities, discrepancies may be detectable between the temperatures selected in the laboratory (low activity) and the temperatures selected in the field where the lizard is likely to thermoregulate for high activity (foraging, digestion, etc) (Bowker et al. 1986; Christian and Weavers 1996). The suitability of using thermal gradients to approximate preferred or optimal temperatures of field active ectotherms needs further examination. The thermal gradient in this study was a thigmothermal gradient designed to remove light intensity as a confounding factor in determining temperature preference in lizards (Sievert and Hutchison 1988). Many studies have used photothermal gradients to determine T_{sel} (Hertz et al. 1993, Bauwens et al. 1996, Grbac and Bauwens 2001), and the potential confounding effects of light gradients paralleling the thermal gradient have been incompletely investigated for diurnal, heliothermic lizards. However, in a study of thermoregulation in an assembly of African lizards, Bowker (1986) tested several different gradient types and found no differences in temperature preference between gradient types.

Another explanation for the lack of correspondence between T_{sel} and T_b is that microhabitat preference (which is correlated with phylogeny) overrides the thermal preference of the lizard, at least within the range of T_e prevalent during this study. This may be a likely explanation due to overall high temperatures that these species had to choose from. The overall mean T_e for all sites, habitats, and microsites over the entire study from 0700 to 1800 hrs was 37.8°C (interquartile range = 28.2°C to

47.4°C). These temperatures are high for temperate-zone lizards but variable enough to allow for effective thermoregulation throughout the day if microsite selection is not hampered by other requirements such as foraging, maintaining territories, reproduction, or predator avoidance. The fact that T_{sel} was not correlated with T_b and that T_b was correlated with microhabitat selection, suggests that microhabitat needs were overriding the need for precise temperature regulation during this study. High environmental temperatures may have released these species from the necessity of careful thermoregulation (as in Shine and Madsen 1996), except to avoid high temperatures, and allowed them to use the microhabitats that would optimize other facets of their ecology. In a study of phylogenetic effects of preferred temperatures and optimal performance, Huey and Bennett (1987) showed that critical thermal maxima and optimal temperatures for sprinting varied less than preferred temperatures. This suggests that if lizards in a hot environment are thermoregulating to avoid high temperatures that would lead to incapacitation, there will be less variation in T_b than is found in T_{sel}. This hypothesis was not confirmed; standard deviations of field T_b were slightly higher than individual lizard standard deviations in the laboratory thermal gradient.

Lack of correlation between T_e and T_{sel} leaves open the possibility that interspecific interactions at this site are leading to displacement of some species away from their preferred thermal environment. Closely related species were more likely to use similar microsites than distantly related species. The same holds true for T_b, and T_b and microhabitat overlaps were also significantly correlated. This suggests that microhabitat partitioning was not occurring because T_e and T_b also showed a significant correlation and it is likely that if lizards were partitioning thermal resources there would be a corresponding partitioning of microhabitat resources due to the strong effect of microhabitat type on T_e. Under field conditions species actually became more similar in their T_b use relative to T_{sel} rather than diverging, as would be predicted under a niche partitioning model.

The pseudocommunity analysis indicated guild structure for both T_b and microhabitat overlap matrices. This result indicates that species tend to congregate on common resource categories which also suggests that thermal niche partitioning is not occurring in this assemblage. The correlation between T_b and microhabitat reinforces this result; in the field closely related lizards are likely to be members of the same microhabitat/T_b guild. Results for T_{sel} indicate no phylogenetic effect on temperature preference. The lack of correlation between T_{sel} and T_b may change in a season or at a site with lower T_e in which thermoregulation would involve primarily heat seeking rather than heat avoidance.

Phylogenetic comparisons indicate that temperature preferences may vary in a way that is consistent with the resource partitioning hypothesis, i.e. closely related species use different thermal resources. However, in the field, closely related species had similar T_b, indicating that partitioning was not occurring there. The high correlation between habitat use overlaps and T_b overlaps suggests that microhabitat selection drives the pattern of correlation between T_b overlaps and phylogenetic similarity and possibly interfering with the "optimal" thermoregulation of the individual species.

This study represents a holistic approach to community ecology in which properties result from innumerable complex interactions (emergent properties) that cannot be adequately predicted using reductionist approaches. As with any study of this kind, the results may only be applicable over the specific time and place that the study was undertaken (Mares 1982). This study was conducted at one place that encompassed a small elevational gradient in one season. The lizards involved are widespread species each having a unique evolutionary history that involves populations that have been both temporally and spatially sympatric and allopatric with each other as well as with species that do not currently occur at the present site. Therefore, it is likely that the thermal ecology of each species at this site represents a complex set of tradeoffs and compromises that is also unique to this time and place. It is only through long-term studies of lizard communities in other biomes, representing unrelated lineages, investigated in sympatry and allopatry, that we will begin to gain a thorough understanding of the relevance of thermal ecology to the interactions of lizard species, and ultimately to their distributions and assembly rules.

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Table 1. Summary of the results of a general linear model of operative temperatures (T_e) from four sites at Peppersauce Canyon, Arizona

Source	df	F value	Probability > F
Season	1,24	901.89	<0.0001
Hour	10,24	405.95	<0.0001
Macrohabitat	2,24	24.89	<0.0001
Microhabitat	8,24	35.31	<0.0001
Site	3,24	182.07	<0.0001

Table 2. Summary of T_{sel} and T_b data for 10 sympatric lizards from Peppersauce Canyon, Arizona. Pooled mean and pooled SD indicate species means of each individual lizard's mean and standard deviation of T_b while in the thermal gradient.

	Field body temperatures						Laboratory thermal gradient						
								Pooled mean		Pooled SD		Pooled median	
Species	*N*	Mean	SD	Median	High	Low	*N*	Mean	SE	Mean	SE	Mean	SE
Cnemidophorus burti	73	38.6	1.758	38.0	41.0	32.1	4	37.5	0.426	1.313	0.171	37.7	0.329
Cnemidophorus sonorae	160	38.4	2.589	39.0	42.1	27.0	5	36.0	0.874	2.574	0.471	36.3	0.626
Cnemidophorus uniparens	14	39.3	1.392	39.2	41.8	36.0	5	35.7	0.271	2.330	0.225	35.7	0.271
Cnemidophorus tigris	95	38.6	2.656	39.1	42.4	24.8	6	36.4	0.363	1.825	0.207	36.4	0.476
Cophosaurus texanus	33	38.2	2.274	38.7	40.7	28.7	5	37.9	0.682	2.048	0.196	38.0	0.802
Callisaurus draconoides	85	39.0	2.596	39.7	41.9	28.0	6	37.2	1.056	2.870	0.482	37.7	0.947
Urosaurus ornatus	116	35.0	2.786	35.4	39.8	25.2	5	35.6	0.527	2.295	0.307	35.3	0.993
Sceloporus undulatus	60	34.5	2.005	34.6	39.0	26.4	5	35.4	0.496	2.330	0.225	35.4	0.714
Sceloporus magister	24	33.9	4.018	34.7	38.4	21.2	5	37.2	0.281	1.483	0.233	37.5	0.328
Sceloporus clarki	46	33.8	2.642	34.3	38.9	26.9	5	35.0	0.511	2.205	0.197	35.6	0.671

Figure Legends

Figure 1. Composite phylogeny of lizards at Peppersauce Canyon, Arizona, based on Estes et al. (1988), Frost and Etheridge (1989), and Weins and Reeder (1997).

Figure 2. Hourly operative environmental temperatures recorded at Peppersauce Canyon, Arizona May – August, 1999. The top panel includes all data from all sites. The middle panel shows variation by between habitat types at the 1219 m site. The bottom panel shows variation between microsites within the wash bottom habitat at the 1219 m site. Error bars represent ± one standard error.

Figure 3. Field-measured body temperatures (T_b), mean operative environmental temperatures during the hour of capture (T_e), and selected temperature ranges (T_{sel}) for ten lizard sympatric lizard species.

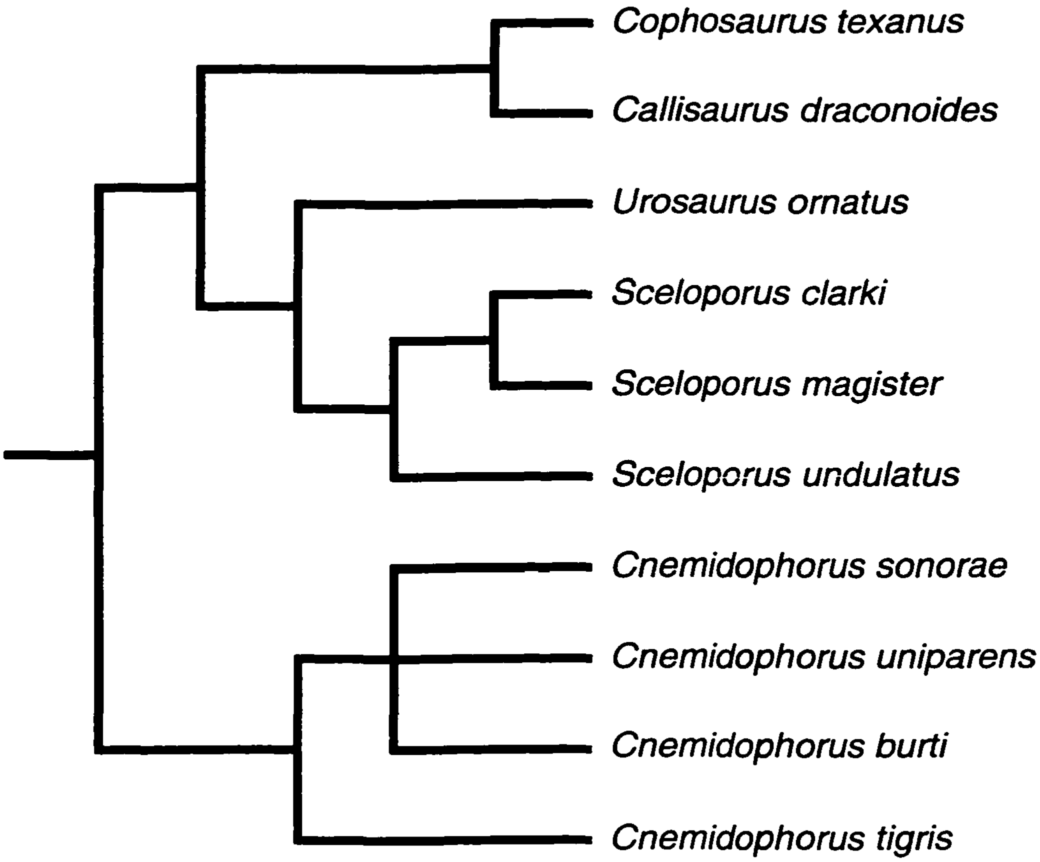
Figure 4. Ranked overlaps and standard deviations in microhabitat and body temperature for the observed community and two types of pseudocommunities. Guild structure is indicated in observed communities by the degree to which observed SD exceeds scrambled zero SD. At each rank, a single asterisk (*) indicates a $P < 0.05$, two asterisks (**) indicates a $P < 0.01$.

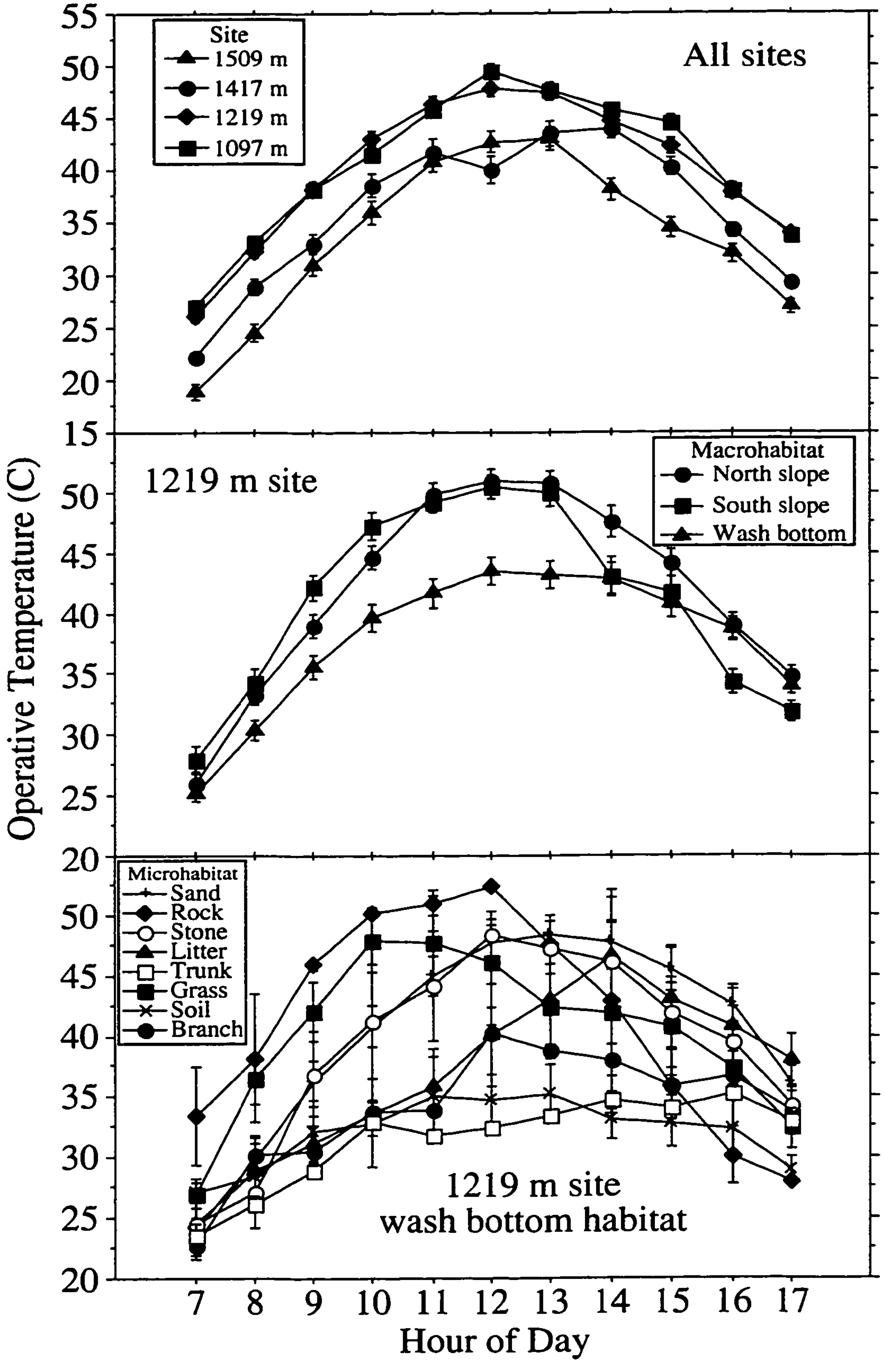
Figure 5. Microhabitats used by each lizard species in the assemblage.

Figure 6. Species means of the d_b (accuracy of thermoregulation) and d_e (habitat thermal quality) indices for ten lizard species. Each species' indices were calculated using that species' selected temperature range (T_{sel}) and the

operative temperatures (T_e) available during the hour that each individual lizard was active. Error bars represent plus one standard error.

Figure 7. Species means of the E index, indicating the degree which field T_b is closer to T_{sel} than is T_e, for ten lizard species in Arizona. Higher E values indicate higher success at maintaining body temperatures within the preferred range.


Cophosaurus texanus
Callisaurus draconoides
Urosaurus ornatus
Sceloporus clarki
Sceloporus magister
Sceloporus undulatus
Cnemidophorus sonorae
Cnemidophorus uniparens
Cnemidophorus burti
Cnemidophorus tigris



