THERMAL ECOLOGY OF THE TEXAS HORNED LIZARD

(*PHRYNOSOMA CORNUTUM*)

By

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Bachelor of Science

University of Central Oklahoma

Edmond, Oklahoma

1997

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
December 2001
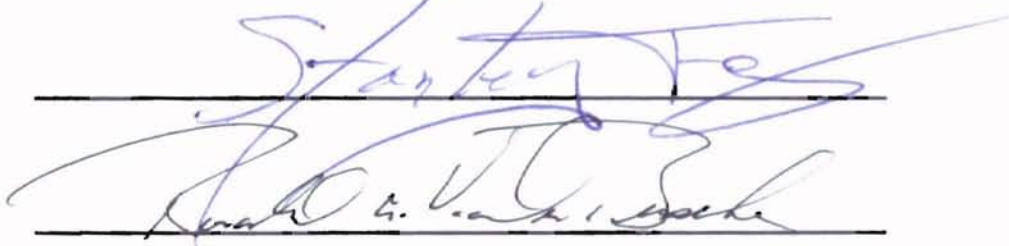
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ACKNOWLEDGEMENTS

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Introduction and Background

Temperature is one of the most important factors affecting rates of chemical reactions, especially biological reactions involving enzymes. Most biochemical rates are increased 2-3 fold with each 10°C increase in temperature, so a 10°C decrease in temperature may decrease any given rate process by one half to two thirds. Accordingly, performance characteristics depending on biological reactions also decrease in rate (Bennett 1990). Therefore, temperature can affect a suite of animal activities such as metabolic rate (Bennett and Dawson 1976), rate of digestion (Huey 1982, Dorcas et al. 1997), and locomotion (Bennett 1980; Hertz et al. 1982, Van Damme et al. 1989, Bauwens et al. 1995), which in turn may influence predator-prey interactions (Greenwald 1974; Christian and Tracy 1981, Bashey and Dunham 1997) and defensive behavior (Hertz et al. 1982, Goode and Duvall 1989, Schieffelin and de Queiroz 1991, Mautz et al. 1992). Ectotherms are particularly sensitive to these effects because they rely on external sources of heat to maintain body temperatures. In the face of changing ambient temperatures and other environmental conditions, poikilothermic ectotherms may experience fluctuating body temperatures, physiological performance, and efficiencies (Huey 1982; Peterson et al. 1993).

The thermal environment can restrict physiological performance by constraining potential body temperatures, thereby limiting growth and reproduction (Huey 1982, Waldschmidt and Tracy 1983, Peterson et al. 1993). For example, environmental temperature may constrain feeding directly by slowing strike speed or indirectly by decreasing the time available for foraging (Grant and Dunham 1988, 1990, Grant 1990, Peterson et al. 1993, Bashey and Dunham 1997, Díaz 1997). The effect of temperature on locomotor performance is especially important because many animals depend on locomotion to escape potential predators, to pursue prey, and fight conspecifics (Mautz et al. 1992, Krebs and Davies 1993). Therefore, regulating body temperature is an important part of a reptile's life, playing a role in physiological, ecological, and reproductive success, which ultimately contribute to the fitness of the

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animal. This apparent link between body temperature and fitness raises the question: how well do reptiles thermoregulate?Physiological processes typically increase in rate with increasing temperature until the rate plateaus at some optimal temperature and declines rapidly thereafter; this pattern is defined as the thermal response curve (Huey 1982). From the response curve, three parameters can be determined: optimal temperature for performance, performance breadth, and critical temperatures. Optimal temperature is the body temperature at which the physiological process is at maximum rate. This is important when determining the significance of the selected temperature range of the animal, the body temperature range the animal would choose if unconstrained by the environment (Huey and Stevenson 1979; Huey 1982). The thermal performance breadth is the range of temperatures over which the animal performs above some arbitrary level, conventionally 80 or 95 percent (Huey and Stevenson 1979; Huey 1982). Performance breadth and optimal temperatures are ecologically relevant measures of performance, indicating temperatures at which the animal performs best (Huey and Stevenson 1979). The upper and lower critical limits are the temperatures at which the animal loses ability to perform the physiological process, which is, in the case of locomotor performance, equivalent to ecological death.

To maintain body temperatures within a selected range that optimizes locomotor capacity (Bennett 1990) and other performance traits, ectotherms may behaviorally control body temperatures by exploiting microhabitat variation in temperature and by postural adjustments, which can affect radiation absorption and exposure to convection (Heath 1965, Peterson et al. 1993). They may also thermoregulate physiologically by changing skin color to alter the absorbance of the skin, thereby changing the amount of radiative heat absorbed (Norris 1967). Reptiles can also change peripheral blood flow (Morgareidge and White 1969) and heart rate (Bartholomew and Tucker 1963), which enables them to heat faster than they cool, thereby reducing the time spent basking (Grigg and Seebacher 1999).

Since Cowles and Bogert (1944) described behavioral thermoregulation in desert reptiles, numerous studies have addressed reptilian thermoregulation. Early studies showed that temperature regulation is a central factor in reptile ecology (Cowles and Bogert 1944; Bogert 1949; Peterson et al. 1993), and most thermal ecology studies have focused on diurnal, heliothermic ectotherms (Huey 1982, Waldschmidt and Tracy 1983, Lichtenbelt et al. 1997, Christian 1998, Brown and Weatherhead 2000).

Traditional methods of earlier studies of ectotherm thermoregulation, such as analyzing the distributions of field-measured body temperatures and interpreting regression slopes of body temperatures on ambient temperatures (Huey and Slatkin 1976), have been criticized (Heath 1964; Hertz et al. 1993).

Examining variance in body temperatures alone is an incomplete description of thermoregulation. Traditionally, a low variance has been interpreted as active thermoregulation to maintain body temperatures within a set-point range, and a high variance suggested thermoconformity. However, these interpretations may be misleading. For example, a non-thermoregulating ectotherm in a homogeneous thermal environment will have a low variance, and an active thermoregulator may have a relatively high variance in a thermally heterogeneous environment (Hertz et al. 1993). In addition, variance only reflects the amount of dispersion or precision of the data points around the mean and is not a correct statistic to use to account for accuracy of thermoregulation relative to a range of selected body temperatures with upper and lower set points (Hertz et al. 1993). The regression slope of body temperature on environmental (air and substrate) temperature has also been used (Huey and Slatkin 1976). Conventionally, a slope near one has been interpreted as thermoconformity and a slope near zero has been interpreted as thermoregulation. However, a single air or substrate temperature is a very incomplete index of true "environmental" temperature, which should integrate long and short-wave radiation, conduction, convection, and evaporation (Hertz et al. 1993; Christian and Weavers 1996, Peterson et al. 1993). Heath (1964) effectively demonstrated such problems with the variance and regression methods by showing that randomly distributed water-filled beer cans had temperature distributions and regression slopes similar to those of presumably thermoregulating, heliothermic lizards. Consequently, when using these techniques, inanimate objects that are obviously not thermoregulating may appear as though they are.

