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Thermal Ecology of the Tropical Iguanid Lizard, Leiocephalus schreibersi

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ABSTRACT.—The Hispaniolan lizard, *Leiocephalus schreibersi,* precisely maintained a narrow range of body temperatures (T_b) ($\bar{x}$ = 36.7, SE = 0.17 C) that was significantly above concomitant air (T_a) and site (T_s) temperatures throughout all but the last hour of their emergence period. Lizards moved frequently between shade and sun throughout the day. Hourly basking frequency of the population was greatest (80%) when most lizards were emerging from their burrows (0900–0959 h), gradually declined to 35% at midday, then oscillated between 20–40% for the remaining afternoon hours. An hour before the majority of lizards entered their borrows (1700 h), movement markedly decreased and T_b declined to overlap T_s, as lizards appeared to relax thermoregulatory behavior.

An important feature of this species' thermoecology is that the elevated and relatively stable T_b of *Leiocephalus schreibersi* permitted the lizards to be physically active during the entire day; rising ambient temperatures during the day never reached the maintained T_b of this stenothermic species. In addition, no seasonal effects (November vs. May–June) were detected in the above thermal profile.

INTRODUCTION

Little or no field data are available on the thermal ecology of *Leiocephalus* lizards, even though they are common on a number of West Indian islands (Schwartz and Thomas, 1975). Here we present the thermal profile of *Leiocephalus schreibersi.* Based on suggestions by Huey (1982), Hertz (1983) and Hertz *et al.* (1983), we will characterize *L. schreibersi* by answering five basic questions. First, do the species' activity body temperatures reflect those of closely related groups? Second, is the range of body temperatures narrow (stenothermic) or wide (eurythermic)? Third, is there evidence for active thermoregulation (precise thermoregulators) or are the lizards thermally passive (thermoconformers)? Fourth, during any portion of the day, do ambient temperatures significantly depress activity? Fifth, are there seasonal differences in the population's thermal profile?

MATERIALS AND METHODS

Leiocephalus schreibersi is a ground-dwelling, territorial lizard that is abundant in many of the xeric, coastal regions of Hispaniola (Schwartz and Thomas, 1975). The males (max. SVL = 92 mm) are brightly colored and larger than the females (max. SVL = 71 mm). These lizards favor semi-open habitat with scattered, moderate-sized rocks which they use for surveillance and basking. They retreat into burrows and rock crevices at night or when disturbed.

Data were gathered at the Kaliko Beach Resort located 55 km N of Port-au-Prince, Haiti, during 11–25 November 1983, 15–29 June 1984 and 14–21 May 1985. The lizards were habituated to humans which reduced the possibility of an observer's effect upon their normal behavior and facilitated their capture by hand and noose.

Following the techniques and precautions of Hertz and Huey (1981) and Hertz (1983), body and ambient temperature data for 157 lizards were recorded with Schultheis thermometers. Cloacal temperatures (T_b) were taken immediately after capture, by holding the subject near the pectoral region while the thermometer reached equilibrium. Temperatures of animals that had been chased for more than a minute prior to capture were not taken, and no temperatures were recorded from animals smaller than 40 mm SVL.

Due to the complexity of lizard-microclimate interactions (Porter and Gates, 1969; Porter *et al.*, 1973; Porter and James, 1979; Tracy, 1982), we could only approximate the ambient temperatures of each lizard by using air (T_a) and site (T_s) temperatures. "Breast height" T_a, a traditional estimator of ambient heat load, was taken with a shaded thermometer bulb 1.5 m above the capture site. The T_s was recorded where the lizard was first seen by placing the shaded thermometer bulb against the lizard's perch site. This method eliminated direct solar radiation, but otherwise facilitated maximum T_s values by including conduction as well as radiation and convection effects. Lowered readings due to sporadic breezes were minimized by waiting for a stable mercury in calm air.

We also recorded whether the lizard had been in the sun or shade when first sighted, time of day, the lizard's snout–vent length (SVL), sex and position on a map of the study area. After marking with an unique toe clip, the lizard was released at the point of capture. No lizard was used twice.