Operative Temperature (C)
Hour of Day
All sites
Site
1509 m
1417 m
1219 m
1097 m
1219 m site
Macrohabitat
North slope
South slope
Wash bottom
Microhabitat
Sand
Rock
Stone
Litter
Trunk
Grass
Soil
Branch
1219 m site
wash bottom habitat
55
50
45
40
35
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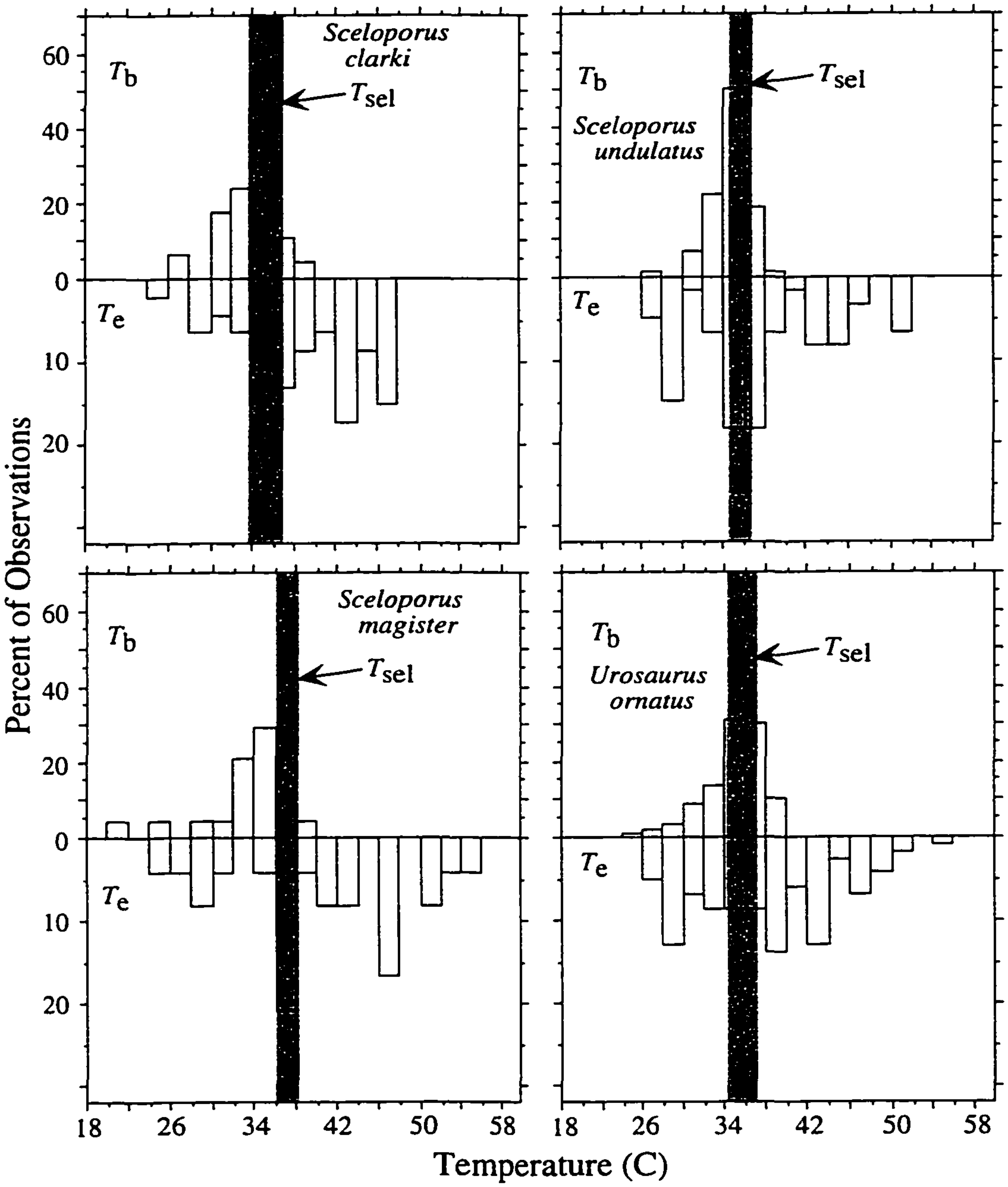
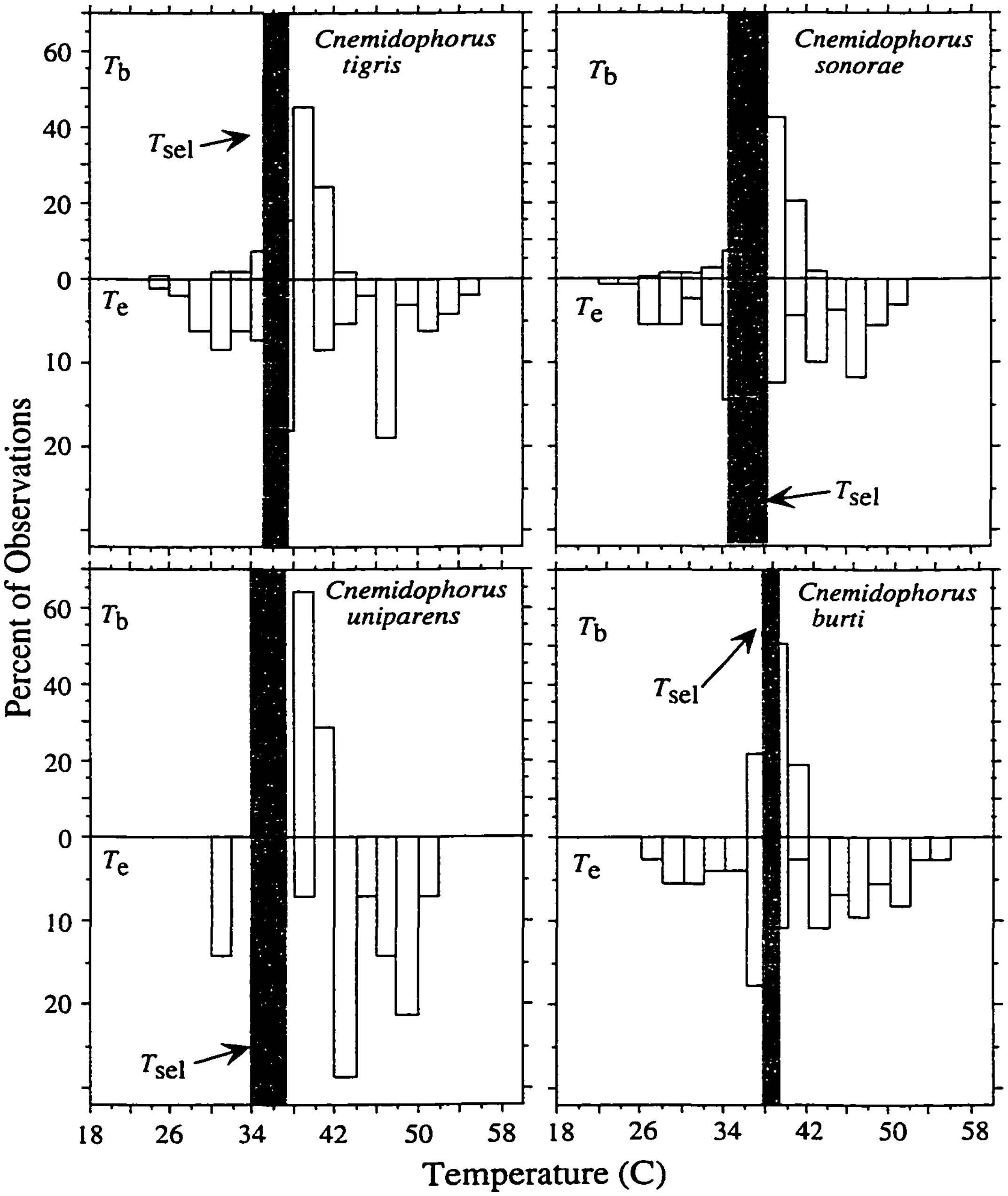
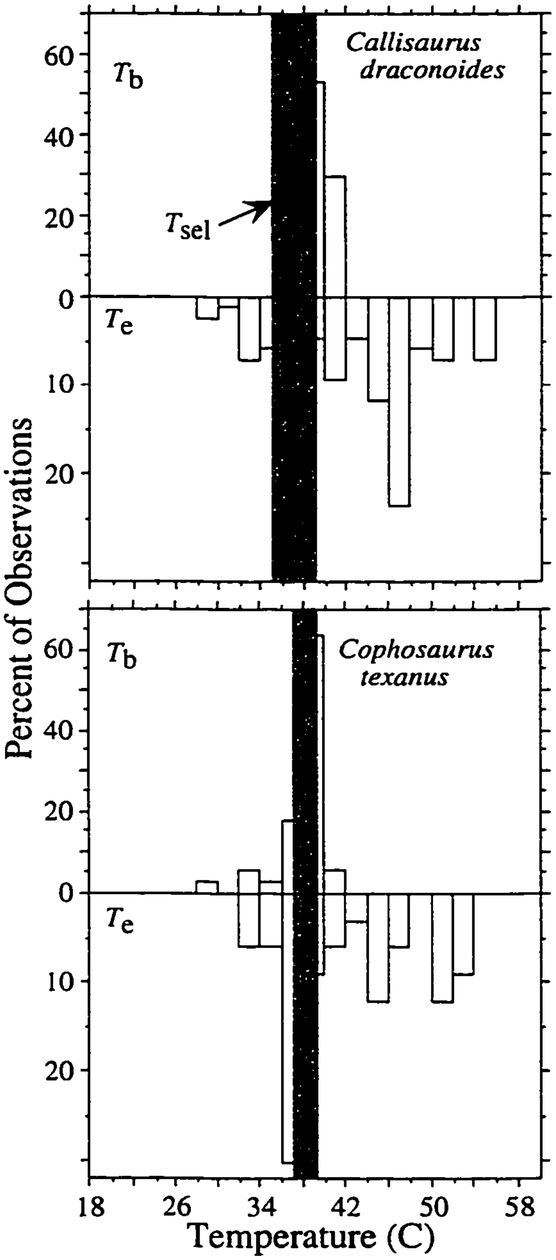
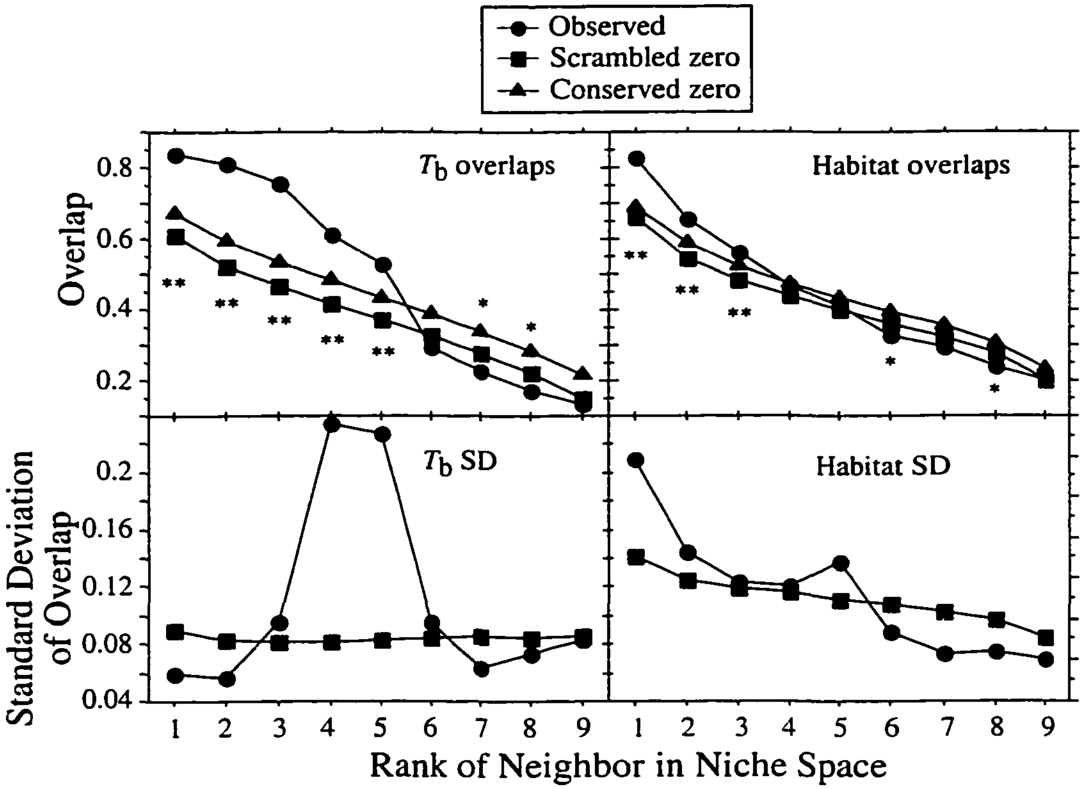
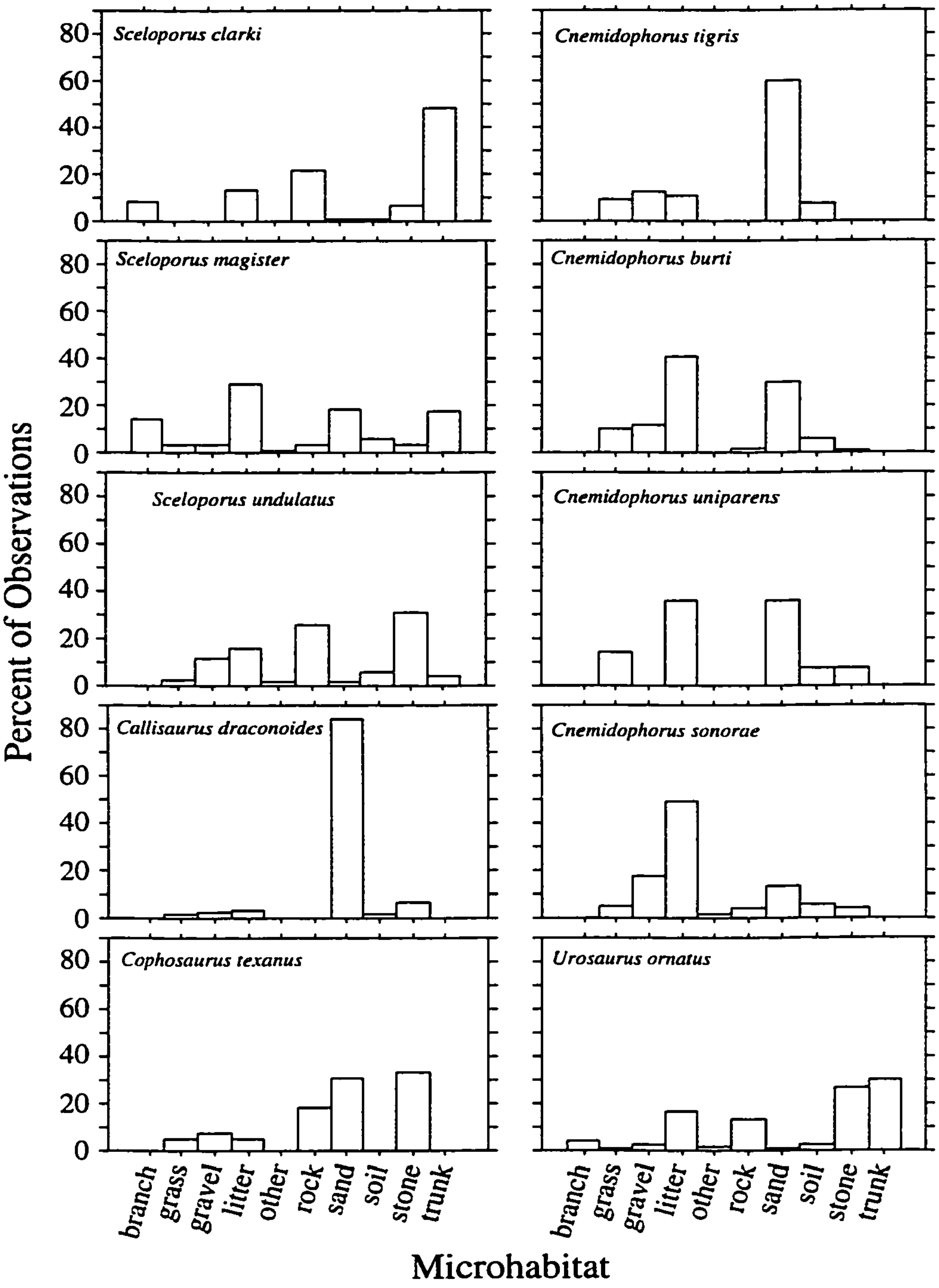


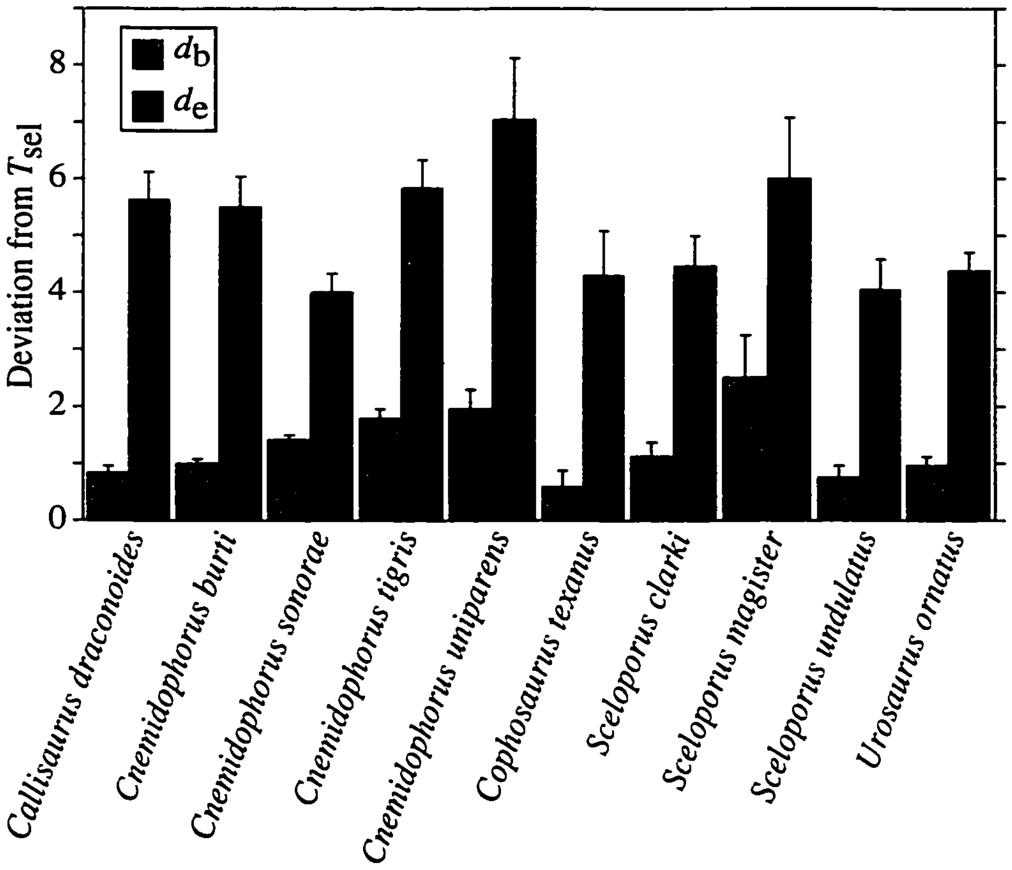
Sceloporus clarki
Sceloporus undulatus
Sceloporus magister
Urosaurus ornatus
T_b
T_e
T_{sel}
Percent of Observations
60
40
20
0
10
20
18
26
34
42
50
58
Temperature (C)

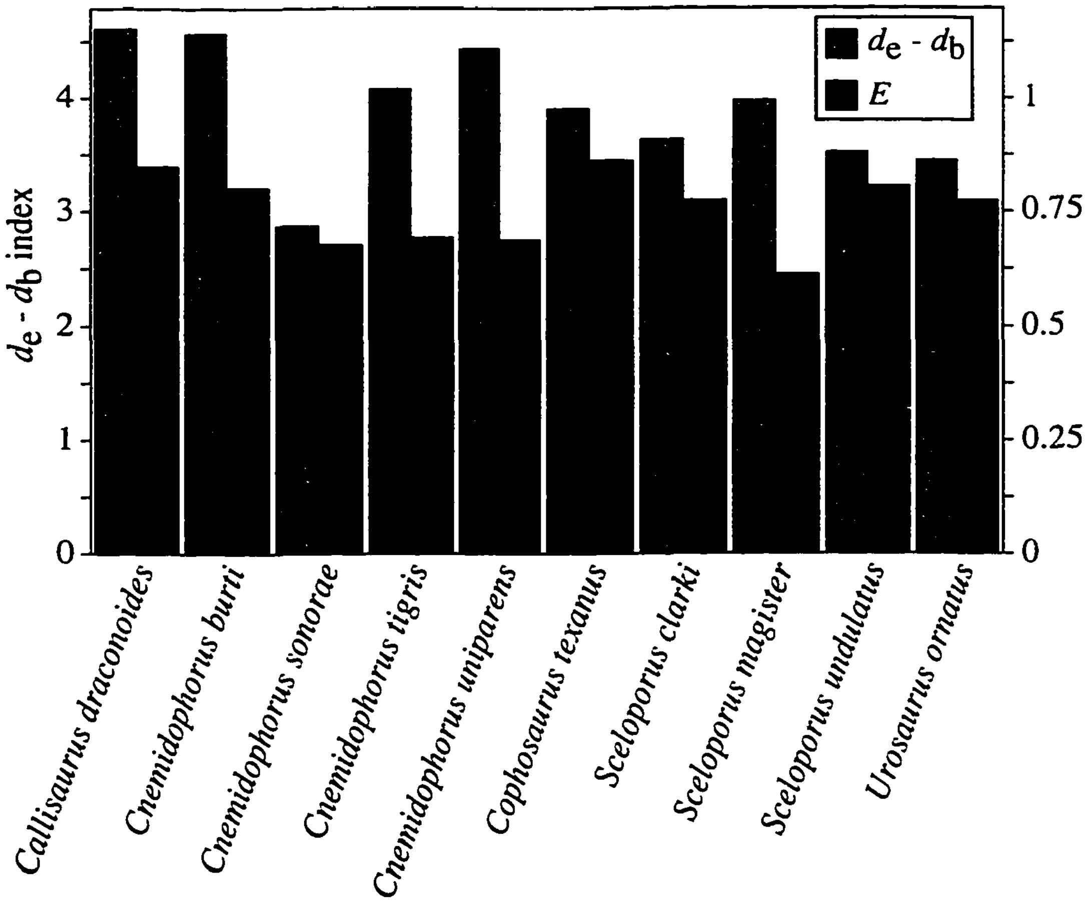

Cnemidophorus tigris
Cnemidophorus sonorae
Cnemidophorus uniparens
Cnemidophorus burti
T_b
T_e
T_{sel}
60
40
20
0
10
20
Percent of Observations
18
26
34
42
50
58
Temperature (C)


Callisaurus draconoides
T_b
T_{sel}
T_e
Cophosaurus texanus
T_b
T_e
60
40
20
0
10
20
60
40
20
0
10
20
Percent of Observations
18
26
34
42
50
58
Temperature (C)

Observed
Scrambled zero
Conserved zero
T_b overlaps
Habitat overlaps
T_b SD
Habitat SD
Overlap
Standard Deviation of Overlap
0.8
0.6
0.4
0.2
0.2
0.16
0.12
0.08
0.04
**
*
1
2
3
4
5
6
7
8
9
Rank of Neighbor in Niche Space


Sceloporus clarki
Cnemidophorus tigris
Sceloporus magister
Cnemidophorus burti
Sceloporus undulatus
Cnemidophorus uniparens
Callisaurus draconoides
Cnemidophorus sonorae
Cophosaurus texanus
Urosaurus ornatus
Percent of Observations
80
60
40
20
0
branch
grass
gravel
litter
other
rock
sand
soil
stone
trunk
Microhabitat


d_b
d_e
Deviation from T_{sel}
0
2
4
6
8
Callisaurus draconoides
Cnemidophorus burti
Cnemidophorus sonorae
Cnemidophorus tigris
Cnemidophorus uniparens
Cophosaurus texanus
Sceloporus clarki
Sceloporus magister
Sceloporus undulatus
Urosaurus ornatus



d_e - d_b
E
d_e - d_b index
0
1
2
3
4
E index
0
0.25
0.5
0.75
1
Callisaurus draconoides
Cnemidophorus burti
Cnemidophorus sonorae
Cnemidophorus tigris
Cnemidophorus uniparens
Cophosaurus texanus
Sceloporus clarki
Sceloporus magister
Sceloporus undulatus
Urosaurus ornatus

Chapter II

Thermoregulation Among Lizard Communities in the Amazon Basin: Historical Effects on and the Importance of Thermoregulation for Tropical Lizards

Abstract

Fifteen lizard species from 3 different localities in the Amazon Basin of Brazil were studied to determine relative potential for thermoregulation among rainforest lizards from a diversity of lineages and to test for phylogenetic effects on lizard thermoregulation. Operative environmental temperatures (T_e) were generally low and showed little variation in undisturbed rainforest habitats. Habitat disturbances that involved canopy removal increased T_e. Lizard mean body temperatures (T_b) were higher than mean T_e for all species and T_b means varied significantly between species. An index of the potential for thermoregulation (P_t) reveals that all species potentially thermoregulate, in that their T_b distributions were different from null T_e distributions. Widespread variation among species in the magnitude of these differences indicates that thermoregulatory activities are employed to varying degrees by different species. Comparisons with measures of T_b and P_t for a lizard assemblage in Arizona revealed that T_b for teiid lizards was similar between biomes but Iguanian lizards had high T_b in Arizona and low T_b in rainforest. Overall mean P_t values for Amazon and Arizona lizards were similar, indicating the likelihood that thermoregulation is quite important for rainforest lizards.

Significant relationships between phylogenetic distance and T_b and P_t differences exist for both Amazon and Arizona lizard assemblages indicating that thermoregulatory traits may be rooted deeply in lizard phylogenies. These relationships remained significant when the two regional faunas were analyzed together, however the amount of variation in T_b and P_t explained by the correlation

was low suggesting that environmental/ecological factors also play a role in the amount of thermoregulation that lizards engage in.