There are many instances in which traditional methods of analyzing thermoregulation have resulted in an inaccurate description of the thermoregulatory patterns of lizards (see Hertz et al. 1993 and Hailey and Coulson 1996). Because of the problems with conventional methods of analyzing ectotherm thermoregulation, improved techniques integrating laboratory and field data should be employed. The question 'how well do reptiles thermoregulate?' actually encompasses a suite of other questions

necessary to describe thermoregulation fully (Hertz et al. 1993; Christian and Weavers 1996): 1) what is the reptile's selected body temperature range and how similar is this to the observed field body temperatures? 2) How precisely does the reptile regulate body temperatures in the field? 3) Over how much of the day do local climate and microhabitat conditions allow the reptile to thermoregulate within the selected temperature range, i.e., what is the opportunity for thermoregulation? 4) How effectively do lizards exploit the environmental opportunity for thermoregulation, i.e., what is the effectiveness of thermoregulation? 5) Are realized body temperatures in the field conducive to optimal performance?

New techniques employ the measurement of operative temperatures to map the thermal environment (Peterson et al. 1993). In the absence of thermoregulation, body temperature will not necessarily equal ambient air temperature (Hailey and Coulson 1996). However, by using biophysical models of an animal, convection, radiation, and conduction are integrated, producing an operative environmental temperature, or the equilibrium temperature that a lizard would achieve in that microhabitat (Bakken 1992). Potential body temperatures available in the environment can be characterized if such models are placed randomly in the environment. These random operative temperatures represent a null model for comparison; i.e., the distribution of expected body temperatures in the absence of thermoregulation (Hertz et al. 1993).

By using operative and body temperatures measured in the field along with thermal preference and performance data obtained in the laboratory (see below), the degree of temperature regulation can be fully characterized (Hertz et al. 1993, Christian and Weavers 1996, Peterson et al. 1993). In essence, accuracy and precision of thermoregulation can be determined by comparing actual body temperatures with the thermal preferences established in the laboratory. The effectiveness of temperature regulation can also be determined, i.e., how close realized body temperatures are to the set point range, relative to the operative temperatures available in the environment. Also, it can be shown how often the environment permits temperature regulation at body temperatures that optimize performance. In addition, the functional importance of thermoregulation can be determined by comparing realized field body temperatures with the temperatures that optimize performance, e.g., locomotion.

Horned lizards (*Phrynosoma* spp.) are interesting subjects for the study of thermoregulation and performance. Despite their impressive variety of thermoregulatory postures and behavior documented by Heath (1965), it has been speculated that horned lizards are, relatively speaking, imprecise thermoregulators (Pianka and Parker 1975; Pianka, 1981). Pianka and Parker (1975) observed a high variance in body temperatures in *P. platyrhinos* relative to sympatric lizards, which may be a result of *Phrynosoma's* rather specialized natural history. Horned lizards are sit-and-wait foragers specializing on small harvester ants, which contain a great deal of indigestible chitin (Pianka and Parker 1975; Pianka 1986). Consequently, large numbers must be consumed, which may necessitate increased activity time over the day to make myrmecophagy economically feasible (Pianka and Parker 1975). This increased activity and foraging in the open may contribute to an increased variance in body temperature because the lizards are active over a large portion of the day and exposed to a large range of environmental temperatures.

To accommodate the large numbers of ants ingested, *Phrynosoma* has a large stomach for its body size and a tank-like body form that may reduce locomotor speed and the ability to escape from potential predators. Therefore, *Phrynosoma* relies on crypsis to escape a predator's detection (Pianka and Parker 1975; Pianka 1986). This lack of a need for fast sprints to escape predators and a broadened time niche required for feeding may reduce the benefits of precise thermoregulation, and may therefore contribute to the increase in body temperature variance observed by Pianka and Parker (1975). As a result of the apparent unimportance of optimal locomotor performance and their unique behavior, anatomy, and diet, horned lizards may not thermoregulate as precisely as other reptiles that are active foragers and that rely on locomotor escape. Additionally, some cryptic lizards are often active at temperatures that are below optimal for sprinting (Hertz et al. 1988). Consequently, for *Phrynosoma*, temperatures maximizing performance may not dominate the range of realized body temperatures over a day.

In this study, I address the following questions: 1) What is the Texas horned lizard's selected body temperature range and how similar is this to observed field body temperatures? 2) How precisely do horned lizards maintain body temperature in the field? 3) Over how much of the day do local climate

and microhabitat conditions (integrated as operative temperatures) allow the reptile to thermoregulate within the selected temperature range? 4) Do horned lizards use the available thermal microhabitats randomly or nonrandomly with respect to availability? 5) Are realized field body temperatures conducive to optimal performance?

Methods

Study Area: Phrynosoma cornutum was studied at the Chaparral Wildlife Management Area (CWMA) in Dimmit and La Salle counties in southern Texas from May through August 1999. The CWMA was purchased by the state in 1969 and is managed by Texas Parks and Wildlife Department. The area is 6,150-ha, composed of 15 pastures with high intensity, short duration rotational grazing from October to May. In addition, a burning regime was implemented in 1997 on a rotational system. Burns ranging in size from 40-80 ha take place every two to three years (Hellgren et al. 2000).

The CWMA is within an area dominated by a mesquite-acacia thornscrub community with varying degrees of vegetative cover. The dominant woody species include honey mesquite (*Prosopis glandulosa*), twisted acacia (*Acacia schaffneri*), blackbrush (*A. rigidula*), granjeno (*Celtis pallida*), guajillo (*A. berlandieri*), brasil (*Condalia hookeri*), and hog plum (*Colubrina texensis*). Common grasses include hooded windmill grass (*Chloris cucullata*), hairy grama (*Bouteloua hirsuta*), introduced buffelgrass (*Cenchrus ciliata*), and introduced Lehmann lovegrass (*Eragrostis lehmanniana*). Common forb species include croton (*Croton* spp.), crown coreopsis (*Coreopsis nuecensis*), lazydaisies (*Aphanostephus* spp.), and verbenas (*Verbena* spp.). Prickly pear cactus (*Opuntia lindheimeri*) is also common on the area (Hellgren et al. 2000).

Characteristic weather conditions are typified by hot summers (mean July temperature = 30.4°C) and mild winters (mean January temperature = 12.5°C). Average annual rainfall is 66 cm (1969-1997; unpublished data, Texas Parks and Wildlife Department). Rainfall peaks in May-June with a smaller peak in September-October (Hellgren et al. 2000).

Selected Temperatures: To determine the selected temperature range (T_{sel}) of *P. cornutum*, a 1.83-m by 0.31-m linear thigmothermal gradient was constructed with a base of 6-mm-thick aluminum covered with

a thin layer of soil from the study site. To provide a smooth heat gradient ranging from approximately 20-50°C, heat lamps were located below to heat the hot end of the gradient. To cool the cold end of the gradient, cool water was circulated through a copper coil there and ice packs were also placed below the cold end. Illumination was provided by overhead fluorescent lights with a photoperiod of 10L:14D.