Emergence activity of the population (*i.e.*, numbers of lizards seen in the habitat) was determined by census over a prescribed 430-m route. A census was made every hour from 0700–1900 h for 4 days (June 1984). An observer and a recorder traversed an open area of high lizard density, scanning both sides of the census path, counting and recording the basking status (sun/shade) of each observed lizard.

In addition to emergence activity, we also used focal animal sampling (Altmann, 1974) to measure the physical activity of individual lizards. Six subjects (three males and three females) were continuously observed from 0800–1800 h, each on separate days in June 1985. Using binoculars and a working distance >10 m to ensure no observer effect, two people made focal animal observations on each subject, noting all moves of more than a body length, elapsed time spent in the sun and shade, and any obvious purpose for the moves (*e.g.*, eating, courting, territorial defense).

RESULTS

November and May–June temperature data were pooled as their respective T_b distributions ($\bar{x} \pm$ SE and range = 36.6 ± 1.80 C and 31.5–39.8 C; 36.1 ± 2.19 C and 28.2–39.8 C) were not significantly different ($t = 1.50$, $P > 0.10$). Likewise no significant difference in T_b was detected between the sexes ($t = 1.49$, $P > 0.40$).

The mean T_b for 157 subjects was 36.3 ± SE 0.17 C (range = 28.2 C at 0920 h to 39.8 C at 1225 h), and was statistically higher ($P < 0.01$) than concurrently recorded T_s or T_a ($\bar{x} \pm$ SE = 32.3 ± 0.14 C, 30.8 ± 0.11 C, respectively). The latter was true in every hour of the day except 1700–1859 h (Fig. 1). On an individual basis, T_b was as much as 11 C above concurrent T_a and 10 C above concomitant T_s. Regression analysis of T_b on T_s and T_b on T_a resulted in the following respective coefficients: $r = 0.42$ and 0.43.

Few lizards were out between 0700–0759 h, the 1st hour after sunrise (Fig. 2). The majority of the population emerged from 0800–0959 h. During this period of emergence, our sample contained a wide T_b range from lizards who had just appeared from their burrows (relatively low T_b) to individuals who had been basking for over an hour (elevated T_b). Therefore, the mean 0900 h T_b was lower than subsequent hourly means, with more variance (Fig. 1). The 0800–0959 h period was also marked by a high percentage of the population in the sun (Fig. 2). By 1000 h, numbers of emerged lizards stabilized, and most of the population had been basking for an extended time; as a consequence, their T_b values