Introduction

The importance of thermoregulation to the ecology of ectothermic vertebrates has been a central issue in studies of spatial and geographic distribution of reptiles since the description of behavioral thermoregulation in lizards (Cowles and Bogert 1944). Temperature is a critical determinant of many performance measures such as sprint speed (Beck et al. 1995; Bennett 1990; Hertz et al. 1988; Huey and Bennet 1987), metabolic rate (Aleksiuk 1971; Brett 1971), digestion (Dorcas et al. 1997; Stevenson et al. 1985), and overall fitness (Huey and Berrigan 2001). Behavioral thermoregulation allows ectothermic animals to escape constraints that environmental temperatures place on their physiological performance by allowing them to utilize the portion of the total environmental temperature distribution that optimizes one or a combination of their physiological needs. Any costs of thermoregulation, whether they be increased exposure to predation or reduced time for foraging or reproduction (Huey and Slatkin 1976), are likely to influence the amount of time and effort that individuals allocate to thermoregulatory activities.

Of central importance to studies of thermoregulation, especially where complex communities of interacting species are concerned, is whether strong evolutionary constraints on preferred temperatures influence thermoregulatory effectiveness for individual animals. A continuing debate in physiological ecology centers on the relative plasticity of thermoregulatory traits (Gvozdík and Castilla 2001; Hertz 1981; Hertz and Huey 1981; Hertz and Zouros 1982; Rosen 1991). One hypothesis posits that temperature preference variation across large taxonomic groups is conservative and not likely to be precisely adapted to local conditions for most species (Bogert 1949; Hertz and Nevo 1981; Rosen 1991). Another hypothesis asserts that changes in thermoregulation correlated with changes in thermal environment point to the adaptability of thermal physiology (Hertz 1981; Hertz et al. 1979; Hertz and Huey 1981). Whether or not traits that are deeply rooted in lizard phylogeny place constraints on lizard thermoregulatory abilities and temperature preferences is of central importance to a thorough understanding of thermal ecology.

Most studies addressing questions of thermoregulation in reptiles have been conducted on lizards in deserts (Cowles and Bogert 1944; Grant 1990; Grant and Dunham 1988; Huey and Pianka 1977; Pianka 1969; Soulé 1963), on Caribbean island anoles (Hertz 1992; Hertz and Huey 1981; Huey 1983; Ruibal 1961; Schoener and Gorman 1968), or on the lacertid lizards of temperate Europe (Bauwens et al. 1996; Castilla and Bauwens 1991; Diaz 1997; Grbac and Bauwens 2001; Martín-Vallejo et al. 1995). Relatively few studies have investigated thermoregulation in reptiles from tropical mainlands, and most of those were conducted in xeric habitats (Bowker 1984; Christian and Bedford 1995; Christian and Weavers 1996; Huey and Pianka 1977; Pianka 1969; Vitt 1982). The studies that have been conducted in wet tropical mainlands have lacked a community context and/or inadequately sampled environmental temperature so that potential for thermoregulation and phylogenetic effects on thermoregulation cannot be evaluated. (Christian and Weavers 1996; Fitch 1968; Hillman 1969; Sartorius et al. 1999; Van Berkum et al. 1986; Vitt et al. 2000a).

Shine and Madsen (1996) recently suggested that thermoregulation may be unimportant for most reptiles because most live in tropical habitats that have an abundance of relatively high (but not extreme) temperatures and a relative lack of seasonal temperature variation, a situation very different from temperate deserts. However, a thorough presentation of tropical lizard thermoregulation in the context of available environmental thermal regimes has never been made and the importance of thermoregulation for tropical lizards remains uncertain. Measurement of the relative amount of thermoregulation for sympatric reptile species from a diversity of lineages, habitats, and regions is necessary to fully evaluate the importance of thermoregulation for tropical species.

Differences between operative environmental temperature distributions and lizard body temperature distributions are a necessary (but not sufficient) condition for demonstrating thermoregulation (Wills and Beaupre 2000). Numerous factors may cause body temperatures to deviate from environmental temperatures, such as pursuing thermoregulating prey, escaping predators, and reproductive activities that may not directly reflect thermoregulatory decisions. A convincing case for thermoregulation can only be made when information on the target body temperature (preferred body temperature) of the animal is known (Hertz et al. 1993). In some cases careful evaluation of field collected body temperatures and operative temperatures combined with behavioral observations (e.g. Rosen 1991) may appropriately measure thermoregulation because they do not rely on laboratory studies that assume "natural" thermoregulatory behavior by their subjects (Gregory

2001). However these methods are somewhat subjective and difficult for other investigators to repeat (Hertz et al. 1993). When data on selected temperature ranges are not available, it may be useful to determine the potential for thermoregulation by looking for differences between T_e distributions and T_b distributions. The hypothesis of thermoregulation can be rejected if no difference between these distributions exists (Wills and Beaupre 2000). If differences are detected, the magnitude of these differences are likely to be related to thermoregulatory effort or conversely, may indicate a specialization for a habitat or microhabitat with an anomalous temperature distribution. This method of estimating the relative amount of thermoregulation among species is straightforward and repeatable.

I present habitat temperature data for three tropical rainforest sites in the Amazon Basin and body temperature data for the assemblage of lizard species at each site. I address several related questions: 1) At what habitat scale do microsite temperatures (T_e) vary in Amazonian rainforest habitats? 2) What is the potential for thermoregulation (P_t) among Amazonian lizards? 3) Is variation in T_b and P_t correlated with phylogenetic affinity? 4) Do phylogenetic trends in T_b and P_t mirror trends found in a lizard assemblage from temperate thornscrub? I used data on T_b and T_e from a lizard community in southern Arizona to compare the potential for thermoregulation among Amazonian lizards with the potential for thermoregulation among an assemblage of lizards with a very different climatic and biotic history. In this comparison I ask what are the relative contributions of phylogeny, habitat use, and behavior to actual body temperatures and address the likelihood of thermal constraints on the use of time and space for lizards in tropical forests. I then compare the relative potential for thermoregulation among both Amazonian and Arizona lizards to ask if thermoregulation is important for lizards in Amazonian rainforest.

Materials and methods

Field Sites

Lizards were observed and collected at three sites in Amazonian Brazil and one site in Arizona, USA, from 1997 to 1999. The Amazonian sites and times sampled were: Rio Ituxí, southern Amazonas state, January to March, 1997; Parqué Estadual Guajara Mirim (PEGM) Rondônia, January to April, 1998 and a site in northern Amazonas, 30 km south of Manaus and the Amazon River, January to February, 1999. Each of these sites is characterized by Amazon rainforest vegetation with moderate drying in the dry season. Canopy in undisturbed areas is continuous and trees are not generally drought deciduous. Each site had varying amounts of disturbance ranging from small artificial clearings to large clearings and tracts of selectively logged forest. Human disturbances reduce canopy to varying degrees and allowed greater insolation of the forest floor, resulting in increased diurnal temperatures (Sartorius et al. 1999). Each site also contained large areas of intact rainforest habitat with continuous canopy except for river banks and natural treefall clearings.

Within these sites, I divided each area into these macrohabitat types: artificial clearing, upland forest, upland forest stream, upland forest treefall, river forest, river forest steam, river forest treefall, and secondary forest. Upland forest is forest that is not flooded during the annual wet season rise and fall of area rivers. River forest (Varzea) areas are flooded for weeks to several months during the wet season resulting in drastically reduced access to terrestrial habitats. Not all macrohabitat categories occurred within all sites but all sites contained both disturbed and undisturbed macrohabitats. Microhabitats were categorized as bare soil, branch of living tree, tree buttress, tree trunk, palm frond, log on ground, stick on ground, and leaf litter. Again, not all macrohabitats contained each microhabitat, e.g. clearings rarely had palm fronds, leaf litter, or tree trunks, but these categories broadly cover most microhabitats in which lizards are found in Amazonian rainforest (Vitt et al. 2000a; Vitt and Zani 1996).

The Arizona field site consisted of four sub-sites distributed along a canyon-wash system in the Santa Catalina Mountains from 1097 m to 1509 m elevation. Each of these sub-sites covered approximately 2 km of canyon with 1 to 2 km between sub-sites. Vegetation ranged from a rich Sonoran desert/thornscrub formation at low elevations to oak woodland at upper elevations making a gradient of increasing vegetative coverage from low elevation to high. Three macrohabitats were recognized: wash bottom, north (facing) slope and south (facing) slope. At each sub-site, north slopes had greater vegetative cover than south slopes, and wash bottoms had the highest density of vegetation consisting of dense thickets of drought adapted trees and shrubs. The distribution of trees and shrubs at these sites provided a complex matrix of sun-exposed and shaded microsites at a relatively small scale. For a more detailed description of the Arizona field site, see chapter 1.

Lizard species

The lizards examined here represent two ancient clades: Iguania and Scleroglossa. Amazonian Scleroglossa comprise two distinct clades: the Gekkota, including the geckos *Gonatodes humeralis* and *G. hasemani*, and the Autarchoglossa including *Ameiva ameiva*, *Kentropyx calcarata*, *K. pelviceps*, and *K. altamazonica* of the Teiidae, *Arthrosaura reticulata* and *Prionodactylus eigenmanni* of the Gymnophthalmidae, and a single member of the Scincidae, *Mabuya nigropunctata*. Scleroglossa in Arizona was represented by four species in a single genus within the Teiidae: *Cnemidophorus burti*, *C. sonorae*, *C. tigris*, and *C. uniparens*. The Amazonian Iguania included *Plica plica*, *P. umbra*, and *Uranoscodon superciliosa* of the Tropiduridae, and *Anolis fuscoauratus*, *A. nitens*, and *A. punctatus* of the Polychrotidae. In Arizona the Iguania were *Sceloporus clarki*, *S. magister*, *S. undulatus*, *Urosaurus ornatus*, *Callisaurus draconoides* and *Cophosaurus texanus* all of the Phrynosomatidae. For a summary of the ecology and site occurrences of each species see Table 1.

Data collection

Lizards were sampled by 3 to 6 investigators using haphazard transects through all available habitats during all hours of diurnal lizard activity (~0700 to ~1900 hrs). We sampled all time intervals approximately equally. When a lizard was observed it was identified to species, and the macrohabitat, microhabitat, and time of day were recorded on micro-cassette recorders. When possible, lizards were collected immediately using a noose, by hand, or with pneumatic (BB) rifle, and T_b

was measured to the nearest 0.1C using a Miller and Weber® rapid-register cloacal thermometer. Lizards were held by a hind foot during temperature measurement to minimize heat transfer between lizard and investigator. Lizards collected by lethal methods were preserved in a 10% formalin, individually tagged and deposited in the Sam Noble Oklahoma Museum of Natural History at the University of Oklahoma in Norman, Oklahoma, USA, or in the Museu Paraense Emílio Goeldi in Belém, Brazil.

Operative environmental temperatures (T_e) were recorded at each site concurrent with lizard observations to generate null distributions of temperatures available for lizard thermoregulation during activity. I used Tidbit® temperature data loggers (Onset Computer Inc.) to approximate lizard T_e. These miniature data loggers are self-contained in a shell of epoxy resin and record equilibrium temperatures similar to small copper lizard models traditionally used in studies of lizard operative temperatures (Shine and Kearney 2001; Vitt and Sartorius 1999). At the Ituxí and PEGM sites, macrohabitat types were compared to identify differences in thermal regimes related to natural and artificial habitat disturbances. At the Ituxí site, 3 data loggers were placed haphazardly in each habitat type and recorded T_e at hourly intervals for 27 consecutive days. At the PEGM site, data loggers were moved every 3 days of recording to increase the sample of microsites, for a total of 48 days of sampling in 16 independent microsite locations within each macrohabitat category. At the Amazonas site, I tested for differences in thermal characteristics between microhabitat types within primary upland forest macrohabitat. Eight microhabitat categories were sampled: bare soil, tree branch at 1.5 m, tree buttress at 1.5 m, leaf litter, log on ground, palm frond at 1.5 m, stick on ground, tree trunk at 1.5 m. Three data loggers were placed haphazardly in each of these microhabitat types and allowed to record temperatures at hourly intervals for 24 hours. Data loggers were then moved to new microsites at least several hundred meters away to sample the same microhabitat categories. Using these methods, thermal regimes for 22 to 24 independent microsites were sampled within each microhabitat category, except for tree buttress for which 11 microsites were sampled.

At the Arizona site I established a 210 m transect at a 90° angle to the direction of flow down the canyon and centered on the center of the canyon bottom. Along this transect I placed 21 data loggers at 10 m intervals so that one data logger was in the center of the canyon bottom with 100 m of transect radiating out and up the canyon slopes on each side. At the 1097 m site the canyon bottom became wider than 200 m and so the transect was divided into two with 10 data loggers placed on each side of the canyon, 4 data loggers running 40 m up the slope and 6 running 60 meters into the wash. This transect was moved within each site a random distance up or down the canyon each day so that within each 24 hr sampling period a new set of random microsites was sampled. Temperatures were recorded at 1 hr intervals for a total of 28 sampling days covering the entire lizard sampling period.

Potential for Thermoregulation

For each lizard captured, the mean T_e was calculated from all T_e recorded during the hour of capture in the macrohabitat type that the lizard was captured in. I used the deviation of T_b from T_e for each individual lizard sampled as an index of the potential for that individual to be thermoregulating at the time of capture (potential for thermoregulation: P_t). Using only T_e from the macrohabitat in which the lizard was found ignores the possibility that macrohabitat choice itself may be a form of thermoregulation. I chose to look only at thermoregulatory choices that lizards could make without traveling long distances, so my estimations of P_t are likely conservative. Lower average deviation values for a species indicate that their T_b was relatively closer to T_e than other species, indicating a lower likelihood that they satisfy one of the necessary requirements for thermoregulation, i.e., that T_b distributions are different from T_e distributions (Wills and Beaupre 2000).

Phylogenetic analyses

To test the hypothesis that phylogenetic affinity influences lizard temperature use and thermoregulation, I constructed a composite phylogenetic tree based on studies by Estes et al. (1988), Frost and Etheridge (1989), Weins and Reeder (1997), Guyer and Savage (1992), Frost (1992), and Presch (1974 and 1980) (Fig. 1). I then constructed a matrix of phylogenetic distances using an arbitrary branch length of 1 for all branches indicated on the tree. Using equal branch lengths in the face of incomplete knowledge of phylogenetic distance has been found to produce the lowest type II error rates in other phylogenetic analyses and is considered a conservative approach (Purvis et al. 1994). I compared matrices of phylogenetic distance computed using the tree to matrices of T_b distance and P_t distance. I computed correlation coefficients for the matrices compared and used Mantel's randomization tests with 9999 randomizations to determine significance levels of test statistics. I then applied a Bonferroni correction to maintain alpha at the 0.05 level following the method of Rice (1989). All matrix comparisons were computed using NTSYSpc 2.02I.

Results

Overall, T_e was low with low variation for all natural (i.e. canopy covered) habitats in Amazonian rainforest (Figs. 2, 3). For example, at the PEGM site where I have the most complete data, T_e ranged from 21.6° to 67.5° C (X = 27.3 ± 0.03). Both high and low values came from artificial clearing habitat. Mean hourly T_e did not exceed 31° C at any time of day in undisturbed habitats indicating that lizards seeking T_b above 31° C must actively thermoregulate, even at midday. Within artificial clearings, the macrohabitat with the highest temperatures, mean hourly T_e only exceeded 30° C from 1000 hrs to 1500 hrs, a brief window of high temperatures compared to desert habitats (see chapter 1). Microhabitat comparisons within primary upland forest revealed very little variation within microhabitats compared to the variation associated with canopy removal (Fig. 4). Temperatures in primary forest were generally low with a lack of thermoregulatory opportunities for lizards that utilize high T_b for activity. Due to the overall similarity in T_e between the three Amazonian sites, T_b and T_e for species found at more than one site were combined for all thermoregulatory and phylogenetic analyses.

Arizona T_es were more extreme (7.7° C to 75.3° C) than those in Amazonian forest and were on average much higher (X = 37.8 ± 0.15). In a general linear model of T_e with hour, locality, macrohabitat and microhabitat as factors, all factors were significant indicating that thermal variation exists at several spatial and temporal scales. Among spatial factors, microhabitat contained the most variation when all other factors were accounted for. This small scale of thermal variation stands in direct contrast to the Amazonian T_e data and suggests that lizards in the Arizona site needed only move short distances to find a variety of thermal opportunities, a situation favorable to behavioral thermoregulation. A thorough presentation of the Arizona T_e results can be found in Chapter 1.

Amazonian lizard species' T_b and associated T_e are summarized in Figure 5. Mean T_b varied widely among species ($X = 31.1 \pm 0.83$, ANOVA, $F_{14,631} = 75.08, p < 0.0001$) with 68 of 105 pairwise comparisons contributing to the overall variation (Fisher's PLSD). Mean P_t values for Amazonian lizards ranged from 1.78 for *Plica umbra* to 8.66 for *Kentropyx pelviceps* with an overall mean of 5.44 ± 0.15 (Fig. 6). Lizard mean T_b exceeded mean T_e for every species in this analysis indicating that thermoregulatory activities for all species were predominantly aimed at increasing rather than decreasing T_b and that overheating was not a danger. P_t means varied among species (ANOVA, $F_{14,630} = 27.99, p < 0.0001$) with 63 out of 105 pairwise comparisons contributing to the overall difference (Fisher's PLSD). Amazonian species differed significantly in the amount that their T_bs differed from T_e, suggesting widespread differences in the amount that each species engages in thermoregulatory activities.

Species' mean T_bs showed less variation in Arizona and a higher overall mean ($X = 36.9° \pm 0.72$). Again, T_b variation was widespread among species with 26 of 45 pairwise comparisons significant (Fisher's PLSD). (ANOVA, $F_{9,696} = 45.652$, $P < 0.0001$).

Thermoregulatory measures were correlated with phylogenetic distance in all cases Table 2. Phylogenetic relationships explained less variability when Amazonian and Arizona communities were combined, indicating that phylogenetic effects are most prominent when environmental factors are held constant.

Discussion

Rainforest environments profiled in this study had thermal regimes characterized by low mean temperatures in undisturbed macrohabitats with higher temperatures related to partial or complete removal of the forest canopy. Natural disturbance events, such as large treefalls, create small canopy breaks and are distributed sporadically throughout the forest. River edges, and to a lesser extent small stream courses, also create canopy breaks. These disturbances make islands of high insolation habitats surrounded by shade and represent the only opportunities for lizards like *Ameiva ameiva* that require high T_b to thermoregulate in primary forests (Sartorius et al. 1999). Artificial clearings offer large tracts of high insolation, high T_e habitats and thus increased opportunities for maintaining high T_b. However, few lizard species take advantage of large clearings, so it is likely that thermal advantages are offset by other disadvantages inherent in these heavily disturbed habitats. These habitats often attract high densities of teiid lizards (especially *Ameiva*), but lizards of other clades tend to avoid them, and at least part of this usage pattern is likely to be linked to thermal physiology (Sartorius et al. 1999). Undisturbed, continuous canopy rainforests do harbor some species with relatively high T_b such as *Kentropyx pelviceps* and *K. calcarata* (Vitt et al. 2000a). Their T_bs tend to be somewhat lower than *Ameiva ameiva* (Table 1), and they thermoregulate by seeking out small (< 1 m^2) patches of sun on the forest floor for basking. The scale of thermal heterogeneity at these rainforest sites is large relative to the movement capabilities of all but the largest forest lizards. Lizards seeking a T_b at the high end of the scale must use large canopy breaks and avoid large tracts of continuous canopy. For individual lizards employing a shuttling thermoregulatory tactic, movement between macrohabitat types is often required, therefore, habitat edges are likely to be choice positions for thermoregulation.

Arizona thornscrub exhibits thermal heterogeneity at a several scales relevant to lizard thermoregulation, including a large amount of variation between microhabitat types within each macrohabitat. Lizards need only move short distances to find a wide variety of thermal conditions, reducing the costs associated with traveling or restricting activities to macrohabitat edges. The scale of thermal heterogeneity is of great importance in studies of behavioral thermoregulation in ectotherms. Investigators should consider this scale, in conjunction with the unique biology of each organism, to determine what part of the total temperature variation at a given site is available to the animal for minute-by-minute thermoregulatory decisions and what part of the variation requires high travel costs in terms of energy, predation exposure and/or time. In this study, Amazonian lizards must generally change macrohabitat type or live on the edge of two macrohabitats to thermoregulate.

The exceptions are those species that are able to quickly exploit small, temporary, high T_e microsites, such as patches of sun on the forest floor which are constantly moving. At the Arizona site, expenditures of energy, time, and predation exposure due to thermoregulation are likely to be smaller due to the close juxtaposition of microsites with highly variable temperatures. This makes it likely that lizards from the Arizona site have lower costs associated with thermoregulation.

Despite the likelihood of high costs, I found that all of the Amazonian species examined maintained mean T_b above T_e. Amazonian lizards appear to thermoregulate to some extent in all cases. Species mean P_t values were similar to those for temperate thornscrub lizards, a group for which high thermoregulatory activity has been measured (Chapter 1). Despite the common perception of tropical rainforests as steamy hothouses, actual temperatures under the canopy are well below T_bs normally recorded for the lizards found in them (Fitch 1968; Vitt et al. 1998a; Vitt et al. 2001; Vitt et al. 2000a; Vitt et al. 2000b). Thus, I conclude that in this widespread tropical environment, thermoregulation is likely to be important for lizards, much as it is in hot deserts and at high elevations. Open tropical formations offer more abundant high temperatures and it is possible that thermoregulation is less necessary there, however in those habitats, overheating becomes a problem and thermoregulation must be employed to prevent it.