Ten adult lizards were imported from the study site to the laboratory at Oklahoma State University within two weeks of capture and held without food. To prevent any social interactions, the gradient was divided longitudinally by cardboard and one lizard was introduced to each side. Lizards were introduced into the gradient 12 hours prior to measurements and allowed to habituate. A thermocouple was taped 1-2 cm into the cloaca, and body temperatures were monitored throughout a 48-h period at 4-sec intervals with a Sable Systems TC-1000 digital thermometer interfaced with a computer. Because of data acquisition problems, only three lizards were recorded for a continuous 48-h period. Temperature data obtained from the other seven lizards were at least six 30-min intervals at various times of the day. The 4-sec intervals were condensed into 5-min means and were compiled for all lizards. The selected temperature range was defined as the central 50% of the observations during the active period (0800-2000 h). Lizards were released at the original capture site.

Field Body Temperatures: Lizards were located in May and June in the west region of the South Jay pasture via road cruising and random ground searches. At the time of first capture, body mass, snout-vent length, and sex were determined, and a toe was clipped. A small passive integrated transponder (PIT tag) was inserted into the abdominal cavity for individual identification. Over the course of the study, 19 lizards were fitted with small radio transmitters (150-151 MHz, L&L Electronics, Mahomet, Illinois, USA) enclosed in a small backpack strapped to the back. The whole apparatus weighed 3 g, which was less than 8% of the lizard's mass. All radio tagged animals were located at least once daily, and the following measurements were taken at the site of capture: body temperature (T_b) at the time of capture (with a 32-gauge type T thermocouple inserted 1-2 cm inside the cloaca), time of capture, the shaded substrate temperature, and shaded air temperature at 10 cm above the ground. In addition, any observed activity (such as basking, foraging, any social behavior), and the microhabitat used (such as road, bare

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ground, or brush clump) were noted, as was the proportion of the lizard's body in direct sunlight (shade, 0-20% sun; partial shade, 25-50% sun; partial sun, 55-75% sun; full, 80-100% sun).

Operative Temperatures: To characterize the temperature range available in the environment (to a hypothetical, randomly distributed, thermoconforming lizard), biophysical models were constructed to obtain operative temperature (T_e) data (Bakken 1992). Models were made from thin copper foil sheets molded over a ceramic form of a horned lizard, painted gray (Western Auto Parts, Grey Spray Primer, total reflectance 18.1% according to Peterson et al. 1993) to approximately match the average reflectance of *P. cornutum* (average reflectivity of *P. cornutum* dorsal skin is 20.2% [Hutchison and Larimer 1960]), and fitted with a thermocouple inside the hollow cavity.

The thermal environment was mapped by choosing a starting site and moving the models through the habitat at a random direction and distance. Each placement of the T_e model was determined by first randomly stopping the second hand of a stopwatch to determine the number of paces to be walked. Next, a direction was determined by randomly rotating the compass dial and the set number of paces was walked. Once the model was placed on the ground, the equilibrium temperature of the model was recorded, indicating the integrated environmental temperature of that microhabitat. To obtain data on the availability of thermal microhabitats, the percent sun of the model was recorded. Because field body temperatures were collected over several weeks, I characterized the operative temperature distribution over a similar time period. Therefore, the procedure was repeated over 13 (randomly chosen) days of the study period during randomly chosen, 1-h periods, in which a minimum of 5 temperatures per hour were recorded.

Throughout the study, the minimum and maximum operative temperatures were recorded each day, remotely, every 15 minutes. Maximum available temperatures were estimated by a horned lizard model equipped with the temperature probe from a HOBO data logger on a fully exposed, south-facing surface. Minimum operative temperatures were recorded by burying a HOBO data logger 5 cm under the soil in constant shade on the north side of a small shrub. Because of differences in temperature distributions between days throughout the sampling period, days were divided into hot and cool days

based on minimum operative temperatures. Days were designated hot when minimum T_e exceeded 40°C, which included days between 25 May 1999 through 12 June 1999 and 19 June 1999.

Locomotor Performance: To determine the optimal temperature range conducive to maximal locomotor performance, sprint speed was measured over a range of body temperatures (22- 42°C) on a 2-m racetrack equipped with photocells at 0.25-m intervals. Prior to the trials, food was withheld for at least 24 hours, and each lizard ran the track twice before trials began. As lizards ran down the track, a computer program calculated the successive times (in msec) that the running lizard broke the photocell beams. Each lizard was raced four times per temperature at one temperature per day with a 1-h break between trials. To obtain a particular body temperature, lizards were housed in an incubator before and between trials. The sequence of temperatures was randomized at 30, 42, 34, 22, 26, 40, and 38° C. To perform each trial, the computer program was initiated, a lizard was removed from the incubation chamber, body temperature was measured, and the lizard was quickly placed on the track and gently prodded to initiate running until reaching a black bag at the end of the track. If the lizard would not run or had to be excessively prodded, the data from that run were not included in the analyses. The fastest 0.25-m interval for each lizard at each temperature was used in analyzing performance.

Seven lizards were raced at temperatures 22-40°C, and three lizards were raced at 30-42°C. Because one individual resisted running, it was eliminated from the analyses, resulting in a total of nine lizards. Average sprint speed over all lizards was calculated for each temperature. The three lizards that ran at the higher temperatures ran fastest at 40°C; therefore, relative performance was obtained by dividing average speed at each temperature by the average speed at 40°C. Critical thermal minimum and maximum temperatures for *P. cornutum* (9.5°C and 47.9°C, respectively), obtained from the literature (Prieto and Whitford 1971), were assigned zero speed. A modified minimum polygon method was used to define thermal dependence of sprint speed, resulting in a performance curve (van Berkum 1985), from which performance breadths were determined. Performance breadths are defined as the temperature ranges over which a lizard sprints at least 95% and 80% of its maximum speed.

Additional Analyses: In accordance with traditional methods of analyzing thermoregulation, regression slopes of T_b on environmental temperatures were calculated to determine the influence of T_s and T_a on T_b. Thermoregulation can also be evaluated by testing the prediction that body temperatures will be closer to the selected temperature range than randomly distributed operative temperatures for the habitat (Hertz et al. 1993). Following Hertz et al. (1993), three indices of thermoregulation were calculated from data for all lizards captured. First, the accuracy of thermoregulation (d_b) was indexed using the absolute deviation of each individual body temperature from the T_{sel} to obtain a mean d_b (d_b=0 when all body temperatures are within T_{sel}). Second, the thermal quality of the environment (d_e) was indexed by taking the absolute deviation of each T_e from the range of T_{sel} to obtain a mean d_e (d_e=0 when operative temperatures do not differ from T_{sel}). Third, the effectiveness of thermoregulation (E) was determined by comparing the accuracy of thermoregulation to the quality of the environment with the equation E=1-(mean d_b/ mean d_e). If mean d_b and d_e are similar, E will approach zero, indicating that animals select thermal habitats at random, i.e., do not thermoregulate. If animals thermoregulate effectively, d_b is smaller than d_e and E will approach one. Finally, E will be negative if animals are avoiding thermally suitable habitats.