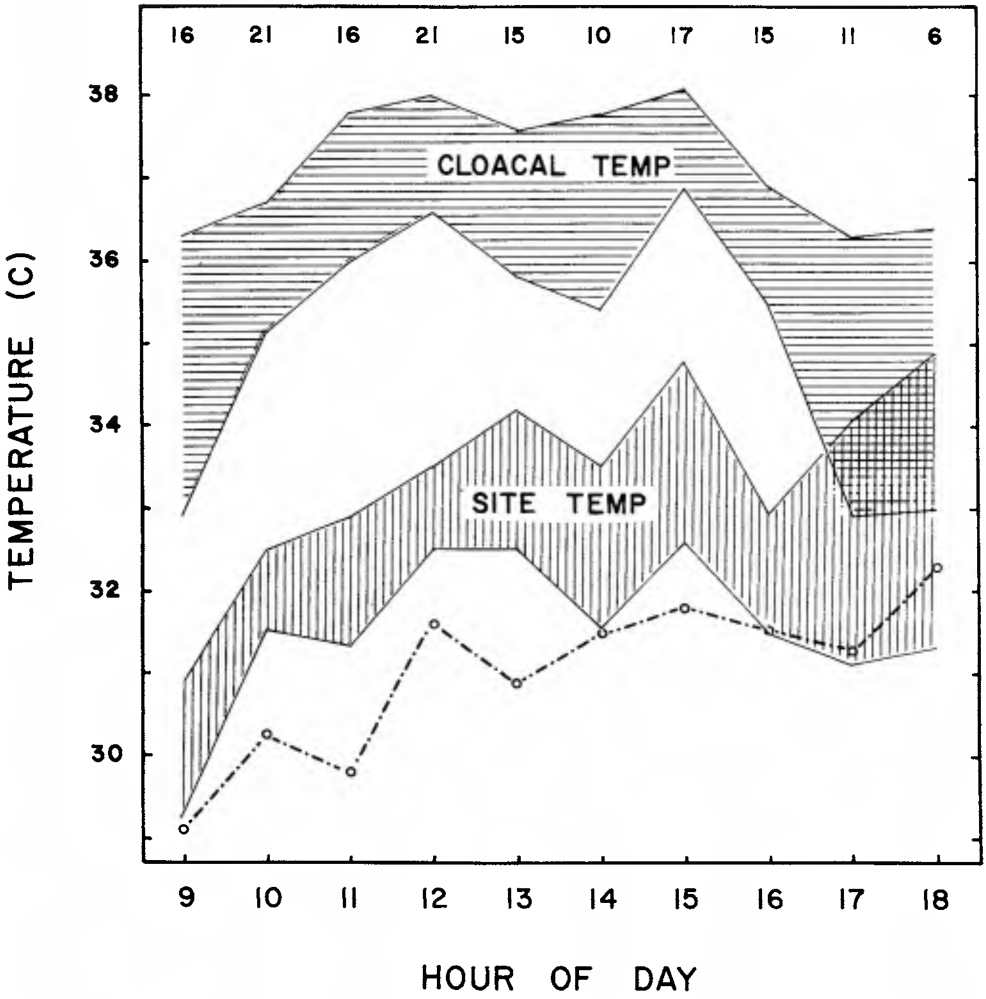

FIG. 1.—Confidence intervals (95%) for mean hourly cloacal and site temperatures of *Leiocephalus schreibersi*. Numbers at top give hourly sample sizes and dashed line represents mean hourly air temperatures

were leveling off at 35.9 C. The proportion of basking individuals in the population gradually dropped off from a maximum of 80% during 1000–1059 h to 35% during midday (1300–1359 h), and then oscillated between 20–40% for the remaining hours of emergence as lizards moved in and out of the sun (Fig.2). At no time were all members of the population entirely in the shade. The same pattern of sun/shade use was also observed in the six lizards placed under continuous focal animal observation; their average percent of time in the sun for each consecutive hour from 0800–1659 h was 92, 87, 59, 35, 26, 28, 27, 16 and 24%. These lizards avoided available shade in their home ranges in the morning, in spite of making frequent moves (*see below*). Then they spent more time in the shade in the afternoon, even though sun-exposed substrate was always nearby (many times within a body length).

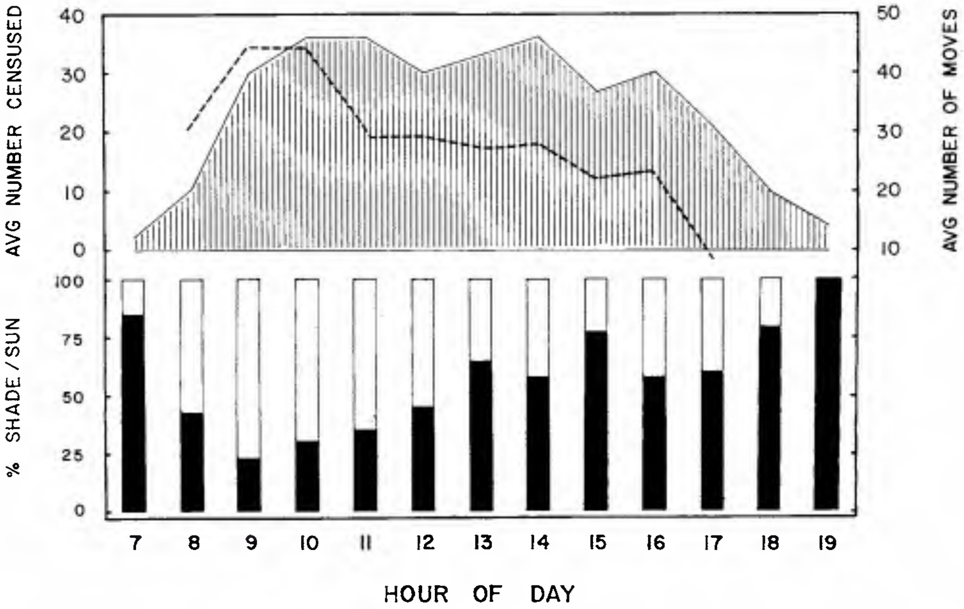

FIG. 2.—Hourly mean number of *Leiocephalus schreibersi* seen during censuses (shaded curve), hourly mean number of movements by six lizards during daylong focal observations (dashed line), and hourly mean percent of lizards in the shade (black portion of bars) and sun (white portions of bars) during censuses