In a provocative paper, Shine and Madsen (1996) used data collected for a single species of python in tropical Australia to support their argument that thermoregulation is unimportant for most tropical reptiles. They observed few overt thermoregulatory behaviors such as basking and also found that overall temperatures were warm and mild at their study site, so that thermoregulation was often not necessary to maintain T_b within their optimal range. Future investigators should consider several important points when evaluating the importance of behavioral thermoregulation in their studies. 1) The scale of thermal heterogeneity is a critical factor in determining the necessity for thermoregulation and the potential costs of engaging in thermoregulatory activities. 2) It is important to measure not only minimum and maximum temperatures but enough microsites must be sampled so that a true non-thermoregulating (null) distribution of T_e can be generated for comparison with T_b. 3) The ecology and behavior of the organism should dictate what behaviors are used to indicate thermoregulation. For example, basking behavior is an appropriate behavioral indicator of thermoregulation for a diurnal, heliothermic lizard but may not be an appropriate indicator of thermoregulation for a semi-nocturnal secretive snake. Lack of basking in a large snake may reflect a predator avoidance or foraging strategy rather than a thermoregulatory decision. Secretive reptiles may employ thermoregulatory strategies that are not easily observed, such as orientation inside retreats (Dorcas and Peterson 1998). It should also be clearly understood that overt thermoregulatory behaviors, such as basking, are not the only way that ectotherms thermoregulate. Avoidance of activity during times of year or day and in microhabitats that are thermally sub-optimal are also forms of thermoregulation. Despite these criticisms, it is possible that the pythons studied by Shine and Madsen thermoregulate relatively little. However, extrapolating that study to other tropical species and environments without corroboration is premature.

Amazonian lizard thermoregulation appears to be correlated with phylogenetic history. Both T_b and P_t showed strong, significant correlations with phylogeny, suggesting that past evolutionary history at least partially dictates the T_b lizards used and how much thermoregulation they employed. This result, along with those in Figures 6 and 7, suggest that T_b and P_t are related to physiological and/or ecological traits that are deeply rooted in the evolutionary history. Amazonian lizards with high T_b are all members of the Autarchoglossa (Camp 1923), an ancient lineage characterized by an active foraging mode, and lack of territoriality (Anderson and Karasov 1981) The active foraging mode means that these lizards move more often and longer distances than sit-and-wait foragers of the Iguania (Anderson and Karasov 1981). This high activity level may necessitate high T_b to maintain high locomotor performance (Van Berkum et al. 1986). It is also conducive to active thermoregulation because a wide range of microsites can be sampled while foraging. The lack of territoriality releases these species from the constraint of remaining within a small area and frees them to search for optimal T_e over a wider range of habitats. Many autarchoglossans tend to have high T_b no matter where they are found (Asplund 1970; Bauwens et al. 1996; Christian and Weavers 1996; Vitt et al. 1997a; Vitt et al. 1997b); however, the two gymnophthalmids in this study had low T_b and relatively low P_t. Low T_bs have been reported for gymnophthalmids from rainforest habitats in the past (Fitch 1968; Vitt et al. 1998b) and low T_b in this group may represent a reversion and a possible adaptation to using cool tropical habitats such as closed canopy rainforest leaf litter.

The Iguania in Amazonian forests appear to maintain T_b only slightly above environmental temperatures. Most of the iguanian lizards that occur in the Amazon are arboreal and as such are tied to the use of habitat structural objects. This use of habitat structure, combined with the iguanian traits of sit-and-wait foraging and territoriality, makes iguanian lizards poor thermoregulators when large distances must be traversed to find optimal microsites. Other iguanians are known to be facultative thermoconformers in habitats where the costs of thermoregulation are high (Hertz 1983) and it may be that in a lower cost environment, Amazonian iguanians would maintain higher T_b, and consequently P_t, values. That no Amazon iguanian lizard was found with a T_b higher than 33.4° C, while each of the teiid species had maximum T_b above 40° C, suggests that iguanians at these sites are not actively trying to increase their T_b to such high levels, even when found in habitats where high T_b are possible to attain.

Correlations between T_b and P_t and phylogeny for the Arizona assemblage were also significant and explained large amounts of the total variation in these two variables. The T_b and P_t results for Arizona iguanian lizards show that in this environment, iguanian lizards thermoregulated similarly to sympatric teiid lizards. There are several likely reasons for this: 1) *Callisaurus draconoides* and *Cophosaurus texanus* are ground dwellers with limited use of habitat structure making them less restricted in their movements. 2) The small spatial scale of thermal heterogeneity at the Arizona site enables lizards with limited mobility to thermoregulate effectively. 3) High T_e forces Arizona lizards to regulate their temperature to prevent overheating, whereas Amazonian lizards face little threat of overheating due to the scarcity of high-temperature microsites.

When the T_b, P_t, and phylogeny data for the Amazon Basin and Arizona assemblages were combined, correlations maintained statistical significance indicating that there were persistent phylogenetic effects. However, the amount of the total variation explained by the correlations was relatively small. This result suggests that if environmental factors are held constant, phylogenetic effects are substantial and easily measured, however, in vastly different habitats, environmental effects can overshadow historical effects and may be a more important determinant of how intensely thermoregulatory behaviors are employed.

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Table 1. Summery of ecological characteristics for 25 lizard species from the Amazon Basin of Brazil and Southern Arizona, USA. Sites are: P = PEGM, I = Ituxí, NA = northern Amazonas, AZ = Arizona. Microhabitats are: Arb = arboreal, Terr = terrestrial, Sarb = semi-arboreal, WM = water margin, LL = leaf litter, Br = branch, Tr = trunk, Vi = vine, Bo = boulder, Cl = cliff, Sa = sand, L = log, So = bare soil. Families are: Tr = Tropiduridae, Po = Polychrotidae, Ph = Phrynosomatidae, Ge = Geckonidae, Sc = Scincidae, Gy = Gymnophthalmidae, Te = Teiidae. See text for site and habitat descriptions. Numbers in parentheses indicate one standard deviation.

Species	Sites	Habitat	Mean T_b °C	Family
Uranoscodon superciliosa	P	Arb, WM, LL	28.3 (1.59)	Tr
Plica umbra	I	Arb, Br	27.8 (1.41)	Tr
Plica plica	P, I	Arb, Tr	28.7 (1.54)	Tr
Anolis punctatus	P, I	Arb, Tr, Br	29.2 (1.64)	Po
Anolis nitens	I, NA	Terr, LL	28.0 (1.68)	Po
Anolis fuscoauratus	P, I, NA	Arb, Br, Vi	29.4 (1.60)	Po
Sceloporus clarki	AZ	Arb, Tr, Br	33.8 (2.64)	Ph
Sceloporus magister	AZ	Arb, Tr, Br	33.9 (4.10)	Ph
Sceloporus undulatus	AZ	SArb, Bo, Cl	34.5 (2.01)	Ph
Urosaurus ornatus	AZ	Arb, Br, Tr	35.0 (2.75)	Ph
Cophosaurus texanus	AZ	Terr, Sa	38.2 (2.27)	Ph
Callisaurus dracanoides	AZ	Terr, Sa	39.0 (2.63)	Ph
Gonotodes humeralis	P, NA	Ar, Tr	30.1 (1.20)	Ge
Gonotodes hasemani	P	Terr, L	30.6 (1.45)	Ge
Mabuya nigropunctata	P, I, NA	Terr, L	33.0 (3.37)	Sc
Arthrosaura reticulata	P	Terr, LL	29.0 (1.34)	Gy
Prionodactylus eigenmanni	P, I	Terr, LL	29.7 (1.53)	Gy
Kentropyx altamazonica	P, I	Terr, LL, So	35.9 (2.96)	Te
Kentropyx pelviceps	I, NA	Terr, LL	35.4 (3.01)	Te
Kentropyx calcarata	P	Terr, LL	35.0 (3.07)	Te
Cnemidophorus burti	AZ	Terr, LL, Sa	38.6 (1.76)	Te
Cnemidophorus sonorae	AZ	Terr, LL, Sa	38.4 (2.59)	Te
Cnemidophorus uniparens	AZ	Terr, Sa, LL	39.3 (1.39)	Te
Cnemidophorus tigris	AZ	Terr, Sa	38.6 (2.67)	Te
Ameiva ameiva	P, I, NA	Terr, LL, So	37.0 (2.55)	Te

Table 2. Results of Mantel's tests after 9999 randomizations. Bonferroni thresholds were calculated using sequential method of Rice (1989). Asterisk indicates a significant result.

Locality	**Comparison**	r	**Percent explained**	**Bonferroni Threshhold**	$p =$
Combined	Phylogeny vs. T_b	0.21	4.45	0.0250	0.0086*
	Phylogeny vs. P_t	0.21	4.58	0.0167	0.0071*
Arizona	Phylogeny vs. T_b	0.71	50.98	0.0125	0.0033*
	Phylogeny vs. P_t	0.44	19.75	0.0500	0.0224*
Amazon	Phylogeny vs. T_b	0.49	24.36	0.0100	0.0021*
	Phylogeny vs. P_t	0.55	30.30	0.0083	0.0010*

Figure Legends

Figure 1. Composite phylogenetic tree depicting relationships between lizard species from 3 sites in Amazonian and 1 site in Arizona, USA. For citations see methods.

Figure 2. Hourly mean operative environmental temperatures for all macrohabitats and microhabitats at three Amazonian rainforest sites in Brazil. Error bars equal 1 standard error.

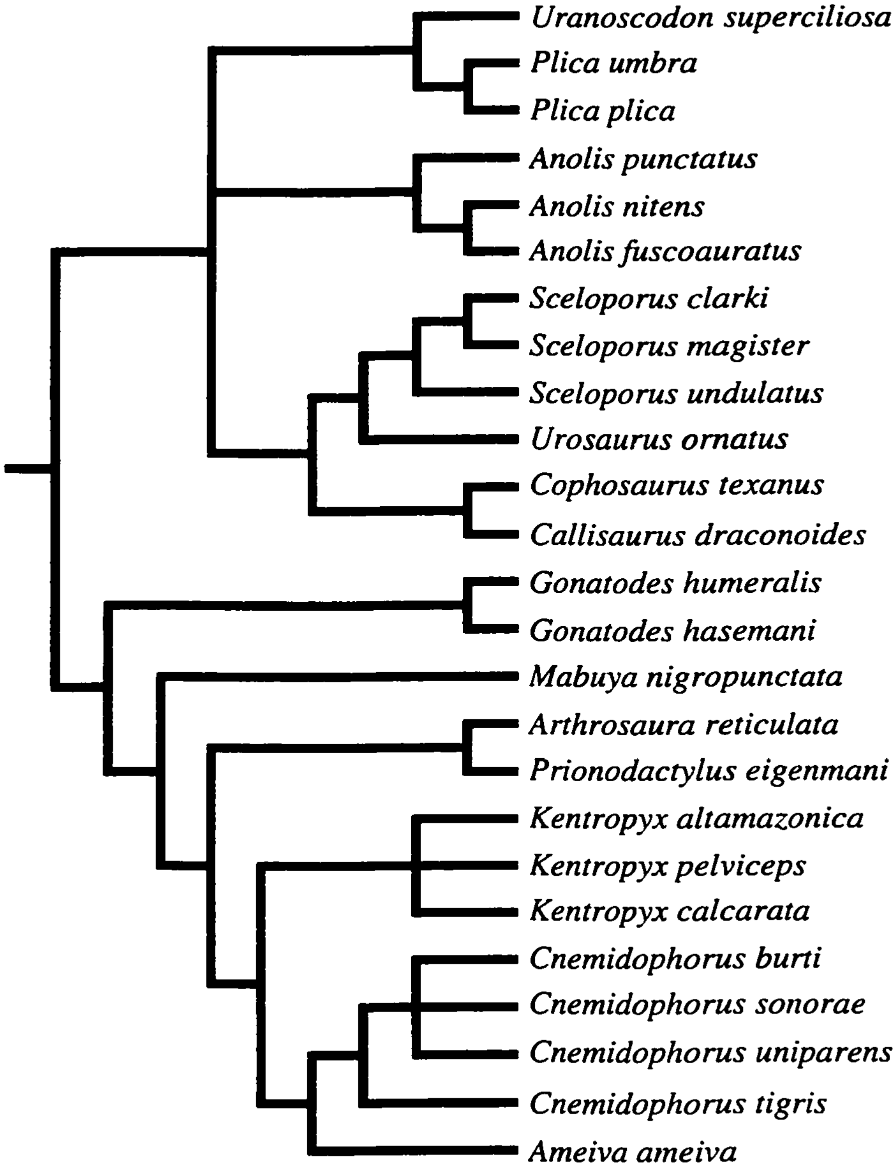
Figure 3. Hourly mean operative environmental temperatures from the PEGM site in the Brazilian Amazon depicting variation associated with macrohabitat type. Error bars represent 1 standard error.

Figure 4. Hourly mean operative environmental temperatures in one macrohabitat type (primary upland forest) depicting temperature variation associated with different microhabitat types at a site in the central Amazon Basin of Brazil (Amazonas state). Error bars represent 1 standard error.

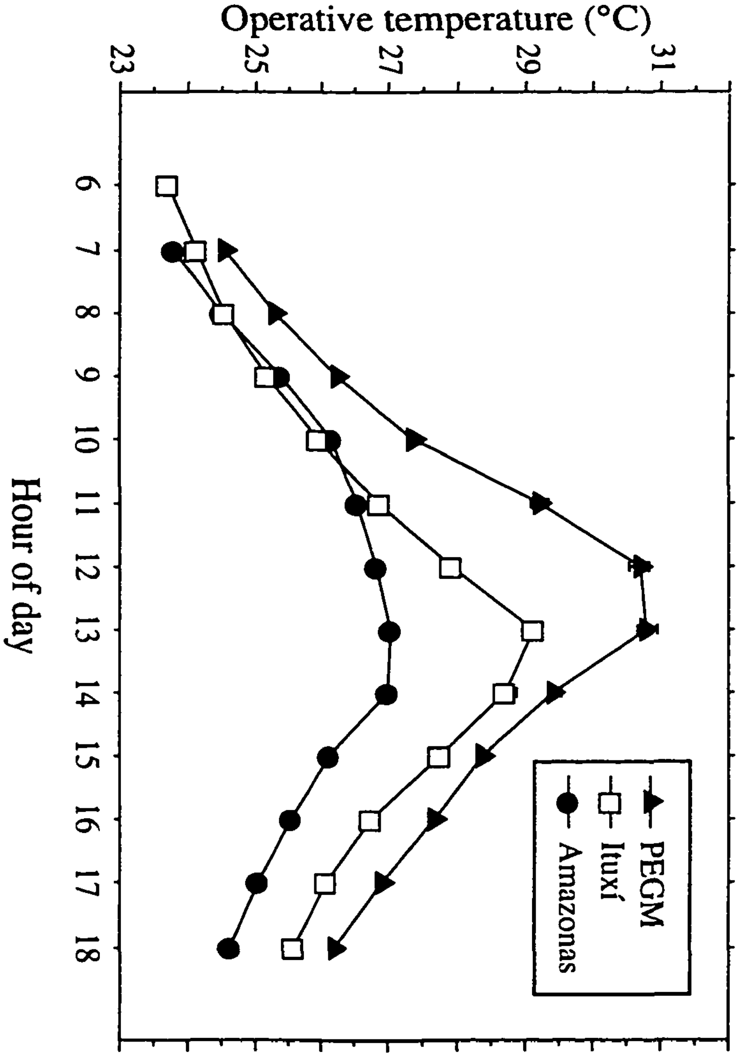
Figure 5. Distributions of body temperatures (T_b) and associated mean operative environmental temperatures (T_e) for 15 lizard species found at 1 or more of 3 Amazonian sites. T_e distribution represents the mean T_e during the hour of capture of each lizard for which T_b was measured.

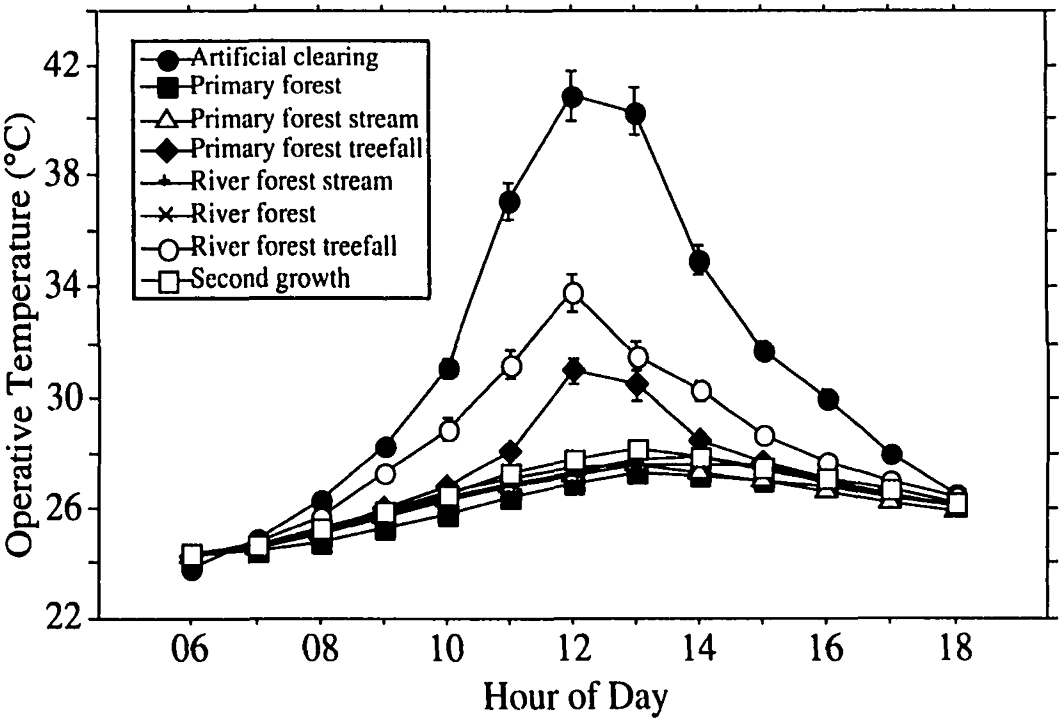
Figure 6. Results of the potential for thermoregulation (P_t) index calculation for 15 lizard species from 3 sites in the Brazilian Amazon Basin. Mean P_t is shown plus or minus one standard error.

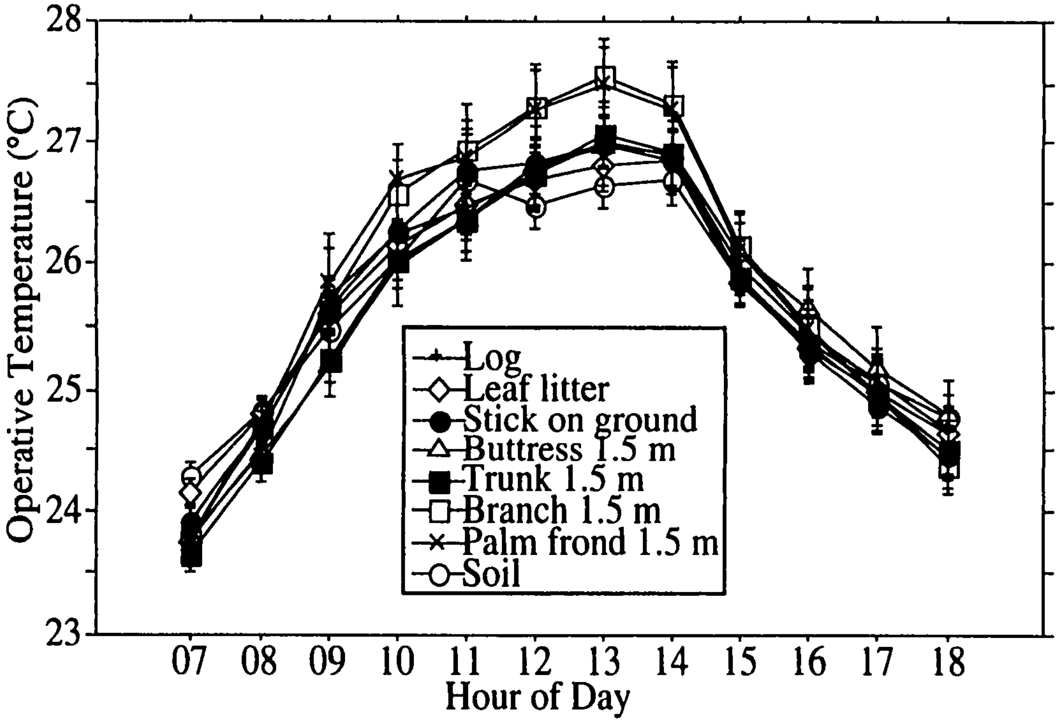
Figure 7. Results of the potential for thermoregulation (P_t) index calculation for 10 lizard species from Peppersauce Canyon in southern Arizona. Mean P_t is shown plus or minus one standard error.