Results

Selected Body Temperatures in the Thermal Gradient: Body temperatures recorded from lizards in the thermal gradient during the active period exhibited a decidedly bimodal distribution (Figure 1). Examination of all temperatures <29°C (n=217 5-min means) showed that 81% of these records were from a single individual that spent several extended periods (during mornings and evenings) at relatively low temperatures (24.5-28.5°C); during these periods body temperatures changed less than 0.5°C over several hours, and this individual spent other extended periods of time (n=104 5-min means) apparently thermoregulating between 34 and 39°C. Low temperature records were also obtained from five other animals over shorter periods (20-30 continuous min), in most cases in the early morning or late evening. I interpret all of these periods as representing inactive, sleeping lizards, or in one or two cases, possible attempts to escape from the cool end of the gradient. This suggests that horned lizards choose to rest and sleep at lower temperatures than they maintain when active. However, it complicates the calculation of a representative T_{sel} range for comparison to body temperatures of lizards in the field. Because I was primarily interested in analysis of temperatures of active lizards, I deleted from the T_{sel} dataset temperatures from lizards believed to have been inactive in the gradient, which included all body temperatures <29°C. The 5-min means of all nine lizards were combined (excluding temperatures <29°C), resulting in 891 temperature records (Figure 1). The mean selected temperature was 36.3°C +_ 2.39 SD and the central 50% (34.9-38.1°C) was defined as the selected body temperature range.

Field Body Temperatures: Fifty-four individual lizards were captured, of which 19 were fitted with radiotransmitters, resulting in 286 total captures and recaptures. Mean body temperatures were not different between May and June (t-test on residuals of Equation 1 [below], t=1.35, d.f.=284, p=0.18), so data were pooled for both months. Mean T_b was 35.2 ± 3.44 SD °C, with a range of 25.2-41.9°C. The T_b distribution was not normal (Figure 2; Kolmogorov-Smirnov test, p<0.005), but was sharply peaked and

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negatively skewed. Forty-five percent of all measured T_bs were within the T_{sel} range, 19% were above T_{sel}, and 36% were below T_{sel}. T_b varied over the course of the day (Figure 3); lizards' heated rapidly in the morning, plateaued, and then cooled after approximately 1600 h. The best-fit quadratic equation described the data as:

$$T_b = -6.3 + 138.3(time) - 107.5(time)^2 \qquad \text{Equation 1}$$

where $r^2 = 0.52$, $p < 0.0001$, $n = 285$, and where time is expressed as a decimal fraction of 24 h (e.g., 1200 noon=0.5). In general, T_b reached T_{sel} at or after 1000 h and remained within or near the T_{sel} in the afternoon until cooling in the evening.

On cool days, body temperature varied over the course of the day (Figure 5), and corresponded closely to the overall pattern of field body temperatures. The best-fit quadratic equation described the data as:

$$T_b = -14.1 + 167.6 \ (time) - 133.8 \ (time)^2 \qquad \text{Equation 2}$$

where $r^2 = 0.57$, $p < 0.0001$, and $n = 177$. Lizards heated quickly in the morning, peaked at 1500 h, and cooled thereafter. Body temperatures were observed within the preference range from 1000 until 1930 h, approximately 79% of the day. Of all lizards captured on cool days, 46% of T_bs were observed within the T_{sel} range, and only 16% were observed above the T_{sel}. Overall mean d_b of all lizards captured on cool days was 1.56°C.

On hot days, body temperatures also varied over the course of the day (Figure 6). The best-fit quadratic equation described the data as:

$$T_b = 4.3 + 97.0 \ (time) - 69.4 \ (time)^2 \qquad \text{Equation 3}$$

where $r^2 = 0.56$, $p < 000.1$, and $n = 114$. Lizards heated in the morning and did not decline throughout the rest of the activity period. Lizards were observed in the preference range from 0920 until after 2000 h, approximately 88% of the day. Of all lizards captured on hot days, 42% of captures were within the T_{sel} range and 23% were above it. Overall mean d_b of all lizards captured on hot days was 1.45 °C.

Active and Inactive Lizards: Because lizards were located with radiotelemetry, both active and inactive lizards were located. Lizards were designated inactive if buried or non-mobile with eyes closed when

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approached. However, some lizards were immobile when captured but had their eyes open, and these were classified as questionable lizards. Active lizards had significantly higher body temperatures than inactive lizards (t-test on residuals of Equation 1, t=5.68, d.f.=195, p<0.0001). Mean T_b for active and inactive lizards was 35.9 °C ± 3.0 SD and 33.9 °C ± 4.27 SD, respectively. The distribution of T_b of active lizards was marginally different than that of inactive lizards (Kolmogorov-Smirnov two sample test, p=0.045; Figure 2). Active lizards were located in all hours of the day, and 50% of all observations were within the T_{sel}, 22% were above, and 28% were below. Inactive lizards were located at all hours of the day except the 1500 hour, and 44% of all observations were within the T_{sel}, 9% were above, and 47% were below.

Slopes of linear regression models of T_b on T_a of both active and inactive lizards were highly significant (Figures 7 and 8; p<0.0001) and were intermediate between zero and one. The linear regression equation described the relationship of active lizard T_b on T_a as:

$$T_b = 15.7 + 0.62 \ (T_a) \hspace{3cm} \text{Equation 4}$$

where $r^2 = 0.57$, 95% confidence interval of the slope = 0.09, and d.f.= 151. The linear regression equation described the relationship of inactive lizard T_b on T_a as:

$$T_b = 12.4 + 0.66 \ (T_a) \hspace{3cm} \text{Equation 5}$$

where $r^2 = 0.76$, 95% confidence interval of the slope = 0.12, and d.f.= 41. However, quadratic regressions explained more variance than linear models and were also significant (Figures 7 and 8; p<0.0001). The quadratic regression described the relationship of active lizard T_b on T_a as:

$$T_b = -33.3 + 3.7 \ (T_a) - 0.05 \ (T_a)^2 \hspace{2cm} \text{Equation 6}$$

where $r^2=0.62$. The quadratic regression described the relationship of inactive lizard T_b on T_a as:

$$T_b = -43.9 + 4.3 \ (T_a) - 0.06 \ (T_a)^2 \hspace{2cm} \text{Equation 7}$$

where $r^2=0.85$. Body temperatures were usually higher than T_a until T_b approached the T_{sel}, at which point some T_bs were lower than T_a, indicating that lizards sought cooler microhabitats to maintain these temperatures.

The regression of active lizard T_b versus substrate temperature showed the same general relationship, and was also significant ($p<0.0001$, Figure 9). The linear regression equation described the relationship of active lizard T_b on T_s as:

$$T_b = 14.9 + 0.61 (T_s) \qquad \text{Equation 8}$$

where $r^2 = 0.61$, 95% confidence interval of the slope= 0.08, and d.f.= 153. However, a quadratic model was also significant ($p<0.0001$) and described the relationship of T_b on T_s with a higher proportion of the variance explained ($r^2 = 0.68$):

$$T_b = -30.6 + 3.3 (T_s) - 0.04 (T_s)^2 \qquad \text{Equation 9}$$

The relationship of inactive lizard T_b and T_s showed a different pattern. The linear regression slope described the relationship as:

$$T_b = 2.8 + 0.93 (T_s) \qquad \text{Equation 10}$$

where $r^2 = 0.88$, 95% confidence interval of the slope = 0.11, and d.f.= 42. The slope of T_b on T_s of inactive lizards was not significantly different than one, indicating a high dependence of inactive T_b on T_s and, traditionally, thermoconformity (Figure 10). Furthermore, unlike the other three regression lines, a quadratic model did not result in a better fit of the data.