At 1000 h, after the population had emerged for an hour or more, the hourly mean T_b remained nearly constant through 1659 h, with hourly means ranging from 35.9–37.5 C ($\bar{x} \pm$ SD = 36.8 ± 0.48 C) (Fig. 1). The coefficient of variation (SD × 100/$\bar{x}$) for hourly mean T_b data during this 7-h period was 1.3% (almost no variance), indicating the T_b was relatively constant. This narrow range of T_b was sustained well above all ambient temperature measurements. The nearest confidence limits between respective hourly T_b and T_s were separated by 2–3 C (Fig. 1). Thus, the stable and apparently regulated T_b of *Leiocephalus schreibersi* was well above the recorded ambient heat levels.

Hourly frequency of movements from focal animal observations showed a 2-h maximum (0900–1059 h) in the morning which coincided with maximum basking activity (Fig. 2). Lizards were averaging 45 position changes/h. As T_b values leveled off at 1100 h and basking decreased, the frequency of movements also decreased to 30/h. Mean hourly position shifts slowly decreased through the afternoon to 23/h (1600–1659). At 1700 h, the lizards appeared to begin preparation to enter their burrows for the night; it was a transition period. During this transition, mean moves/h dropped from 23 to 8, and the mean T_b decreased from 36.2 C to 34.8 C (Figs. 1, 2), marking an apparent relaxation of thermoregulatory behavior. The cooler 1700 h mean T_b was nonsignificant from its T_s mean, even though ambient temperatures were as hot or hotter than during the preceding hour. By 1800 h, most of the population had entered nocturnal retreats in spite of continuing warm ambient temperatures and remaining daylight. At no time during the day did the focal animals leave their predictable activity areas (territories) to enter burrows or seek areas of greater shade.

DISCUSSION

Lizard species have adapted to a myriad of microclimatic conditions. Within the spectrum of adaptive responses, we characterize the T_b of *Leiocephalus schreibersi* as being phylogenetically conservative, stenothermic (within and between seasons), precisely maintained, and never shifting to thermoconformity during the diurnal period.

Conservative T_b.—The average field T_b of *Leiocephalus schreibersi* (36.3 C) is similar to that of related species. *Leiocephalus* is a tropidurine genus (Etheridge, 1964) that belongs to a species group which is osteologically distinct from all other iguanids except the sceloporines (Etheridge, 1966); further, the West Indian species of *Leiocephalus* appear to be most closely allied to the *Liolaemus* species group (Etheridge and de Queiroz, 1988). The range of mean field activity temperatures for eight species of *Liolaemus* (34–37 C; Fuentes and Jaksic, 1979) overlaps the mean T_b of *Leiocephalus schreibersi.* Furthermore, Avery (1982) listed the majority of tropidurine and sceloporine species studied as having activity body temperatures of 34–39 C.

Stenothermy.—The stenothermic response of *Leiocephalus schreibersi* was reflected in several ways. The population was active only during the warmest part of the day. The majority of the lizards did not emerge until 2 h after sunrise (0900–0959 h), and most retired to burrows 1–2 h before sunset (1700–1859 h) while air temperature was still >31 C. After morning emergence and during periods of physical activity (1000–1659 h), the lizards' mean hourly T_b values were very similar, ranging from 35.9–37.3 C. This narrow range of activity T_b was maintained in different seasons (November and May–June) as well. Some species reported to be precise thermoregulators nevertheless have a broad thermal niche due to seasonal effects (*e.g.,* Huey *et al.,* 1977; Christian *et al.,* 1983; van Damme *et al.,* 1987). However, we suspect that the tropical climate, coastal habitat, and behavioral characteristics contribute to the stenothermic T_b of *L. schreibersi.*