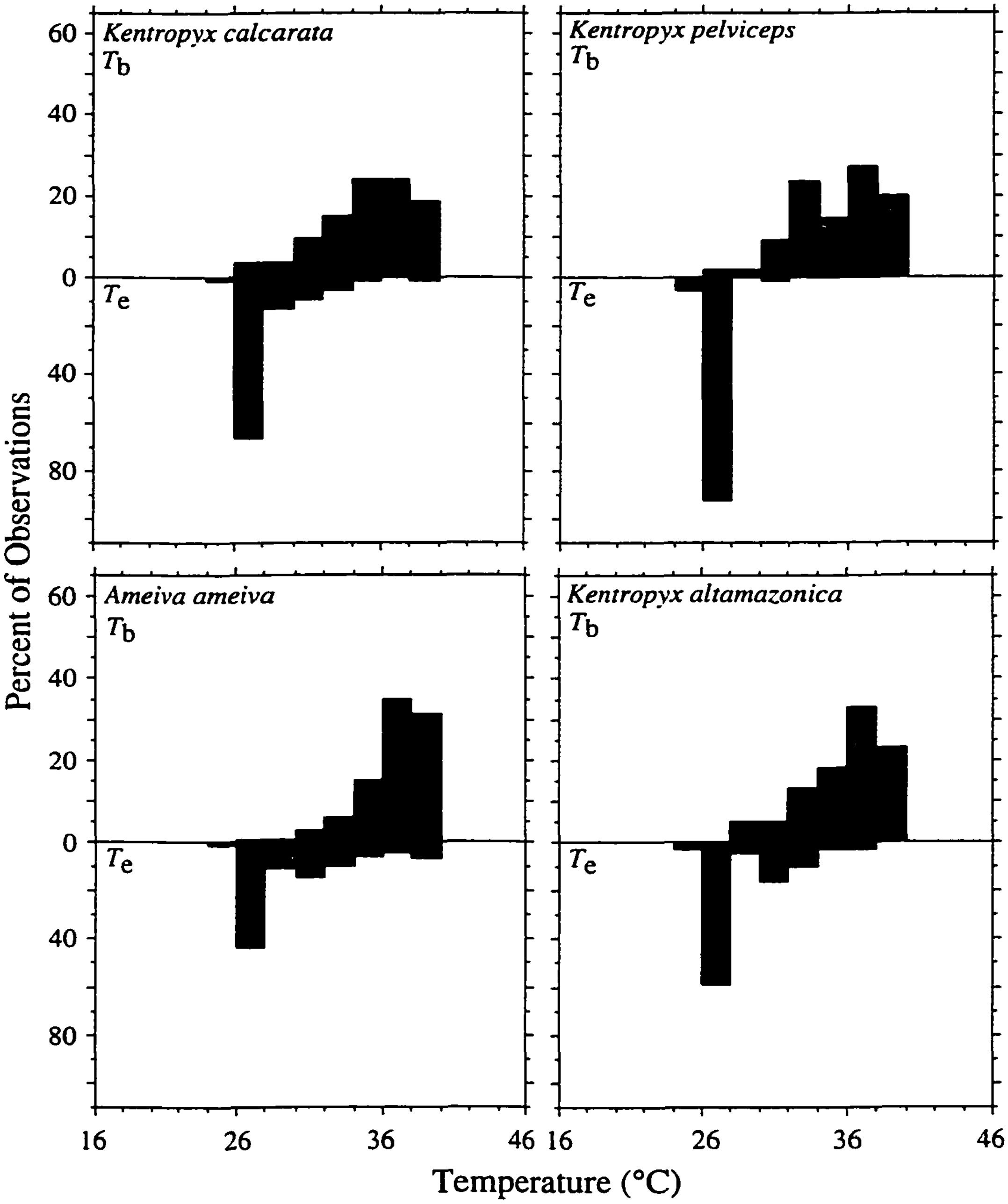


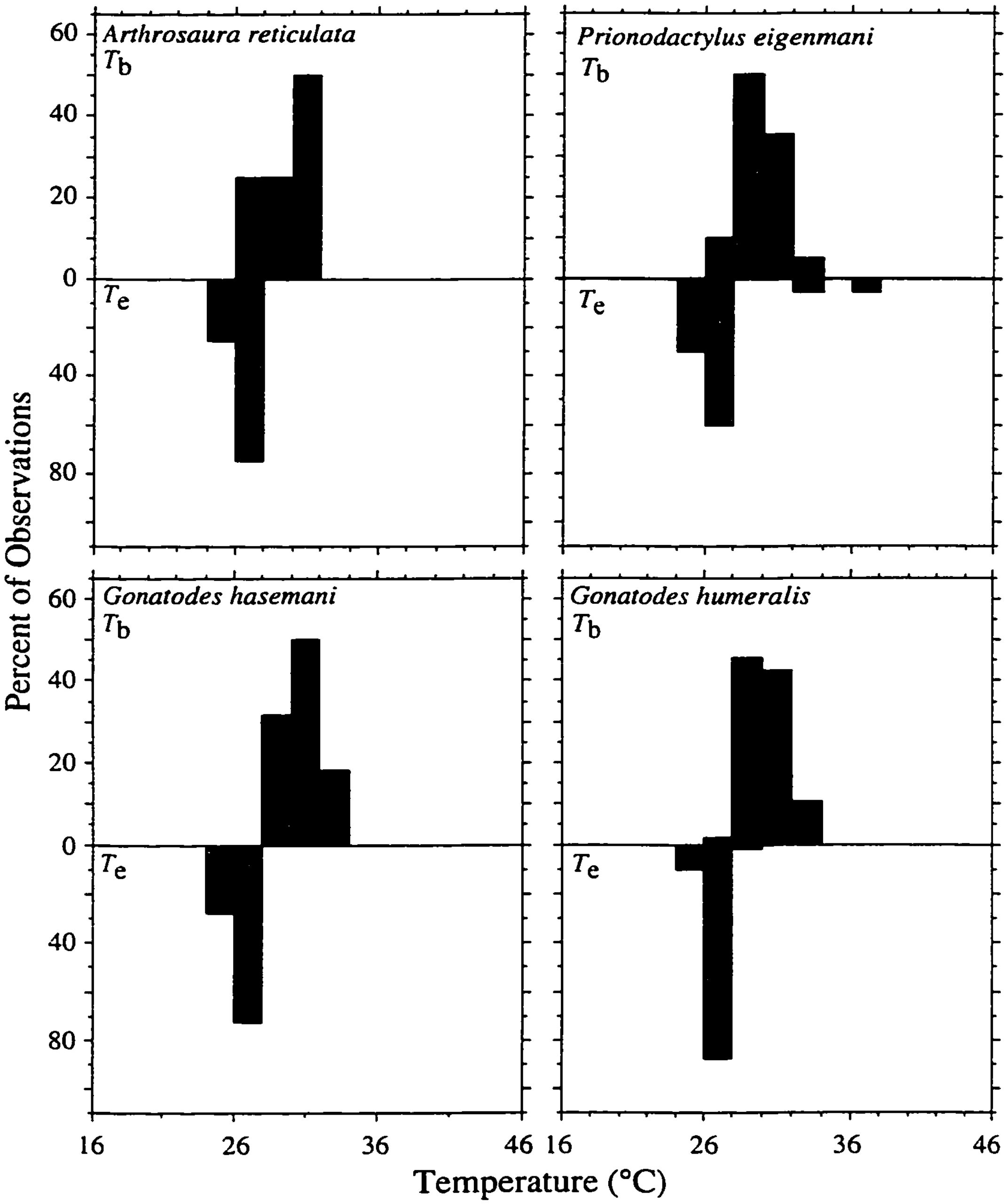
Uranoscodon superciliosa
Plica umbra
Plica plica
Anolis punctatus
Anolis nitens
Anolis fuscoauratus
Sceloporus clarki
Sceloporus magister
Sceloporus undulatus
Urosaurus ornatus
Cophosaurus texanus
Callisaurus draconoides
Gonatodes humeralis
Gonatodes hasemani
Mabuya nigropunctata
Arthrosaura reticulata
Prionodactylus eigenmani
Kentropyx altamazonica
Kentropyx pelviceps
Kentropyx calcarata
Cnemidophorus burti
Cnemidophorus sonorae
Cnemidophorus uniparens
Cnemidophorus tigris
Ameiva ameiva

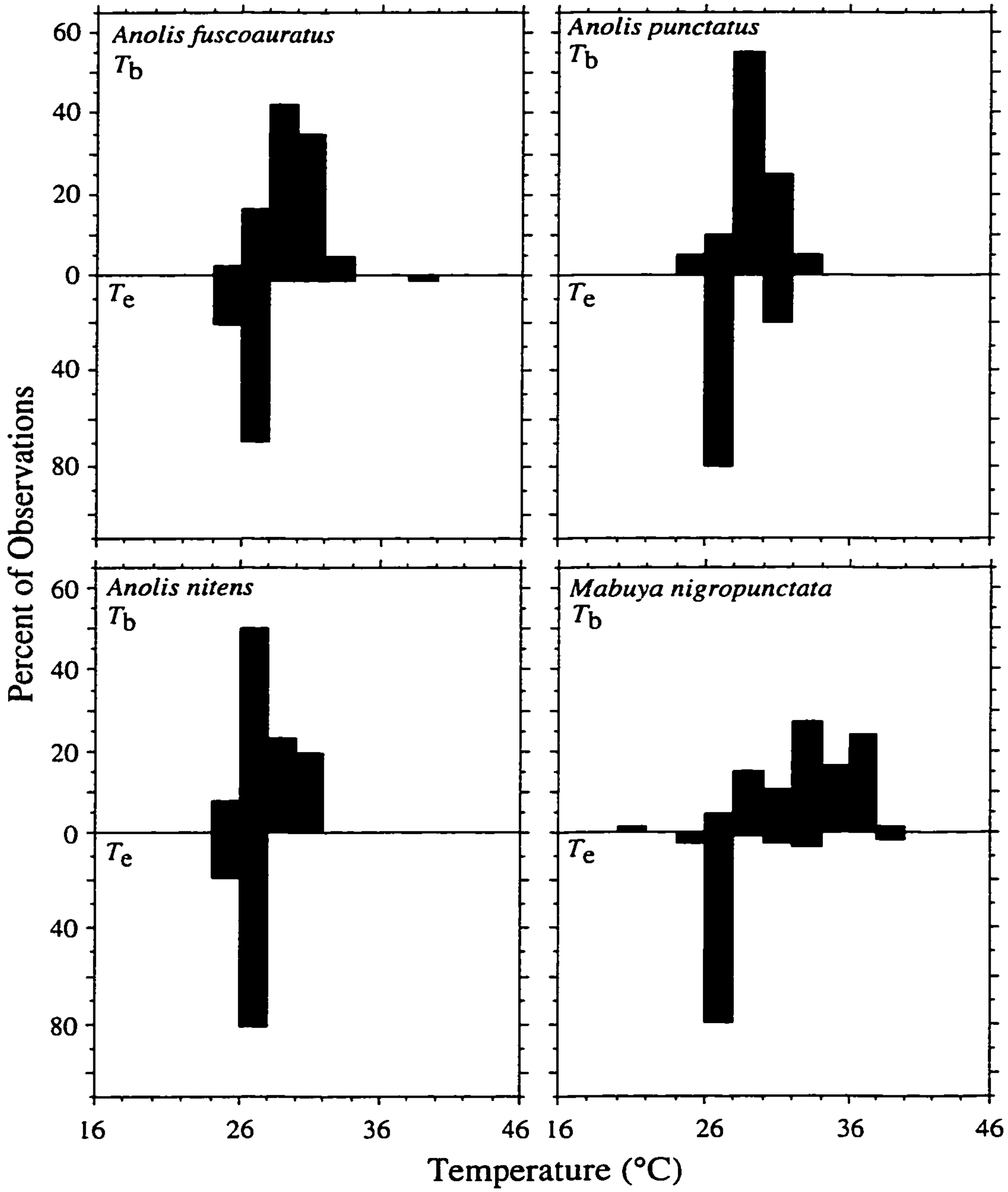

Operative temperature (°C)
23
25
27
29
31
Hour of day
6
7
8
9
10
11
12
13
14
15
16
17
18
PEGM
Ituxí
Amazonas

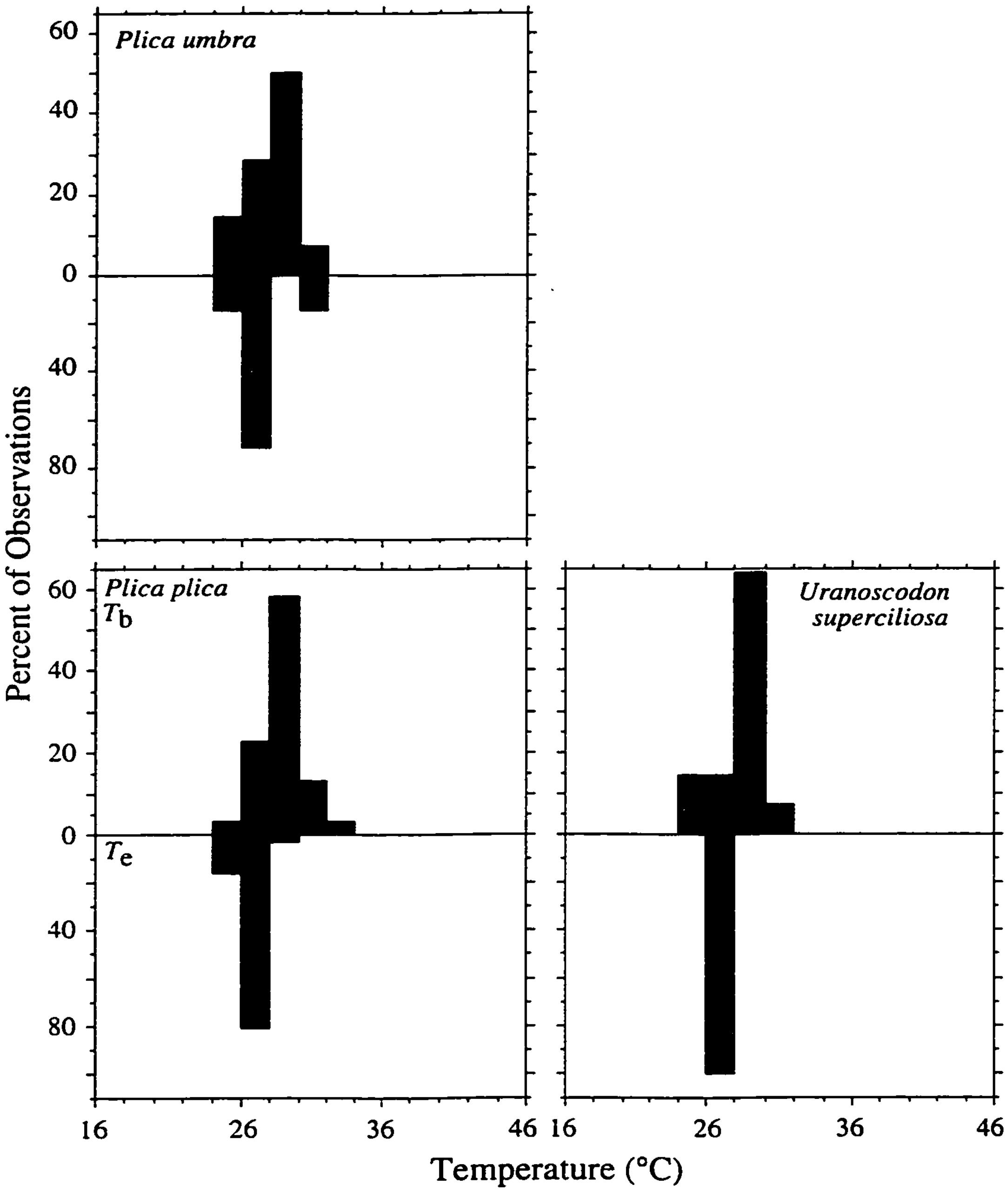

Artificial clearing
Primary forest
Primary forest stream
Primary forest treefall
River forest stream
River forest
River forest treefall
Second growth
Operative Temperature (°C)
22
26
30
34
38
42
06
08
10
12
14
16
18
Hour of Day

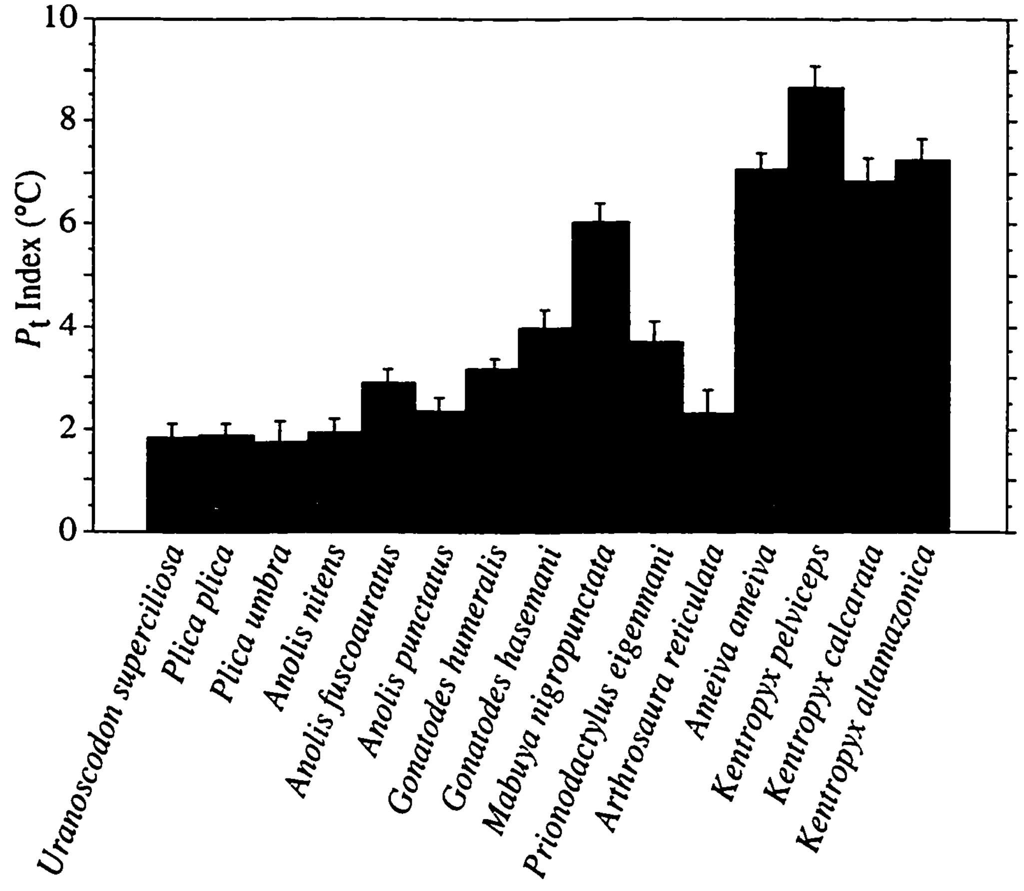

Operative Temperature (°C)
28
27
26
25
24
23
07
08
09
10
11
12
13
14
15
16
17
18
Hour of Day
Log
Leaf litter
Stick on ground
Buttress 1.5 m
Trunk 1.5 m
Branch 1.5 m
Palm frond 1.5 m
Soil

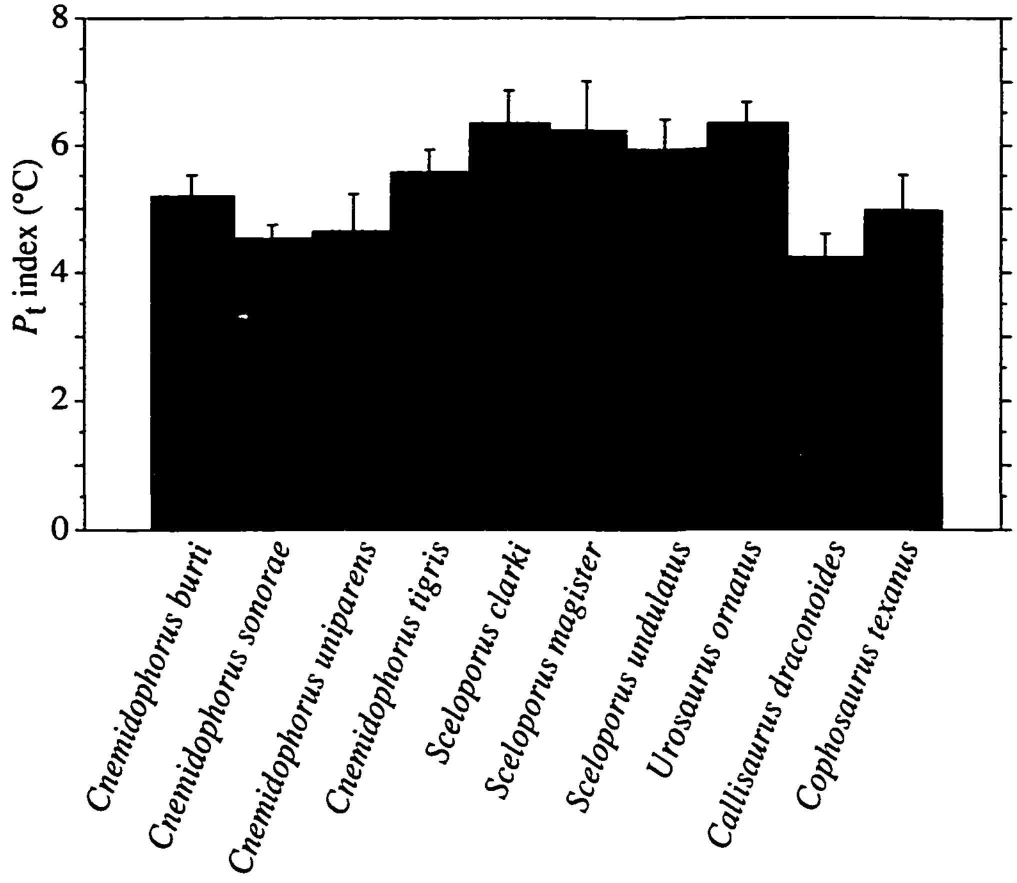

Kentropyx calcarata
T_b
T_e
Kentropyx pelviceps
T_b
T_e
Ameiva ameiva
T_b
T_e
Kentropyx altamazonica
T_b
T_e
60
40
20
0
40
80
Percent of Observations
16
26
36
46
Temperature (°C)