Thermal Quality of the Habitat: Two biophysical models placed in the environment were intended to record the minimum and maximum operative temperatures possible throughout the day on 24 days of the study period. On cool days, during the activity period, models in the sun (maximum operative temperatures) averaged 41.0 °C ± 10.6 SD but routinely exceeded this temperature (Figure 11). Models buried in the shade averaged 31.2 °C ± 4.0 SD. The majority of minimum operative temperatures (T_{min}) fell below the T_{sel} range, and the majority of maximum operative temperatures (T_{max}) were above the T_{sel} range. On cool days, based on average minimum and maximum operative temperatures, lizards were able to achieve T_{sel} from 1000 to 1900 h (Figure 11). Consequently, lizards could regulate within the preference range for nine hours or 75% of the active period. On cool days, inactive lizards were located early in the morning or late in the afternoon; active lizards were located at all times of day (Figure 5).

On hot days, during the activity period, maximum operative temperatures averaged 50.0 °C +_ 12.1 SD and were usually above the T_{sel} (Figure 12). Minimum operative temperature averaged 37.9 °C ± 6.3 SD and were usually above the T_{sel} range. On hot days, based on average minimum and maximum operative temperatures, lizards were able to achieve T_{sel} from 0930 to 1200 h and 1830 to 2000 h (Figure 12). Consequently, lizards could theoretically regulate within the preference range for four hours or 33% of the active period. Active and inactive lizards were located during all periods of hot days (Figure 6).

Operative temperature models were moved randomly through the environment for one hour on each of 13 days of the study period, resulting in 101 temperature readings. Model temperatures ranged from 29.4-70.6°C, and of all readings, only 7% were within the T_{sel} range, and 64% were above (Figure 13). Random operative temperatures varied over the course of the day; they heated in the morning, plateaued in the afternoon with a wide range of high temperatures, and cooled in the evening (Figure 14). Based on this pattern, a randomly moving, thermoconforming lizard would be predicted to achieve body temperatures within the preference range from approximately 0830-1130 h and 1530-1900 h. Consequently, the index of thermal habitat quality d_e varied over the course of the day. Mean d_e increased until the noon hour, at which time it decreased to a low of 1.65°C during the 1800 hour (Figure 4).

Effectiveness of Thermoregulation: Overall, mean d_e was 8.40°C and mean d_b was 1.43 °C, resulting in an overall value of 0.83 for the index of effectiveness (E) of thermoregulation. The daily patterns in mean d_b and d_e (Figure 4) resulted in concomitant temporal changes in E: effectiveness was actually negative during the 0800 hour, after which E increased and remained high over most of the day (Figure 15).

Availability and Use of Microhabitats: Use of thermal microhabitats was compared to microhabitat availability via randomly located lizard models. The distribution of available sunlit areas differed throughout the day (Figure 16); the proportion of shady microhabitats was high in the 0800 hour, and decreased through the afternoon until again increasing during later afternoon. Likewise, the proportion of sunny microhabitats increased, until 1400 at which time the trend was reversed.

Very early and very late in the day, lizards used shady habitats apparently as available. Throughout the rest of the day, lizards used shady habitats more than available, and rarely used sunny habitats, especially in the middle of the day (Figure 17). Overall, lizards used shady microhabitats more than available, and sunny microhabitats less than available (Figure 18; $X^2=42.3$, p<0.001).

Locomotor Performance: Maximal sprint speeds for individuals measured at different temperatures ranged from 0.40 to 1.95 m/sec. In accordance with the minimum convex polygon for creating a performance curve method (van Berkum 1985), the critical thermal minimal and maximal temperatures were assigned zero speed and the remaining relative sprint speeds were plotted against body temperature (Figure 19). Two data points were deleted from the analyses in accordance with the criteria for creating the convex up polygon (van Berkum 1985). The performance curve resulted in an 80% performance breadth (B_{80}) of 29.0-42.9°C, a range of 13.9°C. The 95% breadth (B_{95}) had a range of 6.8°C, spanning temperatures 35.4-42.2°C which includes most of the selected range.

Overall, 91.6% of field body temperatures were within the B_{80}, and 58.9% of T_bs were within the B_{95}. During both hot and cool days, lizard body temperatures were usually within the B_{80} and the B_{95}. With reference to minimum and maximum operative temperature models (Figures 11 and 12), on cool days lizards could achieve temperatures within B_{80} after about 0930 h and within B_{95} after 1000 h and could maintain these temperatures all day. On hot days, lizards could achieve temperatures within B_{80} almost all day, except during the hottest part of the day (1400-1700 h), and within B_{95} after 1000 h, except during the hottest part of the day.

Discussion

Because so much of an ectotherm's life is dictated by its relationship with the thermal environment, it is important to ascertain how precisely the animal regulates body temperature in the field. In this study I collected comprehensive data to describe the relationship of *Phrynosoma cornutum* with its thermal environment. I measured temperatures that the lizards select when unconstrained by the environment, I captured animals in the field to determine actual field body temperatures, I mapped the thermal environment using operative temperature models to determine the range of body temperatures available, and I determined the thermal dependence of sprint speed to determine the importance of body temperature regulation for locomotor performance. Furthermore, this study is different than many other studies of thermoregulation. Because of the cryptic nature of *P. cornutum*, locating individuals was difficult. To facilitate the location of lizards and acquire an adequate sample size, radio transmitters were used and the time span of the study was increased from a matter of days, as in other studies, to months. This allowed me to locate and capture animals in all habitats used at all times of day and integrates their responses to environmental variation over an ecologically meaningful period of time. In addition, I was able to capture inactive lizards in retreat sites that would have otherwise been undetectable.

Selected Body Temperatures: In the laboratory, unconstrained by the environment, active lizards regulated body temperatures within a range of 34.9-38.6°C (T_{sel}, central 50% criterion) and had a mean selected body temperature of 36.3 ± 2.39°C SD. These temperatures are very close to the mean temperatures at which *P. cornutum* shuttles from shade into sun (34.8°C), and from sun into shade (37.5°C) (Heath 1965). Additionally, the preference range for Texas horned lizards in my study population coincides with other studies of *Phrynosoma* spp. In a population in New Mexico, the mean selected temperature range for *P. cornutum* was 37.5-39°C with a mean selected temperature of 38.5°C

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(Prieto and Whitford 1971). This value is slightly higher than the population I studied, which may be a result of postprandial thermophily since the lizards in Prieto and Whitford's study were fed prior to placement into the thermal gradient. *Phrynosoma douglassi* generally has lower body temperatures than *P. cornutum*, (mean selected temperature = 35 °C) (Prieto and Whitford 1971). Other members of the family Phrynosomatidae also show similar mean selected body temperatures, such as *Uma notata* (37.5 °C), *Sceloporus undulatus* (36.3 °C) (Dawson 1975), and *Holbrookia maculata* (35.7 °C) (Hagar 1994). However, *P. cornutum's* T_{sel} is higher than the similarly measured central 50% of observations for other iguanian lizards, such as *Pogona barbata* (summer: 29.2-33.1 °C) (Schauble and Grigg 1998), *Anolis cooki* (29.6-31.6 °C), and *Anolis gundlachi* (24.3-26.1 °C) (Hertz et al. 1993). When comparing thermal preference ranges between studies, caution must be used. All selected body temperature ranges are arbitrary as a result of the investigators' choice of methods and the choice of central bounds for calculation of the preference range (Wills and Beaupre 2000). For example, I conservatively chose the central 50% of all body temperature records as the selected body temperature range. If I had instead chosen the central 70% range (33.7-38.8°C), lower d_b and d_e values would have resulted. Additionally, results may have changed if I had fed the lizards prior to measurements. Reptiles often undergo postprandial thermophily (Dawson 1975, Schall 1977), which would result in different d_b, d_e, and E values (Hertz et al. 1993).