Precise thermoregulator.—However controversial, all evidence indicates that *Leiocephalus schreibersi* is a precise thermoregulator. Heath (1964) cautioned that the thermodynamics of inanimate objects (*e.g.,* water-filled cans) can at times mimic the very field data of cloacal temperatures which were offered as evidence for behavioral thermoregulation. Inferring thermoregulation from field T_b data requires a control (*e.g.,* grey body temperature index; Roughgarden *et al.,* 1981) or direct behavioral observations (Huey *et al.,* 1977). To aid in this distinction, Huey and Slatkin (1976) and Huey (1982) offered two criteria for identifying thermoregulation: (1) the frequency of thermoregulatory behavior and (2) the slope of the linear regression of T_b on T_a. Regarding the first criterion, it is not always clear whether a lizard shifted its sun/shade status for purposes of thermoregulation or for other reasons such as feeding, predator avoidance or social functions (Hillman, 1969; Avery, 1978; Rose, 1981; Waldschmidt and Tracy, 1983). If animals move between sun and shade during the day in a proportion independent of available shade (*i.e.,* nonrandom), then it can be assumed that at least one significant motivation for these movements was thermoregulation (Huey *et al.,* 1977). Our continuous daylong observations of six lizards indicated such a nonrandom use of shade and sun. At all times of the day, sun and shade conditions were readily available to each lizard; yet the lizards' hour to hour exposures to direct sunlight showed a nonrandom pattern by varying widely (16–92%). This inter-hour variability and its distribution across the day cannot be explained by random lizard movements, even within a habitat of shifting amounts of shade. Predictably, sun movement produces maximum shade in the morning and afternoon, and minimum shade at midday. No such morning–afternoon symmetry is evident in the data. Actually, maximum basking occurred when maximum morning shade is predicted, and infrequent basking occurred during midday when minimum shade is predicted. Nor were there obstructions (*e.g.*, mountains) which blocked the sun from the study area at the beginning or end of the lizards' activity period.

The second criterion, regression slopes of T_b on T_a, produces r values which can vary from 0 to 1, where 0 indicates total independence of T_b from T_a (precise thermoregulator) and 1 indicates complete thermal conformity; such values offer quantification of relative thermoregulatory behavior. These measures sometimes have limitations (Hertz and Huey, 1981; Huey, 1982; Dreisig, 1984). For example, van Damme *et al.* (1987) found that with seasonal effects a slope near 1 (thermal conformity) might still be generated from thermoregulating lizards. Van Damme *et al.* (1987) added the criterion of the y-intercept value from the regression equation; if this is well above 0, regardless of slope value, thermoregulation is still occurring. In a thermally conforming species, the intercept should be close to 0, with a slope near 1. For our *Leiocephalus schreibersi* data, the y-intercept was 21.3 (well above 0), and the slope of 0.43 was much closer to 0 than that of purported precise thermoregulators (*e.g.*, 0.70 for *Anolis sagrei*; characterization from Huey, 1982; data from Ruibal, 1961). Thus, evaluation by criteria of direct observation and the T_b–T_a regression analysis showed *L. schreibersi* to be a precise thermoregulator.

Continuous activity period.—Lizards of many species begin their day by thermoregulating, but frequently become thermoconformers because rising ambient temperatures surpass the lizards' thermal activity ranges. During this extended period of thermal stress, microhabitat utilization is restricted, as lizards retreat to the coolest available shade (usually elevated perches) and curtail their nonthermoregulatory activities (*e.g., Anolis nebulosus,* Jenssen, 1970; *Agama agama,* James and Porter, 1979; *Sceloporus merriami,* Grant and Dunham, 1988). In species which utilize burrows, intolerable heat loads will force lizards into their subterranean retreats (*e.g., Dipsosaurus dorsalis,* Porter *et al.,* 1973).

Unlike the above species, *Leiocephalus schreibersi* experienced no midday inactivity and no extended periods in the shade or burrows. The broad differential between midday T_b and the cooler concomitant T_s (site temperatures) largely emancipated *L. schreibersi* from any thermoregulatory crisis. The lizards were physically active throughout the day (0900–1659 h) (Fig. 2), feeding and socially interacting (DLM and TAJ, unpubl. data). By having a higher thermal setpoint than most all microhabitat temperatures in its habitat, *L. schreibersi* was able spacially and temporally to exploit fully its environment.

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