Arthrosaura reticulata
Prionodactylus eigenmani
Gonatodes hasemani
Gonatodes humeralis
T_b
T_e
60
40
20
0
40
80
Percent of Observations
16
26
36
46
Temperature (°C)


Percent of Observations
Anolis fuscoauratus
T_b
T_e
Anolis punctatus
T_b
T_e
Anolis nitens
T_b
T_e
Mabuya nigropunctata
T_b
T_e
60
40
20
0
40
80
16
26
36
46
Temperature (°C)


Plica umbra
Plica plica
T_b
T_e
Uranoscodon superciliosa
Percent of Observations
60
40
20
0
40
80
16
26
36
46
Temperature (°C)


P_t Index (°C)
10
8
6
4
2
0
Uranoscodon superciliosa
Plica plica
Plica umbra
Anolis nitens
Anolis fuscoauratus
Anolis punctatus
Gonatodes humeralis
Gonatodes hasemani
Mabuya nigropunctata
Prionodactylus eigenmani
Arthrosaura reticulata
Ameiva ameiva
Kentropyx pelviceps
Kentropyx calcarata
Kentropyx altamazonica


P_t index (°C)
0
2
4
6
8
Cnemidophorus burti
Cnemidophorus sonorae
Cnemidophorus uniparens
Cnemidophorus tigris
Sceloporus clarki
Sceloporus magister
Sceloporus undulatus
Urosaurus ornatus
Callisaurus draconoides
Cophosaurus texanus

Chapter III

Use of natural and anthropogenic disturbances in Amazonian rainforest by *Ameiva Ameiva*

Abstract: We studied the effects of natural and anthropogenic habitat disturbances on environmental temperatures and their consequent effects on thermoregulation and habitat use of *Ameiva ameiva* in a complex habitat matrix of primary tropical forest and several types of disturbed forest in Amazonian Brazil. Data on *Ameiva ameiva* from other regions in Brazil with habitats that have little canopy coverage are compared with data from rain forest sites to determine if activity of rain forest *Ameiva* is temporally or spatially limited by the thermal opportunities available in shaded environments. *Ameiva ameiva* preferentially used disturbed habitats in rain forest regions. These sites had significantly higher environmental temperatures than did surrounding undisturbed rain forest. Environmental temperature distributions indicate that closed canopy rain forest is thermally marginal habitat for *Ameiva ameiva* and that high temperatures resulting from forest clearing are likely to enable *Ameiva ameiva* to increase foraging activity in adjacent forest edges above what is possible in continuous interior forest. *Ameiva ameiva* from rain forest, cerrado and savanna regions of Brazil had significantly lower body temperatures than *Ameiva* from caatinga, an open habitat type with little canopy coverage. This difference is probably due to high ambient temperatures and the high availability of basking sites in open habitats and suggests a thermal constraint on habitat use and time of activity for *Ameiva* in closed canopy habitats.

INTRODUCTION

Small scale local alteration and fragmentation of tropical forests may affect more than just the altered area. The species assemblage in remaining undisturbed habitats may also be affected by isolation and edge effects such as altered microclimate, invasion of exotic species, increased sun exposure and increased leaf fall (Harris, 1988; Saunders et al., 1991; Andrén, 1994; Murcia, 1995). Fragment margins typically show increased temperatures, solar radiation, and wind and water flux (Geiger, 1965; Lovejoy et al., 1986; Kapos, 1989). Such changes in microclimate may contribute to changes in species assemblages and species interactions or may prevent re-colonization of altered habitats either directly, because the new microclimate regime is unacceptable, or because the new microclimate regime favors competitors or predators over members of the original fauna. The size of the fragment and its degree of isolation may affect genetic diversity as well as species diversity (MacArthur and Wilson, 1967). These isolation effects may decrease as fragment size increases and they may increase as a function of time since isolation (Whitmore, 1997). Most studies of edge effects and the effects of fragmentation have been conducted in temperate areas and focused on plants (Sork, 1983; Hester and Hobbs, 1992; Matlack, 1993, 1994), insects (Kruess and Tscharntke, 1994), or avian nest success (Gates and Gysel, 1978; Chasko and Gates, 1982; Angelstam, 1986; Paton, 1994; Santos and Tellería, 1992) and habitat use (Kroodsma, 1982). The several studies on fragmentation and edge effects in tropical areas have examined abiotic effects such as microclimate and soil moisture (Williams-Linera, 1990a; Camargo and Kapos, 1995), effects on plant structure and species composition (Janzen, 1983; Johns, 1988; Kapos, 1989; Williams-Linera, 1990b; Laurance, 1991; Burkey, 1993; Kapos et al., 1993; Malcolm, 1994), edge effects on bird communities and habitat use (Thiollay, 1992; Burkey, 1993; Jullien and Thiollay, 1996), effects on mammals (Young et al., 1995), or projected effects on animals based on habitat data (Zimmerman and Bierregaard, 1986). The effects of microclimate change on forest species after habitat alteration are poorly understood and the effects of small scale habitat alteration on terrestrial vertebrates in tropical areas have been little explored (but see Vitt et al., 1998). Detailed information about reactions of individual species to habitat alteration and fragmentation is required to predict the effects fragmentation will have on ecosystems at local and regional scales (Saunders et al., 1991).

The teiid lizard *Ameiva ameiva* is a ubiquitous resident of lowland tropical South America. It is a medium sized (snout - vent length: x = 129 mm, n = 47), fast moving, and active lizard that feeds on a variety of arthropod and vertebrate prey (Vitt, 1982; Vitt and Colli, 1994; Magnusson et al., 1985). *Ameiva ameiva* is widely distributed in the neotropics, occurring from Panama to central Brazil (Peters and Donoso-Barros, 1986; Schwartz and Henderson, 1991). They occur in nearly every low elevation habitat type from rain forest to thornscrub and even invade neighborhoods in large cities (Vitt and Colli, 1994; pers. obs.). This species has been found to be a natural reservoir for *Salmonella* in Panama where it may serve as a potential vector for this pathogen (Kourany et al., 1970) Heatwole (1966) attributed the absence of *Ameiva ameiva* from the Darién Gap region of Panama to post-Colombian reforestation of the region after Native American cultivation ceased in the 16th century. He observed that *Ameiva* was again colonizing this area as deforestation progressed and agricultural activities resumed in the early 1960s. Of 312 observations of *Ameiva ameiva* in Ecuador reported by Duellman (1978), all were from open habitats and most (56%) were from cleared areas that were once rainforest. Other species of the genus Ameiva also use disturbed habitats to varying degrees and maintain precise, high body temperatures. Hillman (1969) reported on three species of Central American *Ameiva.* All had mean body temperatures between 37°C and 38°C and one species, *Ameiva* *quadrilineata*, was found in open areas such as roadsides and never ventured into closed canopy forest. The wide distribution, open habitat association, colonizing ability, and ecological plasticity of *Ameiva ameiva* make it a likely invader of recently disturbed rain forest habitats. There, increased access to warm basking sites due to canopy removal, along with the rich foraging opportunities offered by adjacent forest are likely to release *Ameiva ameiva* from previous constraints on habitat use and population density. Elevated numbers of *Ameiva ameiva* may detrimentally affect terrestrial animal assemblages in altered habitats and in undisturbed forest adjacent to disturbed areas.

Here we present data on thermal ecology and habitat use of *Ameiva ameiva* from several sites from disparate regions and climates in Brazil. We show that at natural rain forest sites with a continuous canopy this lizard is present but largely restricted to localized and temporally variable habitat patches. We also show that the resulting altered thermal environment following natural and human-caused canopy breaks in rain forest opens large areas of habitat that were previously marginal for this species by increasing ambient temperatures and solar insolation, making it possible for this species to thermoregulate more effectively and exploit the newly opened areas as well as forest edges adjacent to them. Finally, we suggest that increased abundance of *Ameiva ameiva* is likely to affect forest leaf litter vertebrate communities in these newly available habitats through predation and competition.

METHODS

Field work was conducted at six non-rain forest sites, comprising three major tropical ecosystem types in Brazil: Amazonian savanna, cerrado and caatinga, and also at five Amazonian rain forest sites, over a period of 20 years from 1977 to 1997. See figure 1 for localities and distribution of ecosystems in Brazil.

Amazonian savanna

Amazonian savanna exists on the periphery of some portions of the Amazon Basin as well as in isolated enclaves surrounded by rain forest within the basin. Savannas generally receive less than 1700 mm of rain annually and are dominated by grasses and sedges with scattered trees and shrubs. The plant assemblage is closely allied to cerrado (described below) though it is less diverse. These savanna enclaves may be remnants of a more extensive Pleistocene savanna that covered much of the Amazon Basin previous to the encroachment of tropical forest (Haffer, 1969; Vanzolini and Williams, 1970). Amazonian savanna sites were: 1) Boa Vista, Roraima state, in 1992, 2) Humaitá, Amazonas state, in 1991, and 3) Macapá, Amapá state, in 1991.

Cerrado

Cerrado is an upland savanna-like ecosystem with a diverse structure that is variously categorized as grassland, scrubland, or open woodland (Eiten, 1972). It lies between the Amazonian rain forests to the west and the dry caatinga to the east and receives an intermediate amount of rainfall (750-2000 mm/yr) with distinct wet and dry seasons (Eiten, 1972). Cerrado study sites were 1) Alto Araguaia, 50 km N of the headwaters of the Rio Araguaia on the border of the states of Mato Grosso and Goiás, in 1989 and 2) several sites near the city of Brasília, Distrito Federal, in 1987 and 1988.

Caatinga

Caatinga is the most xeric habitat type profiled here. It generally receives less than 500 mm of rain each year (Mares et al., 1981). Caatinga is characterized by frequent, extreme and unpredictable droughts, with rainless periods often lasting as long as one year or more. Vegetation is thornscrub with stunted leguminous trees and columnar cacti (Vitt, 1982). The caatinga study area consists of several sites centered around the town of Exu, Pernambuco state, and was studied in 1977. Dates and detailed descriptions of non-rain forest sites and the three general ecosystems they represent are in Vitt and Colli (1994) and citations therein.

Rain forest

Amazonian rain forest is a widespread ecosystem covering most of the Amazon river basin. Annual precipitation varies by locality from 1000-4500 mm and there may or may not be a distinct dry season. Forest formations range from "terre firme" forest which is never flooded, to "Varzea" or seasonally flooded forest, but in general canopy coverage is nearly complete and the canopy is 25-35 m high (Pires and Prance, 1985). Rain forest sites were: 1) Rio Juruá, Acre, 1996, 2) Rio Ituxí, Amazonas, 1997, 3) Central Rondônia, 1985, 4) Caracaraí, Roraima, 1993, and 5) Rio Curuá-Una, Pará, 1995. Site descriptions for four of the rainforest sites; Rio Juruá, Rio Curuá-Una, Rondônia, and Caracaraí sites appear elsewhere (Vitt and Colli, 1994; Vitt and Zani, 1996; Vitt et al., 1997; Vitt et al., 1998). A detailed description of the Rio Ituxí site is given below.

The Rio Ituxí study site is located in southern Amazonas state in the Rio Purus Basin approximately 700 km southwest of Manaus. This site was studied continuously from February 1 to April 4, 1997. Habitats include elevated islands of "terre firme" forest surrounded by "Várzea" forest that is flooded for periods lasting a few weeks to several months during the wet season. Within the primary rain forest at this site are several types of natural and anthropogenic habitat disturbance including natural forest treefalls, eroded river bluffs, and selectively logged forest.

Within this main study area we distinguished four macrohabitat types, based on vegetative structure and amount of canopy coverage, to generate environmental temperature (T_{env}) distributions for use as null temperature distributions available to *Ameiva*. Temperatures were measured in: 1) high forest— unaltered upland forest containing large trees (25-35 m) with a continuous canopy and a thick leaf litter substrate. Understory plants included dense stands of saplings and palms. Canopy gaps were few in high forest and sunlight reached the ground only in small patches that continually moved with the sun so that no microsites were continuously illuminated for long periods; 2) Treefall— a naturally disturbed habitat that occurs within high forest when large trees topple over, dragging with them other trees and opening a sizable gap in the forest canopy. Microsites within treefalls receive direct sunlight for longer periods than any microsites in high forest, but because of the canyon-like nature of treefalls direct sunlight is available only when the sun is high overhead. Substrate is thick leaf litter; 3) Open forest—a naturally disturbed, localized habitat type found on river bluffs and river bank slopes where exposure to wind damage and water erosion has eliminated large trees. Vegetation is dominated by *Heliconia* and *Cecropia* with very little canopy coverage. Soil is sandy with little leaf litter and much of the area is exposed to direct solar radiation for most of the day; 4) River forest—a tract of "varzea" forest adjacent to the Rio Ituxí. This forest was selectively logged 15 years prior to this study when large trees were removed with minimal disturbance to surrounding forest leaving frequent breaks in the once-continuous canopy. In addition, several dirt access roads were cut at the time of tree removal creating open corridors and long stretches of forest edge through this forest. The road surface is bare laterite soil with little leaf litter cover. These roads had been abandoned for several years previous to this study. Together, these habitats offer a wide range of temperatures and basking opportunities for lizards. Because patches of disturbed and undisturbed habitats are in close proximity, the total range of temperatures available in this complex habitat mosaic is available to highly mobile animals such as *Ameiva.*

Field data collection

Lizards were collected by hand and by pneumatic (BB) rifle. Cloacal body (T_b), substrate surface (T_{sub}) and air at 5 mm (T_{air}) (shaded bulb) temperatures were taken at the site of capture to within 0.2°C with a rapid register (Miller and Weber®) cloacal thermometer. Lizards were held by the head during body temperature measurements to reduce heat exchange between the investigator and lizard. Temperatures taken more than 10 seconds after capture or temperatures taken from animals that were pursued before capture were not included in the analysis. Habitat and microhabitat types at the point where lizards were first seen were recorded. Sun exposure of the lizard (sun, filtered sun, shade) and sun availability (sunny vs. cloudy) were recorded as well as lizard activity (basking, foraging, social encounter, etc.) at the time of capture. Random searches were used to maximize the number of lizards encountered in the time spent searching (Vitt and Colli, 1994). Lizards were returned to the laboratory, usually within 2-3 hr, and live lizards were killed with an injection of sodium pentobarbital. Snout-vent length to within 1 mm was measured with a rule and body mass (to within 0.1g) was measured with an Acculab® electronic balance. Lizards were then fixed in 10% formalin and later preserved in 70% ethanol for deposition in the Museu de Zoologia da Universidade de São Paulo, the Coleçáo Herpetológica Da Universidade De Brasília, the Museu Paraense Emílio Goeldi in Belém, or the Oklahoma Museum of Natural History in Norman, Oklahoma.

Environmental temperatures

In addition to T_{sub} and T_{air} recorded for each individual lizard, environmental temperatures (T_{env}) were measured continuously in each of the habitat types at the Rio Ituxí site for 27 consecutive days to generate a null distribution of temperatures available to lizards over a continuous series of daily activity periods. T_{env} were measured with TidBit® electronic data loggers containing internal temperature probes in high forest, river forest, open forest and treefall habitats. These small data loggers are entirely self contained in a cast of clear, waterproof epoxy which acts as a thermal buffer. Temperatures recorded by the data loggers result from a combination of environmental factors such as substrate and air temperatures, sun exposure and wind speed and so are more indicative of the conditions encountered by terrestrial lizards than simple spot temperature measurements. We have tested TidBits® against conventional copper biophysical lizard models under varying field conditions in desert and in rain forest habitats and have found no statistical differences in the temperature distributions generated by these two methods (Vitt and Sartorius, unpbl. data). We consider the environmental temperatures recorded using these methods to estimate operative temperatures in the sense of Bakken (1992) and Porter et al. (1973). Three data loggers each were placed in high forest, treefall, open forest, and river forest habitats. Data loggers were placed randomly on the ground or leaf litter and not moved during the 27 day measurement period. Half-hourly means for each data logger were calculated and these means were used to calculate half-hourly means and variances for each habitat type. Lizard field active T_b were divided into 1 hour intervals and the means (± 1 SE) were calculated within each time interval for comparison with T_{env} distributions.

Habitat temperatures for all days were then pooled to generate a distribution of temperatures that represents available T_{env} in the habitat and the relative distribution of those temperatures throughout the day. T_{env} data from days in which no *Ameiva* were observed were excluded so that the temperatures reported represent only days when *Ameiva* were active. Generally these were days when sun was available continuously for more than one hour within 3 hours of midday. These temperatures are presented as individual data points (and not means) in figure 2 because *Ameiva* are mobile animals and have the ability to seek rare extremes in their environment. Presenting only measures of central tendency would hide the occurrence of extreme temperatures in the environment which are likely to be important to the thermoregulation and habitat use of mobile ectotherms with high heat requirements.

Lizard heating and cooling rates were measured for *Ameiva* from the Ituxí site to estimate how long it would take for lizard body temperatures to rise from minimal activity to high activity temperatures when exposed to sun and how long it would take for a lizard's T_b to fall from a high activity temperature to a low one when in the shade (in the absence of physiological control of heat exchange). Lizards were killed, a temperature probe attached to an electronic data logger (Hobo® XTI, Onset Computer Corporation) was inserted into the cloaca, and each lizard was placed in the sun. The time required for the lizard to heat from 33°C to 40°C was measured. After a T_b of 40°C was surpassed, each lizard was placed in the shade of the forest edge and the time required to cool from 40°C to 33°C was measured there. These data allowed us to measure time to heat and cool between 33°C and 40°C, a range that includes most field T_b from our data set (see Vitt and Colli, 1994). Van Berkum et al. (1986) found that *Ameiva festiva* in Costa Rica thermoregulated at high T_b, and that the mean upper and lower threshold temperatures for shuttling between sun and shade in the field was 39.4 and 34.5 respectively. Thus, our temperature interval represents a realistic range for activity in lizards of this genus. All trials were run between 1100 and 1400 hr on hot, clear days during high *Ameiva* activity. Substrate was bare laterite soil.

An ANCOVA was performed to determine if *Ameiva* body temperature varied by ecosystem type in Brazil (rain forest, savanna, cerrado, caatinga) with substrate temperature as the covariate. This analysis showed that the slopes of the regressions of T_{sub} and T_b were significantly different between ecosystem type, indicating that T_b varied differently with T_{sub} between these environments. For this reason an ANOVA was used to test for differences in T_b between ecosystem types without attempting to correct for environmental temperatures. T_b and T_{air} distributions from different sites were compared using ANOVA to identify differences between sites and ecosystem types and pairwise multiple comparison procedures (Toothaker, 1993) were used to determine the sources of differences. Heating and cooling rates were analyzed over a range of body sizes with regression analysis. T_{env} were compared using ANOVA for times between

1100 and 1400 hrs, the peak activity time interval for *Ameiva* in this study encompassing 63% ($n = 274$) of our total observations. All statistics were computed using Statview 4.01 (Abacus Concepts, 1992) and SuperANOVA (Abacus Concepts, 1989) statistical packages for the Macintosh.

RESULTS

Environmental temperatures and habitat availability

Environmental temperature (T_{env}) varied considerably between habitats at the Rio Ituxí (Fig. 2) (ANOVA, $F_{3,8} = 33.47$, $P < 0.0001$). Five of the six possible pair-wise comparisons were significant (Games Howell multiple comparison procedure) indicating that this complex rain forest landscape offered a wide variety of temperatures for terrestrial lizards. The comparison between treefall and river forest habitats was not significantly different in this analysis. The high forest habitat temperatures were significantly lower than those of each of the disturbed habitat types indicating that both naturally disturbed and selectively logged habitats had increased environmental temperatures. Minimum available temperatures varied little between habitats, thus it appeared that low temperatures were generally available to rain forest *Ameiva*, even in relatively open habitats, and that the risk of overheating at any time was small. The highest daytime temperatures were recorded within river forest habitat, from probes placed on an abandoned dirt logging road.

Ameiva was active only on days when sunlight was available continuously for long periods (> 1 hour) and, indeed, there was a significant difference between T_{env} for days when *Ameiva* were observed versus days when *Ameiva* were not seen ($T_{11} = 7.093$, $P < .0001$). *Ameiva* were not observed on 24 of the 62 days of the study. Furthermore, lizards were active only for short periods on many other days when afternoon activity was precluded by thunderstorms. In all habitats temperatures were warmer on days that *Ameiva* were active (Fig. 3) although this difference was not significant for high forest.