Field Body Temperatures: Documenting precision of thermoregulation in the field has historically entailed measures of central tendency, ranges of field body temperatures, and regression slopes of body temperature on environmental temperatures. I documented a mean field body temperature of 35.2 + 3.4 SD °C (Figure 2). Although lower than some other North American iguanians inhabiting arid areas, such as *Dipsosaurus dorsalis* (40.0 ± 2.3 SD °C), *Urosaurus graciosus* (36.2 ± 1.5 SD °C), *Gambelia wislizenii* (37.4 ± 2.2 SD °C) (Pianka 1986), and *Cnemidophorus* spp. (39.9-40.4°C) (Schall 1977), the mean field body temperature of my population of *P. cornutum* was within the range of mean body temperatures of other phrynosomatids, such as *Sceloporus merrriami* (32.2 ± 2.1 SD °C) (Grant and Dunham 1988), *Uta stansburiana* (35.3 ± 2.4 SD °C), *Uma scoparia* (37.3 ± 2.2 SD °C), and *Callisaurus draconoides* (39.1 ±

2.6 SD °C) (Pianka 1986). Furthermore, mean field body temperature of my population of *P. cornutum* was consistent with other studies of *Phrynosoma* spp. For example, Brattstrom (1965) documented *P. cornutum* as having a mean field body temperature of 35.7°C, and Pianka (1986) documents *P. platyrhinos* as having a mean of 34.9 ± 3.2 SD °C. Christian (1998) showed a mean of 35.5 +_ 2.8 SD °C in a montane population of *P. douglassi* of western Texas, which is higher than populations of *P. douglassi* in Alberta, Canada (32.1 ± 3.6 SD °C) (Powell and Russell 1985), and in Idaho (33.4 +_ 4.4 SD °C) (Guyer and Linder 1985).

Horned lizards have been documented to experience wide ranges of field body temperatures. For example, I documented a range spanning 25.2-41.9°C. Likewise, Powell and Russell (1985) found a wide range of field body temperatures (18.5-38.5°C) in their population of *P. douglassi*, and Christian (1998) showed a range of 25.4-40.7°C in another. Similarly, *Phrynosoma* spp. have been documented to have consistently larger standard deviations in mean field body temperature than other phrynosomatids (compare data above).

Traditionally, a large range in field body temperature in a thermally heterogeneous environment has been interpreted as imprecise thermoregulation. Pianka and Parker (1975) speculated that horned lizards are imprecise or relaxed thermoregulators due to their wide range of body temperatures. Considering *P. platyrhinos*, Pianka (1986) stated that decreased movement and the extensive amount of time that the lizards must stay active to forage sufficiently contributes to this high variance in body temperature, and presumably imprecise thermoregulation. However, the population of *P. cornutum* I studied did not follow this scenario; although I observed a wide range of field body temperatures and a higher standard deviation than some other phrynosomatids, these lizards were very capable at finding and exploiting thermally suitable microhabitats and maintaining selected body temperature in a very unsuitable environment; they were very effective thermoregulators. I conclude that the wide range results from two factors. First, the relatively wide preference range may result in a relatively wide range of body temperatures seen in the field, even though this population of horned lizards were regulating within the selected range. Second, temperature varied according to a daily pattern (Figure 3). Body temperatures differed early and late in the day, but within any given hour there was much less variation.

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Similarly, a population of *P. douglassi* had a standard deviation of almost twice that of sympatric *Sceloporus graciosus* because *P. douglasii* were captured during morning and evening hours when few *S. graciosus* were captured (Guyer and Linder 1985).

Horned lizards undergo a regular series of behavior each day (Heath 1965). They arise at or before sunrise regardless of temperature, and as the sun strikes the substrate, horned lizards begin to bask by orienting toward the sun. When the substrate heats, the lizards flatten themselves against it to maximize conductive heating. Once high body temperatures were obtained in the afternoon, during the hottest part of the day, burrowing occurrs. Horned lizards then emerge in late afternoon and shuttle between sun and shade, and activity ends in late evening. These generalizations correspond closely to the activity pattern seen in my study population. I found that body temperatures in early morning hours were below the preference range, as indicated by high d_b values. Lizards then were not found in the most thermally suitable areas available, as indicated by negative effectiveness values (Figure 15). At these times, most lizards were still buried in a tuft of grass or a shallow layer of soil from the night before and had not yet emerged. In early morning, such sites did not afford opportunities to raise body temperature like habitats in the open, exposed to solar radiation. After emerging in the morning, lizards heated quickly, and the average deviation of body temperature from the selected body temperature range (d_b) decreased and remained low throughout the day, indicating that the animals remained close to the preference range. Christian (1998) and Guyer and Linder (1985) demonstrated very similar patterns over the day in their populations of *P. douglassi*, in which body temperatures were below the preference range in the early morning, but rose and remained within the preference range throughout the day until late in the evening. A similar daily pattern is seen in other lizards as well, such as *Sceloporus merriami* (Grant 1990).

As a result of this time-of-day effect, the overall (time integrated) mean and standard deviation are not good indicators of the precision of thermoregulation. A more relevant measure is the percentage of body temperatures that fall within the selected body temperature range (Hailey and Coulson 1996). Overall, 45% of all body temperatures were observed within the selected body temperature range and few

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were above it (19%). Thus, lizards were usually within or below the preference range and seldom reached the much higher temperatures that were prevalent in their environment.

The daily pattern of body temperatures differed slightly between cool and hot days (Figures 5 and 6). On cool days, lizards were found in the preference range from approximately 1000 until 1930 h; earlier and later, lizards were found below the preference range. Lizards also declined to below the preference range earlier in the evening than on hot days. Interestingly, inactive lizards were found only early and late in the day. Unlike on hot days, none were found inactive during midday, indicating that inactivity was not essential on these days to escape high temperatures.

On hot days, lizards heated, plateaued, and remained in the preference range until 2000 h. Inactive lizards were found mainly in the middle of the day (1200-1830), usually buried in retreat sites within the preference range, presumably escaping the midday heat out in the open. Lizards were found within the preference range earlier and later than on cool days, and despite the extremely high environmental temperatures during midday, lizards were found in the preference range almost all day. Although a higher proportion of body temperatures were above the preference range on hot days than on cool days, d_b values were actually lower on hot days, indicating body temperatures deviated less, on average, from the preference range. These data show the significance of microhabitat selection (see below) and inactivity during hot periods.

I also determined the relationship between field body temperature and environmental temperatures. Body temperatures of both active and inactive lizards were more similar to substrate temperatures than air temperatures, as indicated in Figures 7-10 by their closer proximity to the isotherm. Furthermore, it has been shown that *P. cornutum*'s thermoregulatory patterns are more dependent on substrate temperature (Heath 1965). In general, body temperatures of active lizards were usually above air and substrate temperatures, indicating the use of solar radiation as a heat source to approach the thermal preference range. Once selected temperatures were met, lizards found cooler microhabitats that were within their preference range.

Linear regression slopes of active lizard body temperatures on air and substrate temperature were intermediate between zero and one, indicating that active lizards were neither absolute

thermoconformers nor perfectly precise thermoregulators. Other populations of *Phrynosoma* spp. show the same trends. In a population of *P. douglassi*, body temperatures were usually above air and substrate temperatures, and body temperatures were highly dependent on substrate temperatures rather than air temperature (Powell and Russell 1985). These authors also concluded that horned lizards in their population were neither strict thermoregulators nor thermoconformers. Pianka (1986, appendix D) lists several relationships between body temperature and air temperature for North American desert lizards, in which many show neither strict thermoconformity nor thermoregulation, including *P. platyrhinos* (slope = 0.40), *Callisaurus draconoides* (0.41), *Sceloporus magister* (0.34), *Coleonyx variegatus* (0.76), and *Xantusia vigilis* (0.71). However, he also provided two examples of lizards in which the slopes indicate body temperature is almost independent of air temperature: *Uta stansburiana* (slope = 0.02) and *Uma scoparia* (0.07).

In the population of horned lizards I studied, inactive lizards showed a different relationship than active lizards. Body temperatures of inactive lizards were highly dependent upon substrate temperature, and the slope was not different than one, indicating strict thermoconformity. Lizards' body temperatures were usually within the body temperature preference range and rarely exceeded it. This pattern of body temperature selection via retreat site selection suggests a form of 'passive' thermoregulation. Lizards usually chose areas hidden under vegetation or buried underground, and apparently chose these sites in part based on their thermal properties (seemingly, substrate temperature). This form of passive thermoregulation by selection of retreat sites has been documented in other ectotherms, such as garter snakes (*Thamnophis elegans*), which chose intermediate-sized rocks with adequate thermal properties, and as a result stayed in their selected body temperature range for long periods of time despite inactivity (Huey et al. 1989). Broad-headed snakes (*Hoplocehalus bungaroides*) selected retreat sites that were thermally suitable and thus were able to attain body temperatures within the preference range for most of the day while passing up opportunities to thermoregulate on the surface, presumably because of other costs involved with basking in the open (Webb and Shine 1998). The gecko *Christinus marmoratus* has also been shown to select retreat sites that were closer to the performance range than null models (Kearney and Predavec 2000).

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Regulating body temperature while inactive, buried in vegetation or underground, may have advantages and may also reduce costs associated with basking in the open. There are many predators of horned lizards in this area of southern Texas, including snakes and birds; for example, roadrunners (*Geococcyx californianus*) were observed in high density and are known predators of horned lizards. Additionally, lizards incur an increased expenditure of energy while active (Huey and Slatkin 1976). However, there are also costs associated with periods of inactivity, at which times these lizards were not involved in social interactions or foraging (Pianka 1986).

Thermal Quality of the Habitat and the Effectiveness of Thermoregulation: Ectotherms living in thermally harsh environments are constrained to certain activity periods and microhabitats (Grant and Dunham 1988, Grant 1990, Bashey and Dunham 1997, Díaz 1997). Undeniably, the thermal habitat in my study area of southern Texas is very harsh. Over the day, operative temperatures are often high, and usually higher than the animals' critical thermal maximum (Figures 11 and 12). As environmental temperatures rose throughout the day, the average deviation of operative temperatures from the selected temperatures (d_e) also increased. However, even during the hottest periods of the day, lizards usually remained within their thermal preference range despite these poor conditions (Figures 3- 6).

Compared to randomly placed operative temperature models, lizards were very adept at finding thermally suitable habitats. When the models indicated very few optimal habitats, lizards routinely found cooler sites, even though they were restricted to inactivity. Lizards could find adequately cool habitats at midday when operative temperatures were high, and they were able to maintain temperatures within the preference range for most of the day even during hot days (Figure 6).

The frequency distributions of operative temperatures and body temperatures were also very different, another indication that these lizards were actively thermoregulating (Figures 2 and 13). Operative temperatures ranged extensively and were usually above the selected body temperature range. Wills and Beaupre (2000) outline a randomization method to compare the two distributions statistically, but in this case visual inspection seems sufficient to make the point.

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When comparing accuracy of thermoregulation and habitat quality, overall, these horned lizards were effective thermoregulators (E=0.82) relative to other lizard populations. For example, Díaz (1997) showed two populations of *Psammondromus algirus*, a medium-sized lacertid lizard, thermoregulates with high effectiveness (E=0.9). Hertz et al. (1993) refer to *Anolis cooki* as a "moderate" thermoregulator with effectiveness values ranging from 0.38 in the summer to 0.67 in the winter. In the same study, *Anolis gundlachi* is described as a nonregulator because of low effectiveness values ranging from 0.0-0.21.

Effectiveness was actually negative during the 0800 hour, and increased after 1000 h and stayed high throughout the day until declining slightly in the evening as lizards became increasingly more inactive. Brown and Weatherhead (2000) show a similar pattern in *Nerodia sipedon*. These water snakes were moderate thermoregulators with an overall effectiveness of 0.48; hourly E decreased overnight to negative values in early morning and then rose throughout the day.

Surprisingly, on hot days, horned lizards are able to remain within the preference range and are able to thermoregulate effectively. Lizards were theoretically able to thermoregulate for longer periods of time on cool days (75% of the day) than on hot days (33%). On cool days, the minimum and maximum operative temperatures dictated that lizards should be able to thermoregulate from 1000 until 1900 h. Hot days averaged much higher maximum and minimum operative temperatures than cool days, and even minimum temperatures were usually above the preference range, especially at midday. On hot days, these operative temperatures dictated that lizards should be able to thermoregulate only from 0920 until 1200 h and 1830 until 2000 h, during which time active lizards were found within the preference range despite the extreme environmental temperatures.

This population of lizards inhabits a very heterogeneous habitat with a wide range of thermal microhabitats available. On a given day a lizard could potentially experience a range of body temperatures from approximately 29-70°C as indicated by the randomly placed operative temperature models. However, actual body temperatures were often lower than 29°C, indicating that the models were not sampling all of the available microhabitats. In any case, if these lizards were thermoconformers we

would see a much wider, more variable range of body temperatures. Faced with such high operative environmental temperatures, how did members of this population thermoregulate so effectively?