Habitat availabilities, and our ability to search them, were not equal. High forest and river forest habitats were expansive, and our search time was mostly spent in these areas. Although we did not record the exact time spent searching in each habitat we attempted to alternate field days between river forest and high forest areas and our search times for these habitats are approximately equal. Treefalls and open forest habitats were localized within high forest, occurring as small patches surrounded by continuous canopy. Typically these areas were methodically searched when they were encountered but much less overall time was spent in these habitats. Consequently, lizard use of these habitats is underrepresented in our sample and is included only as a qualitative comparison. When the habitat data for all other lizard species encountered at the Rio Ituxí (25 spp.) are compared to our *Ameiva ameiva* observations we find that all other species combined used the two expansive habitats approximately equally, while *Ameiva* were found predominately in river forest (Fig. 4). Our large number of records for other species from high forest (n = 184) suggests it is unlikely that *Ameiva ameiva*, which are large and active, were overlooked in higher proportions in high forest because of increased understory cover or that search intensity was low in this habitat. Our recorded differences in habitat use are striking for the two expansive habitat types (river and high forest) at the Rio Ituxí and, while not strictly standardized, most likely reflect the true habitat use patterns at rain forest sites.

Lizard body temperatures

At the Rio Ituxí, *Ameiva* maintained body temperatures above mean T_{env} over the entire active period ($x = 37.2 \pm 0.3$, $n = 73$) (Fig. 5) indicating that lizards actively sought the warmest patches within the thermal mosaic. Lizards maintained high body temperatures within a narrow range throughout most of the day, with slight drops in body temperatures in the morning and late afternoon when high T_{env} were not available (Fig. 5). T_b was not significantly correlated with body mass in a linear regression with

T_b as the dependent variable ($R^2 = 0.023$, $P = 0.409$, $n = 32$). No differences in lizard body temperatures among the four different habitat types were detected in a one-way ANOVA ($F_{3,68} = 0.442$, $P = 0.7241$), but warmer habitats (river forest, open forest, high forest treefall) were used disproportionately more by *Ameiva* (Fig. 2, Fig. 4). Most lizards were encountered in open habitats with little canopy coverage, high sun exposure and high T_{env}. T_bs of *Ameiva ameiva* from all other rain forest sites followed a similar pattern. In 127 T_bs measured in six different habitats all means occurred within a narrow range around 37.5°C with no significant differences between means (Fig. 6).

The trend in T_b from *Ameiva* collected in different regional ecosystems, including open and closed canopy habitats, showed that lizard body temperatures were higher in ecosystems with open vegetation structure than they were in closed canopy ecosystems (Table 1). An ANOVA performed on the T_b means from different ecosystems was significant ($F_{3,744} = 5.91$, $P = 0.0005$). Pairwise tests for differences between each ecosystem type revealed that *Ameiva* from caatinga, the most xeric ecosystem and the one with the most open vegetative structure, had body temperatures that were significantly higher than in the other three ecosystem types (Games-Howell multiple comparison procedure). Thus, field active T_bs of *Ameiva* did vary between ecosystem type with the warmest T_bs associated with the most open vegetative structure.

Heating and cooling rates

Heating and cooling rates were nearly linear over the temperature interval of 33°C to 40°C so least squares linear regressions were used to generate best fit lines for the data on each lizard. These lines were used to estimate instantaneous heating rates for each run. Heating and cooling times for the interval correlated significantly with body mass (natural log transformed) ($R^2 = 0.606$, $P < 0.001$ and $R^2 = 0.505$, $P < 0.001$ respectively) (see Fig. 7) but no significant effect of T_{sub} or T_{air} was found, probably due to the limited range of variation in these conditions. For a lizard of average mass in this study (x = 73 g, n = 47) the ratio of cooling time to heating time over the 7° interval was 2.38 from the equations in Fig. 7. The difference in heating and cooling rates can be explained by the difference between the starting temperatures and the equilibrium temperatures in the two habitats used for the test and that solar energy contributed to heat gain in the warming tests. The warming runs started at 33° C with an equilibrium temperature of approximately 50° C (from Fig. 2) while the cooling runs started at 40°C with an equilibrium temperature of approximately 30°C. Thus the temperature gradient for the different tests differed by about 10° C. These data are not intended to represent a precise measurement of heating and cooling rates for *Ameiva ameiva*, they are merely estimates of the proportion of time that must be spent basking when lizards are foraging in shaded habitats (see Tracy (1982) for a detailed explanation of energy balance in lizards). If *Ameiva ameiva* does control heat gain and loss physiologically, then heating rates will likely be faster and cooling rates slower for live lizards that are physiologically as well behaviorally controlling their T_b around some optimum. Given these values for heating and cooling rates, an *Ameiva* of average body mass starting at a T_b of 40°C can forage in the shade of the forest for 24 min before reaching a T_b that limits activity (33°C). It would then have to bask (or forage) in sunlight for 10 min to increase its T_b to 40° once again.

DISCUSSION

Ameiva ameiva is an active foraging heliothermic lizard of open habitats and high T_b wherever it occurs (Table 1) (Vitt, 1982; Vitt and Colli, 1994; Vitt, 1995). *Ameiva ameiva* is active throughout the year in all of the ecosystem types studied. At rain forest sites this lizard is largely restricted to habitats with microsites that provide basking opportunities for long periods of the day. These microsites are uncommon in primary rain forest habitats but abundant in altered habitats whether alteration is due to natural or human caused factors. In addition, *Ameiva* from caatinga ecosystems in arid areas have higher field active T_b than lizards from rain forest, Amazonian savanna, or cerrado habitats, all of which have more canopy coverage and lower surface temperatures (Table 1). This trend in T_b most likely reflects the difficulty that these lizards have in finding suitably hot basking sites in shaded habitats, but could reflect regional variation in T_b preference.

T_{env} distributions from the Rio Ituxí show that the high T_{env} required by *Ameiva* for activity are rare in high forest and are distributed unevenly in space and time. Moreover, *Ameiva* were not active at all on cool, overcast days, further restricting activity. High forest offered a nearly uniform, cool T_{env} distribution throughout the day. Naturally disturbed habitats such as treefalls and open forest on river bluffs, as well as selectively logged river forest, offered higher T_{env} over the entire active period, but the truly high T_{env} required by *Ameiva* for activity usually were available only for a few hours near midday. Days when *Ameiva* were observed had significantly higher T_{env} than days when *Ameiva* were inactive, reflecting their apparent inability to achieve T_bs within their active range on cool days. *Ameiva* are not active on overcast or rainy days when sunlight is not available. If sun is temporarily unavailable, *Ameiva* take basking positions until sun becomes available again; if sun remains unavailable for long periods they seek shelter in burrows.

Like many other heliothermic active foraging lizards (Bauwens et al., 1996; Christian and Weavers, 1996; Rocha and Vrcibradic, 1996; Vitt et al., 1997), *Ameiva* maintain high and relatively stable T_bs throughout the active period despite an environment that is thermally heterogeneous both spatially and temporally. *Ameiva* from regions with an open vegetative structure tend to have higher T_bs as well as higher T_{sub} and T_{air} than *Ameiva* from rain forest. This disparity in body temperature likely reflects the difficulty that rain forest lizards have in finding suitable basking sites with high ambient temperatures. Alternative hypotheses could include that *Ameiva* from open habitats have a higher "selected temperature range" (Hertz et al., 1993) and deliberately thermoregulate around a higher mean than rain forest animals or that hot open habitats force *Ameiva* to be active at temperatures that are higher than their preferred range. Whichever is the correct hypothesis, removal of the rain forest canopy appears to release *Ameiva* from a thermal constraint on habitat use and activity and allows them to exploit previously unavailable areas. Our data show that *Ameiva* cope with suboptimal thermal conditions by avoiding low temperature microsites and habitats and not being active at all when temperatures are low, not by engaging in activity at low body temperatures.

At natural rain forest sites, *Ameiva* activity is largely restricted to the immediate vicinity of fragmentary habitat patches that offer basking opportunities and high T_{env} such as forest edges (e.g. river banks) and natural clearings (e.g. treefalls, eroded hillsides) (fig 2, fig 4). In these areas they occur at modest densities and must continually find new open habitat patches as treefalls fill in with vegetation and rivers rise and fall. Large tracts of undisturbed Amazonian rain forest are thermally marginal habitats for *Ameiva* due to cool ambient temperatures and the rarity of basking sites. We have shown that human disturbance at one rain forest site by selective logging has provided abundant thermal opportunities for *Ameiva* that were not available before the disturbance and that these new habitats are used disproportionately more often than undisturbed sites. At the Rio Ituxí site *Ameiva* were extremely abundant in these disturbed habitats and also in the forest edges adjacent to them. The environment of forest edges near clearings in the Amazon is hotter and drier than deep forest (Lovejoy et al., 1986), a situation that is favorable for teiid lizard thermoregulation.

Ameiva ameiva are dietary generalists that feed on a wide variety of arthropod and vertebrate prey (Magnusson et al., 1985; Vitt and Colli, 1994; Vitt, 1995; Vitt and Carvalho, 1995). Their large size, high sprint speed, and high activity level make them formidable predators on leaf litter animals. Human disturbances that involve the opening of gaps in forest canopy, especially linear ones that infiltrate otherwise undisturbed forest (e.g. roads), may allow *Ameiva* to build up unusually large population densities at forest edges and to infiltrate undisturbed forest in large numbers, potentially creating a detrimental edge effect. Even small roads or trails may provide enough of a canopy gap to allow for increased exploitation of forest by *Ameiva*, extending edge effects far into the core of large fragments of otherwise intact forest. Edge effects caused by predatory animals may be larger than the portion of the edge actually used by the predator if the predator's activity causes a population sink for prey species at forest fragment margins. In this case prey animals from the interior may migrate toward the exterior as they fill the vacancies created by the decline of prey species in the edge zone.

Ameiva ameiva also is likely to compete directly with other teiid lizards that occupy forest habitats. The family Teiidae (which includes the Amazonian genera *Ameiva*, *Kentropyx*, *Tupinambis*, *Cnemidophorus*, *Crocodilurus*, and *Dracaena*) is a morphologically and ecologically conservative lizard taxon whose members are all fast moving, active foragers with streamlined bodies. At most rain forest sites several species occur together where they generally use different habitat types or have different body sizes and hence eat different prey sizes (Vitt, 1995; Vitt and Carvalho, 1995). The three species of *Kentropyx* that commonly occur in Amazonian forest (*K. pelviceps, K. altamazonica, K. calcarata*) are not found in large clearings. In these areas *Ameiva ameiva* is often extremely abundant and represents a formidable competitor and predator for these smaller lizards. Body sizes of the different life history stages of *Ameiva ameiva* range from medium to large on the size scale of forest lizards and this species is likely to compete for food with a wide range of species.

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Table 1. Summary of temperature data for *Ameiva ameiva* from four ecosystem types in Brazil. Means are presented ± 1 standard error. Range is given in parentheses.

Ecosystem	Climate	Habitat structure	Body Temperature	Substrate Temperature	Air Temperature
Rain forest	Long wet season, predictable	Continuous canopy forest	37.5±0.21(28.2-41.2) N = 127	31.81±0.21(26.1-40.8) N = 140	30.02±0.18(24.6-39.1) N = 142
Savanna	Variable length dry season, predictable	Grassland, low tree cover	37.9±0.20(29.6-42.2) N = 133	34.2±0.31(29.4-47.0) N = 122	31.3±0.18(27.4-35) N = 133
Cerrado	Moderate dry season, predictable	Grassland, variable tree cover	37.7±0.10(26.4-41.8) N = 462	30.6±0.18(21.0-45.4) N = 462	28.2±0.09(23.0-35.5) N = 462
Caatinga	Long dry season, unpredictable	Thorn forest	39.4±0.27(36.0-42.7) N = 26	37.0±0.46(31.9-41.2) N = 25	32.2±0.38(29.2-35.3) N = 26

FIGURE LEGENDS

Figure 1. Map of Brazil, showing locations of study sites and the morphoclimatic domains identified by Ab'Saber (1977): 1, Rio Juruá, Acre (8° 15′ 31″ N x 72° 46′ 37″ W), 2, Rio Ituxí, Amazonas (8° 20′ S x 65° 42′ W), 3, Humaitá, Amazonas (7° 31′ N x 63° 02′ W), 4, Central Rondonia (10° 30′ S x 62° 25′ W), 5, Boa Vista, Roraima (2° 49′ N x 60° 40′ W), 6, Caracaraí, Roraima (2° 0′ N x 62° 50′ W), 7, Rio Curuá-Una, Pará (3° 9′ S x 54° 50′ W), 8, Macapá, Amapá (0° 02′ N x 51° 03′ W), 9, Exu, Pernambuco (7° 31′ S x 39° 43′ W), 10, Brasília, Distrito Federal (15° 47′ S x 47° 55′ W), 11, Alto Araguaia, Goiás (17° 19′ S x 53° 12′ W).

Figure 2. Distribution of environmental temperatures (T_{env}) for each habitat type at the Rio Ituxí site. Data for all days when *Ameiva ameiva* were observed to be active are included.

Figure 3. Comparison of environmental temperature (T_{env}) distributions at the Rio Ituxí site in all open habitat types (river forest, treefall and open forest) for days when *Ameiva ameiva* were and were not active. There was no significant difference between the two groups for high forest habitat and these data were excluded. means are presented ± 1 SE.

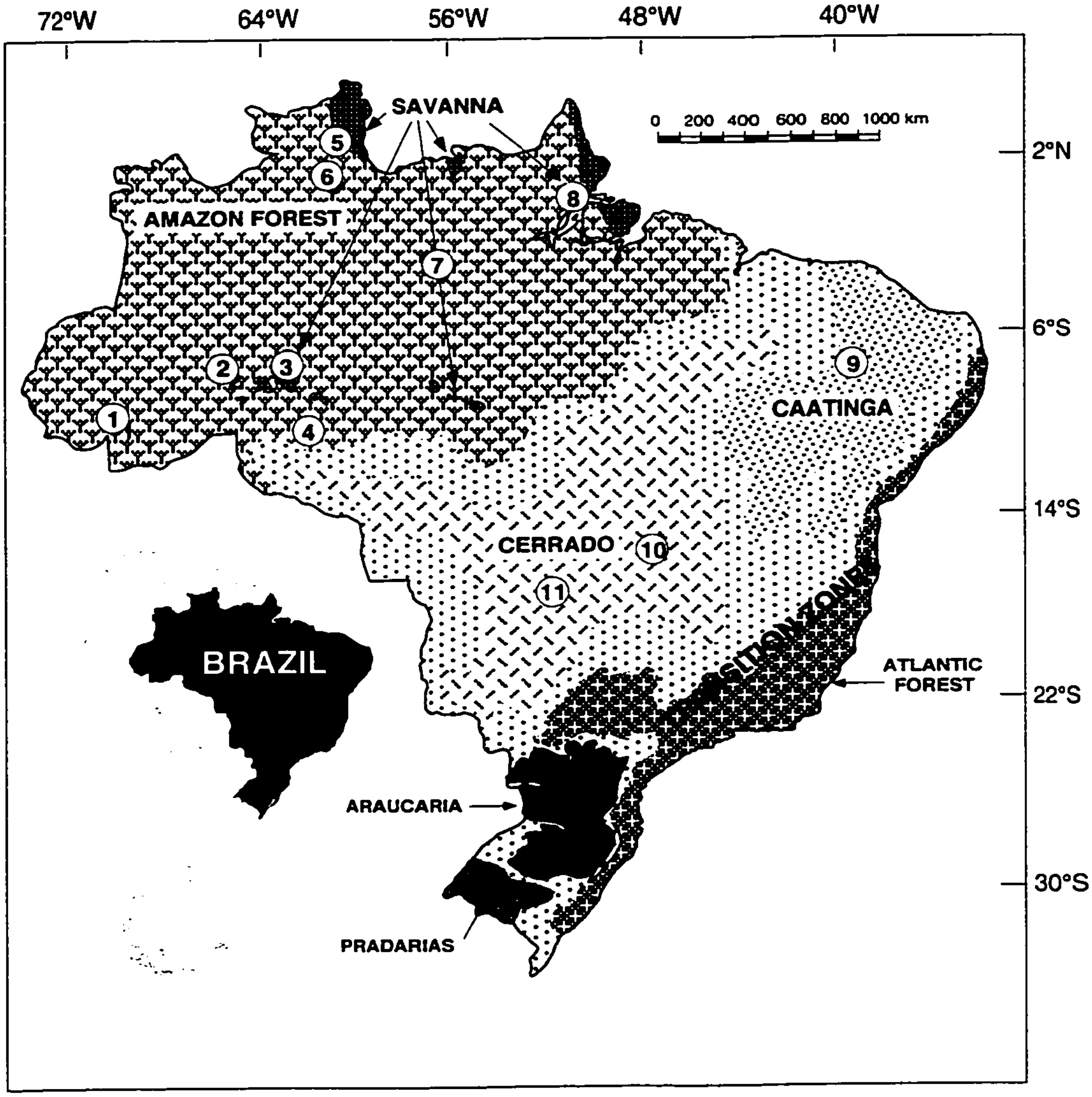
Figure 4. Histogram of habitat use for all lizards (25 spp.) encountered in 189 person days of field work at the Rio Ituxí, Amazonas Brazil. River forest and High forest were widespread habitats and were searched equally. Less search time was spent in High forest treefall and Open forest habitats.

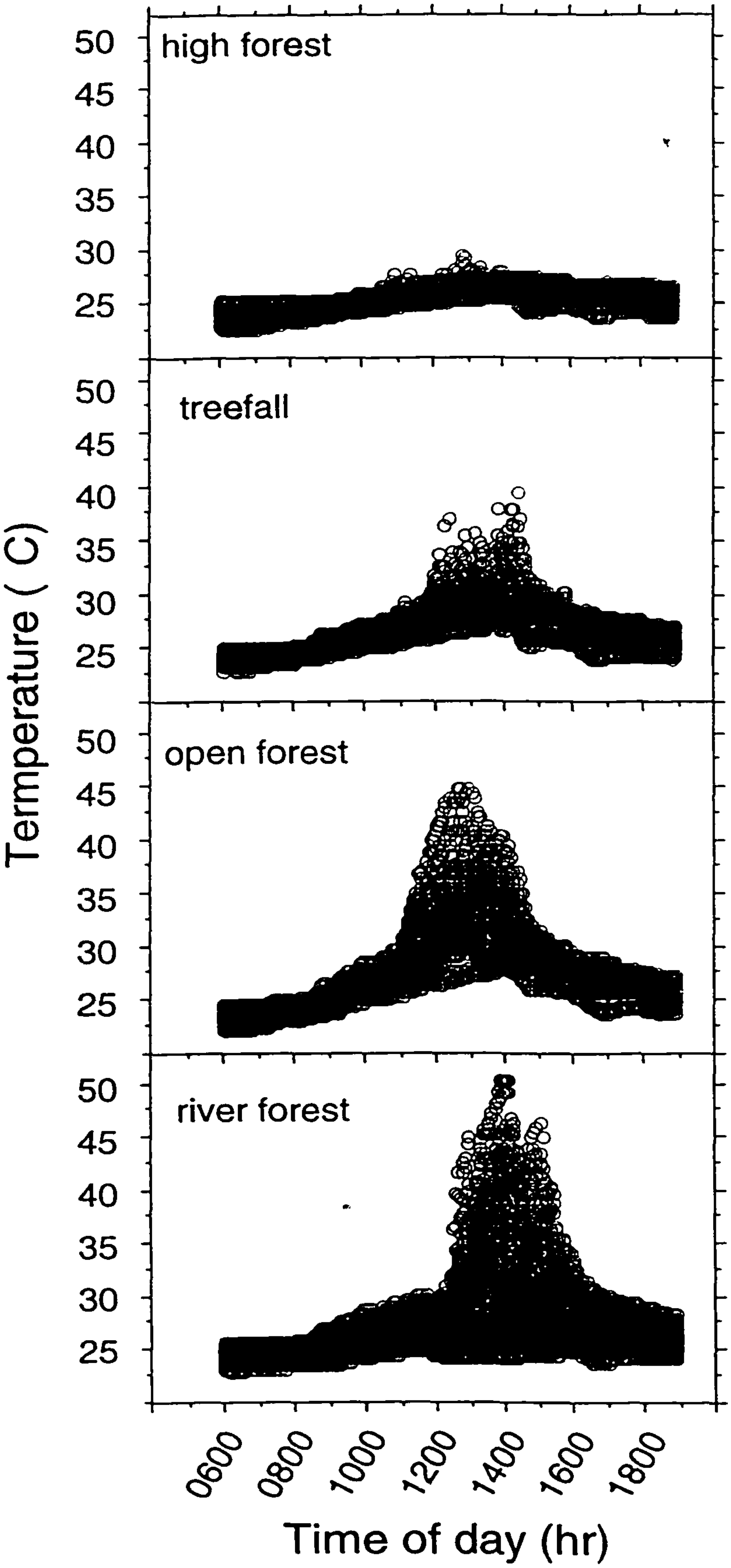
Figure 5. Hourly distribution of active body temperatures for *Ameiva ameiva* at the Rio Ituxí, Amazonas, Brazil, plotted with half-hourly environmental temperatures (T_{env}). All points are means. Error bars indicate standard error. Sample size for lizards appears above each mean.

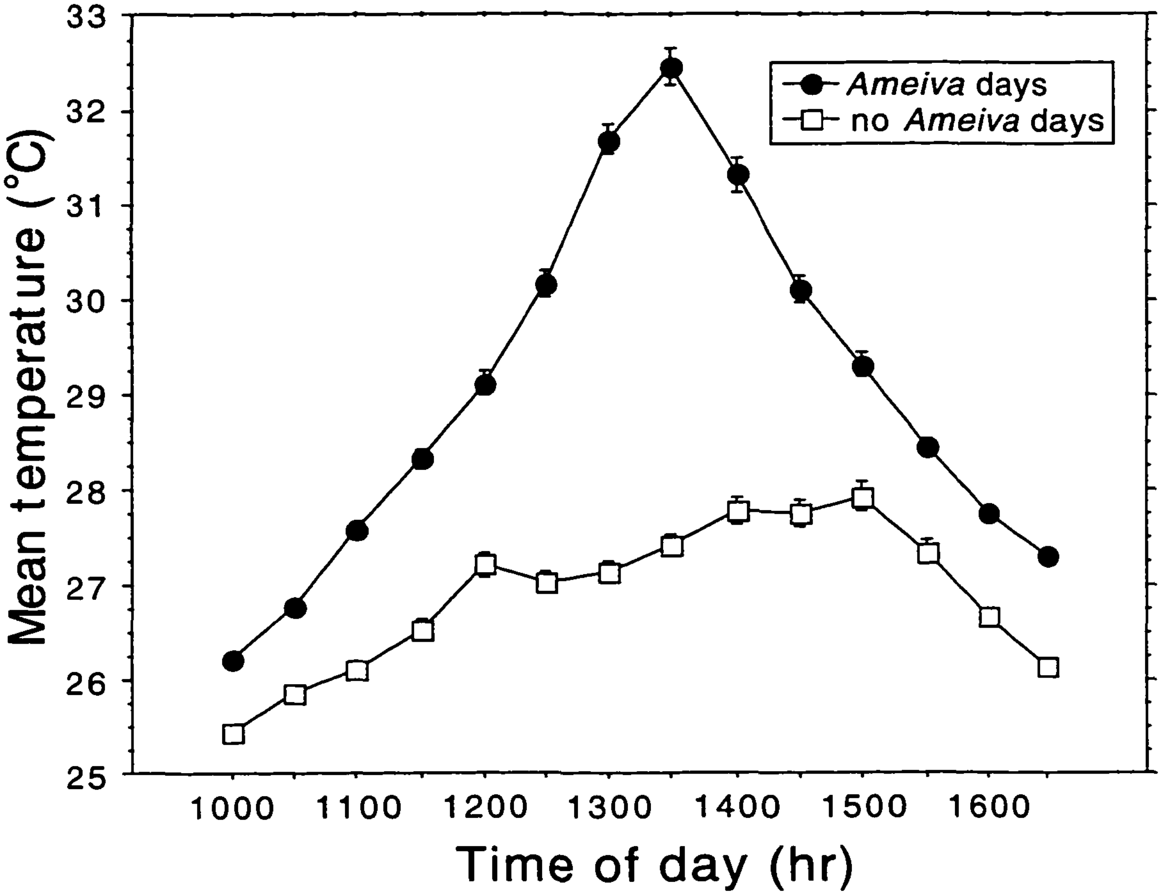
Figure 6. Box plot of body temperatures of *Ameiva ameiva* from several Amazonian rain forest sites separated by habitat type. Horizontal lines indicate 10th, 25th, 50th, 75th

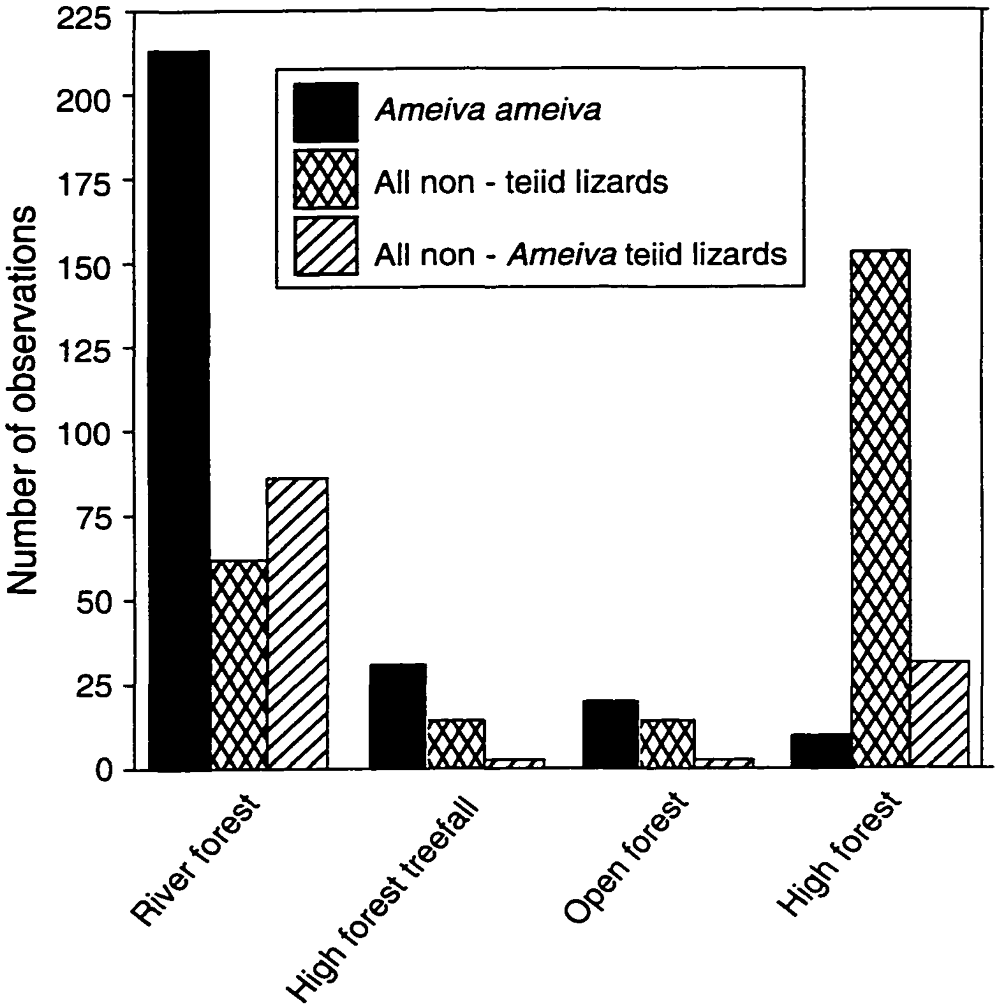
and 90th percentiles for each box. Circles indicate data points outside of the 10th or 90th percentiles.

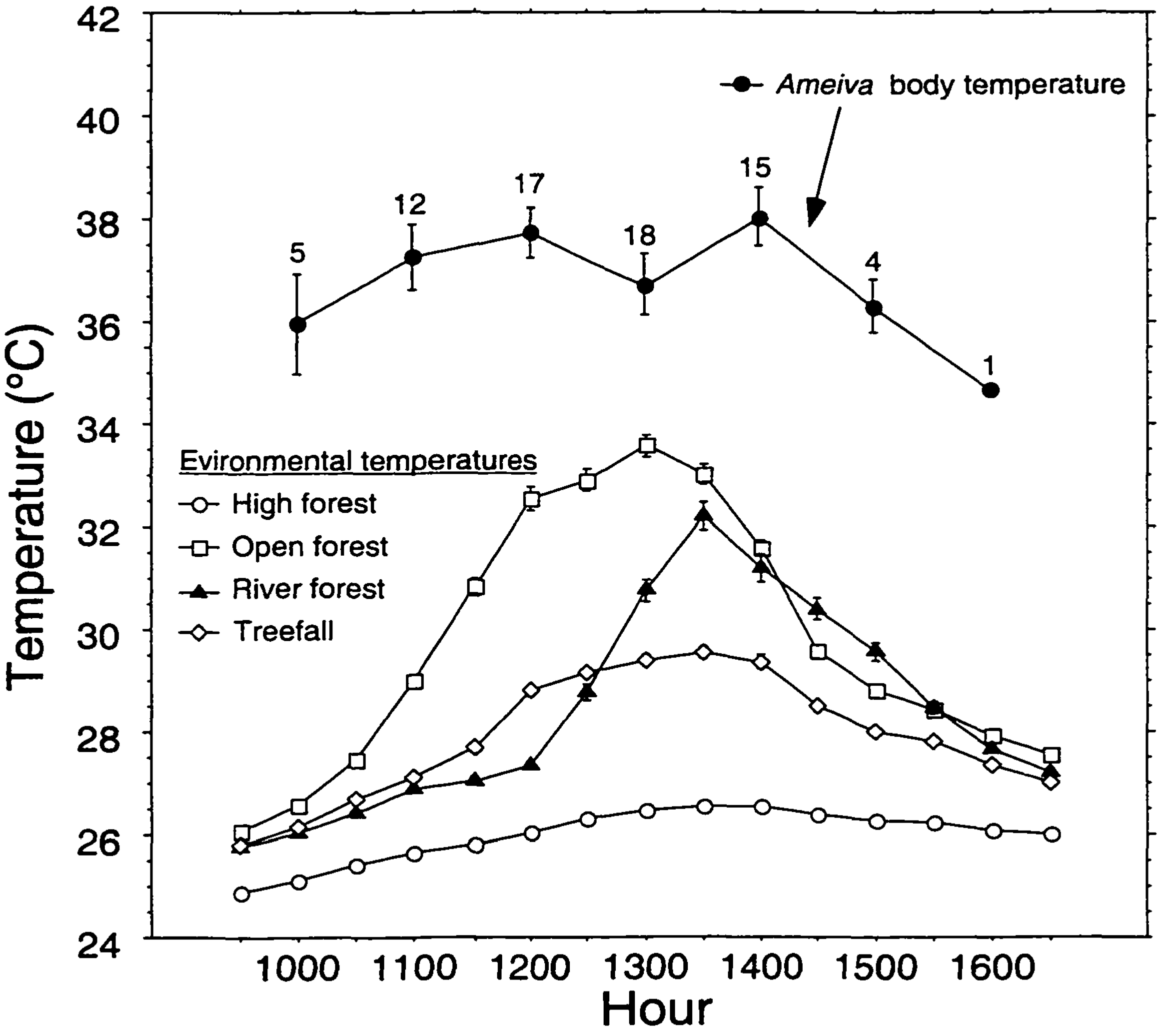
Figure 7. Linear regressions of body mass and the time needed for a temperature change of 7°C (33°C - 40°C) during heating and cooling experiments on *Ameiva ameiva* from the Rio Ituxí, Amazonas Brazil.

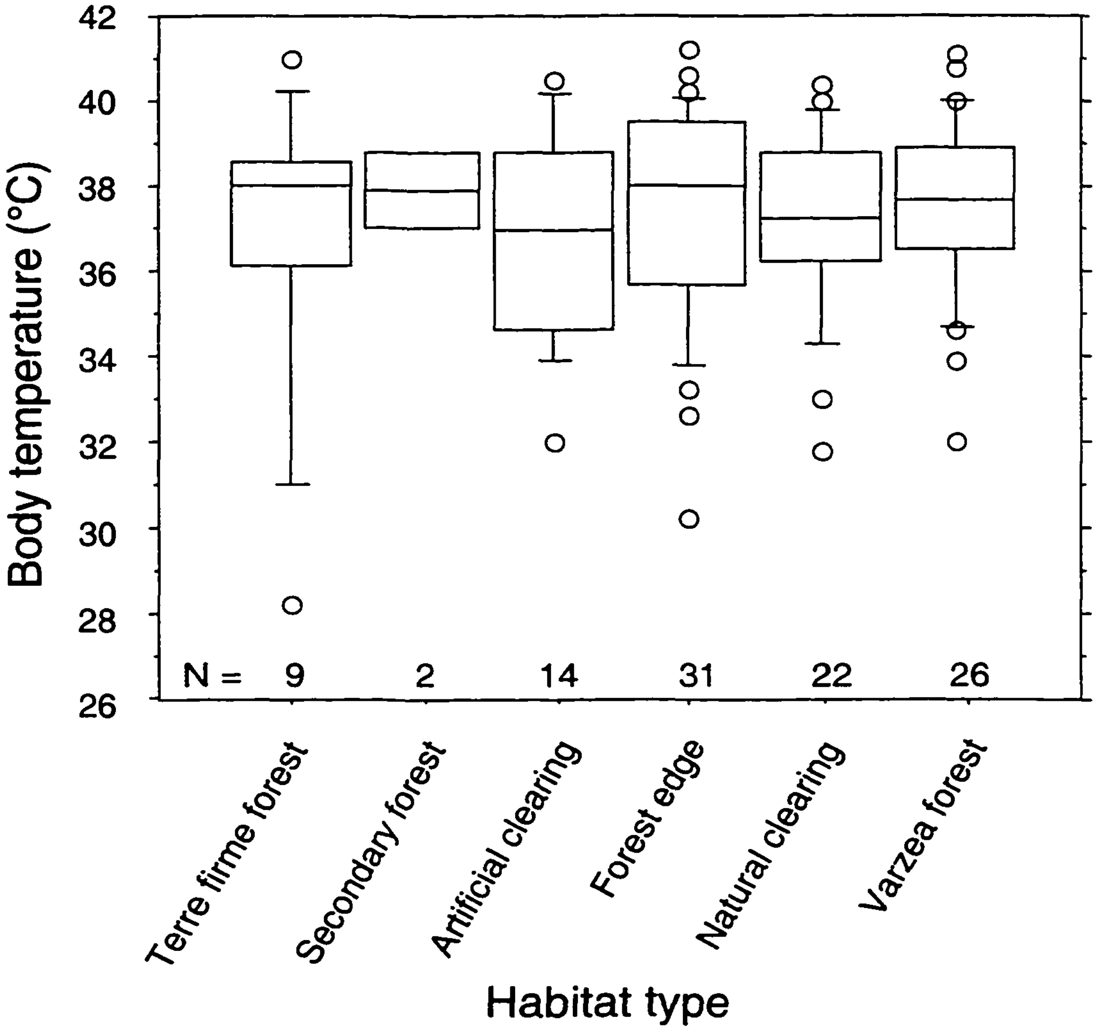

72°W
64°W
56°W
48°W
40°W
2°N
6°S
14°S
22°S
30°S
0 200 400 600 800 1000 km
SAVANNA
AMAZON FOREST
CAATINGA
CERRADO
TRANSITION ZONE
ATLANTIC FOREST
ARAUCARIA
PRADARIAS
BRAZIL
1
2
3
4
5
6
7
8
9
10
11

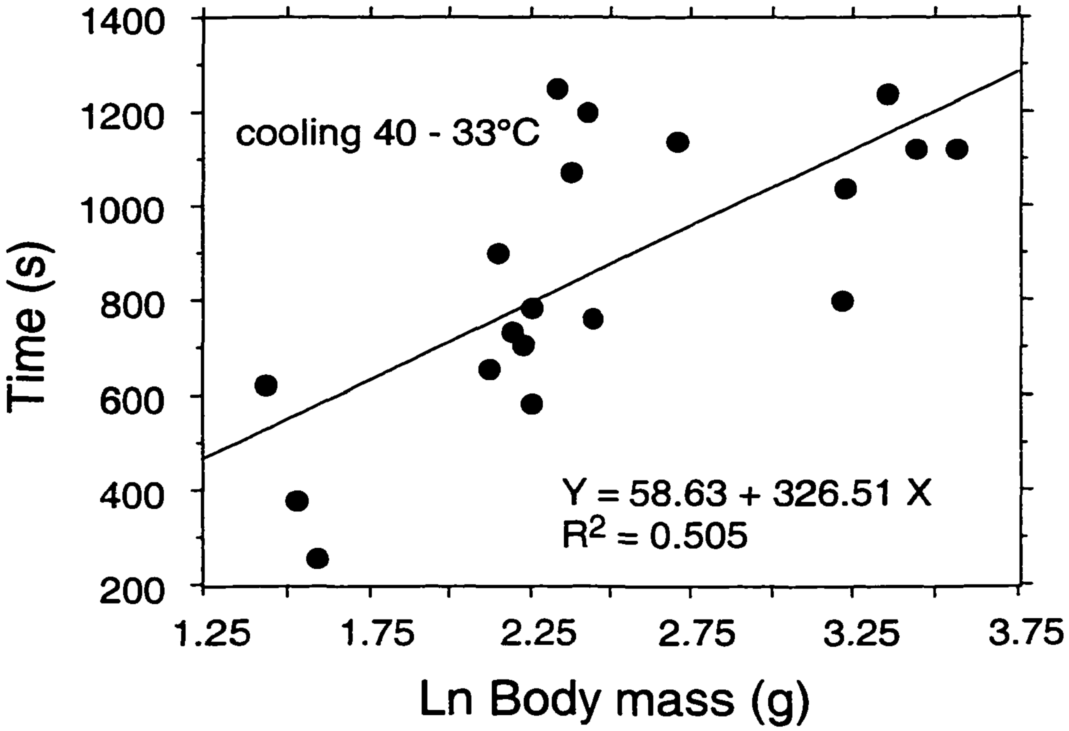

high forest
treefall
open forest
river forest
Termperature (C)
50
45
40
35
30
25
0600
0800
1000
1200
1400
1600
1800
Time of day (hr)

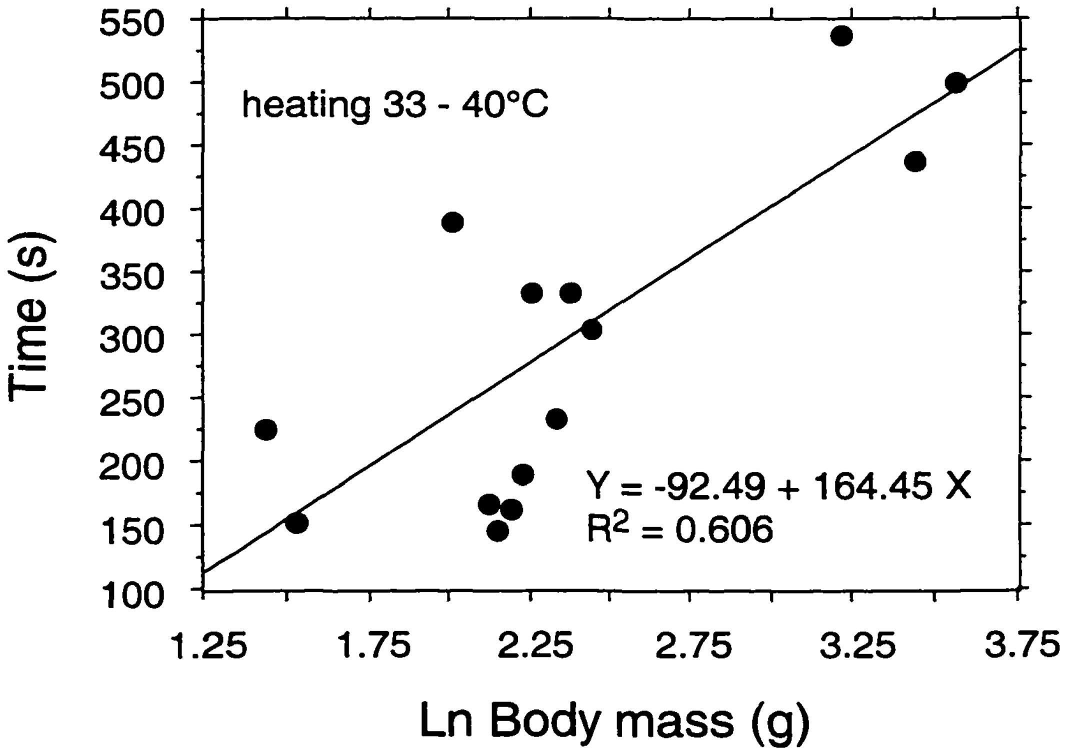

Ameiva days
no Ameiva days
Mean temperature (°C)
33
32
31
30
29
28
27
26
25
1000
1100
1200
1300
1400
1500
1600
Time of day (hr)


225
200
175
150
125
100
75
50
25
0
Number of observations
Ameiva ameiva
All non - teiid lizards
All non - Ameiva teiid lizards
River forest
High forest treefall
Open forest
High forest


Ameiva body temperature
5
12
17
18
15
4
1
Evironmental temperatures
High forest
Open forest
River forest
Treefall
Temperature (°C)
42
40
38
36
34
32
30
28
26
24
1000
1100
1200
1300
1400
1500
1600
Hour


42
40
38
36
34
32
30
28
26
Body temperature (°C)
N = 9
2
14
31
22
26
Terre firme forest
Secondary forest
Artificial clearing
Forest edge
Natural clearing
Varzea forest
Habitat type


cooling 40 - 33°C
Y = 58.63 + 326.51 X
R^2 = 0.505
Time (s)
1400
1200
1000
800
600
400
200
1.25
1.75
2.25
2.75
3.25
3.75
Ln Body mass (g)


heating 33 - 40°C
Y = -92.49 + 164.45 X
R^2 = 0.606
Time (s)
550
500
450
400
350
300
250
200
150
100
1.25
1.75
2.25
2.75
3.25
3.75
Ln Body mass (g)