Habitat Selection: Like other lizard species, the chief reason for the difference between the distributions of body temperature and operative temperature was that horned lizards selected thermal microhabitats. For example, *Podarcis hispanica* thermoregulates very effectively (E=0.95), primarily via habitat selection (Bauwens et al. 1996). My study population of *P. cornutum* showed a similar pattern. The relatively narrow range of body temperatures in the field (when compared to operative temperatures) was a consequence of thermal habitat selection. Lizards used proportionately different sun exposures than were available (Figure 18). During the early morning, lizards used sun exposure in proportion to what was available, but, like Heath (1965), I showed the use of less sunny areas through morning and increased use of shade (Figures 16 and 17). Throughout the rest of the morning and afternoon, lizards used thermal habitats non-randomly, in that they used less sunlit habitats and more shaded habitats than were available, presumably to reduce heat loads and to keep body temperatures from rising and exceeding the thermal preference range. Furthermore, lizards used shady areas most during all periods of the day, in contrast to other studies in which horned lizards were found most often in open areas (Heath 1965, Pianka and Parker 1975, Powell and Russell 1985, Christian 1998). (This disparity probably is a result of my use of telemetry and the consequent ability to find cryptic, inactive lizards, rather than relying on fortuitous captures that would yield just active lizards in the open.) Once environmental temperatures increased, especially on hot days, lizards became increasingly more inactive and thermoregulated passively by choosing thermally suitable retreat sites.

Implications for Performance: The act of regulating body temperature reduces exposure to thermally lethal or critical temperatures and optimizes performance parameters (Dawson 1975). Presumably, selected body temperatures and temperatures that optimize most performance characteristics coincide (Bauwens et al. 1995; Garland 1999). Temperatures that optimize performance may even be a better

reference to judge accuracy of thermoregulation and thermal quality of the habitat than the preference range itself (Díaz 1997).

Horned lizards are very slow sprinters in the field and were easily caught by hand. Lizards rarely ran too fast for me to capture them. Once a lizard was approached it usually remained stationary, and a few sprinted short distances for cover under the nearest shrub or cactus. However, these lizards were difficult to convince to run in the lab, perhaps because of their typical reliance on crypsis rather than locomotory escape. Members of this population were also slow sprinters (0.40-1.95 m/sec) compared to other *P. cornutum* (2.18m/sec) that were measured on a high-speed treadmill (Bonnie and Garland 1999); however, Zani (1996) reported a maximal speed of 1.06 m/sec on a hardwood track. Other species of *Phrynosoma* such as *P. modestum* (1.45m/sec) and *P. mcallii* (1.60 m/sec) are slow as well (Bonnie and Garland 1999). In any case, these speeds are lower than other phyrnosomatids, such as *Sceloporus merriami* (2.10 m/sec) (Huey et al. 1990), *Uta stansburiana* (2.55 m/sec), *Holbrookia maculata* (3.12 m/sec), *Cophosaurus texanus* (4.57 m/sec), and *Callisaurus draconoides* (5.72 m/sec) (Bonnie and Garland 1999). Additionally, the 80% performance breadth of my study population of *Phrynosoma cornutum* spanned 13.9°C, which is wide to relative to other species, such as *Anolis carolinensis* (10.7°C), *Cnemidophorus tigris* (13.1°C) (van Berkum 1988), *Sceloporus merriami* (9.9°C) (Huey et al. 1990), and *Amevia festiva* (10.1 °C) (van Berkum 1986). Huey et al. (1989) calculated the mean 80% performance breadth for 13 species of diurnal lizards as 12.3 °C.

This population of *P. cornutum* has a wide performance breadth, and it thermoregulates within this range very effectively. Hertz et al. (1988) concluded that, in general, active lizards thermoregulate carefully in order to reserve the potential for performing at maximum. The preference range (34.9-38.1°C) was well within the 80% performance breadth (29.0-42.9°C), so by regulating within the preference range, lizards were able to maintain performance at least 80% of the maximum. I found that lizards regulated body temperatures within the 80% performance breadth almost all day, indicating these lizards maintained the potential for near-maximal sprint speed most of the time even though they were reluctant to run.

Conclusions: In conclusion, I showed that lizards of this population of *P. cornutum* were precise thermoregulators, and had to be in such a thermally harsh environment. Even though environmental temperatures were hot, selected body temperatures and mean field body temperatures were comparable to other phrynosomatids. As temperatures rose to above critical and lethal temperatures throughout the day, lizards found suitable sites, even cooler than the random models suggested were available. Active and inactive lizards were able to thermoregulate effectively throughout the day via habitat selection. Horned lizards became increasingly more inactive over the midday period to avoid the heat, nevertheless remaining in the preference range nearly at all times. As a result of microhabitat selection, effectiveness of thermoregulation was very high throughout the day. Additionally, horned lizards of this population were able to maintain the potential for optimal locomotion by regulating body temperature within the preference range.

Armed with just traditional methods of analyzing thermoregulation, one may come to incomplete conclusions. The relatively high standard deviation and regression slopes of body temperatures on ambient temperatures suggest that horned lizards are only moderate thermoregulators, however after considering additional information including the thermal preference range, operative temperatures, and the performance breadth, a more complete picture is created.
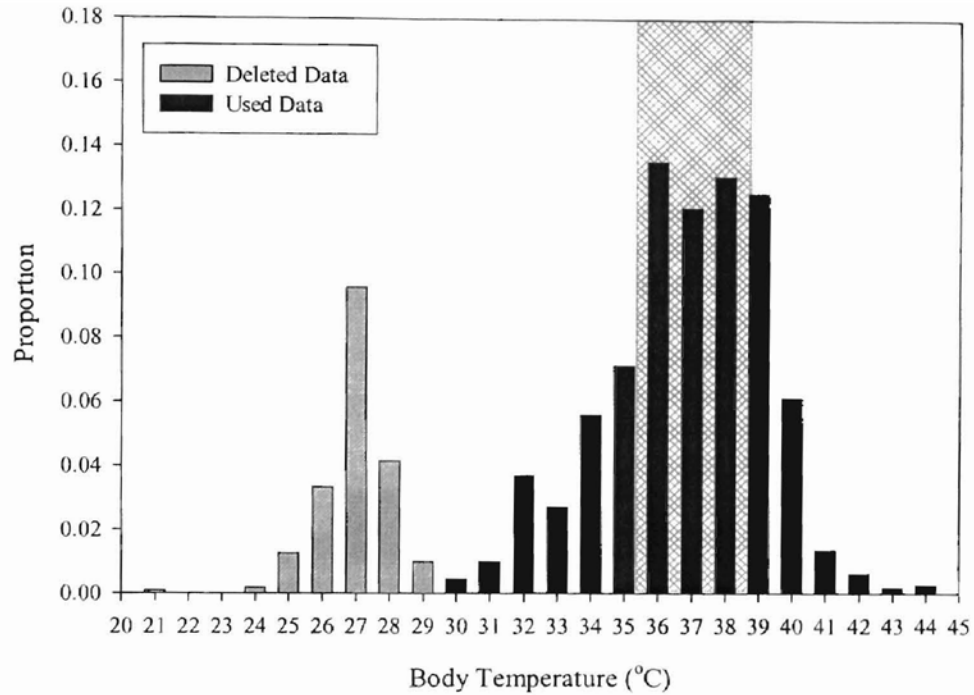
Figure 1. A histogram of all 5-min mean body temperatures selected by *Phrynosoma cornutum* in a thermal gradient. Hatched bars represent deleted data from lizards deemed inactive. Solid bars represent presumably active lizards, and also the data used for the calculation of the preferred body temperature range. The shaded area indicates the central 50% of selected body temperatures; i.e. T_{sel}. Note in all histograms, bins contain temperatures $\leq$ the indicated temperature (e.g. the bin for $30^{\circ}C$ includes temperatures from $29.01\text{-}30.00^{\circ}C$).
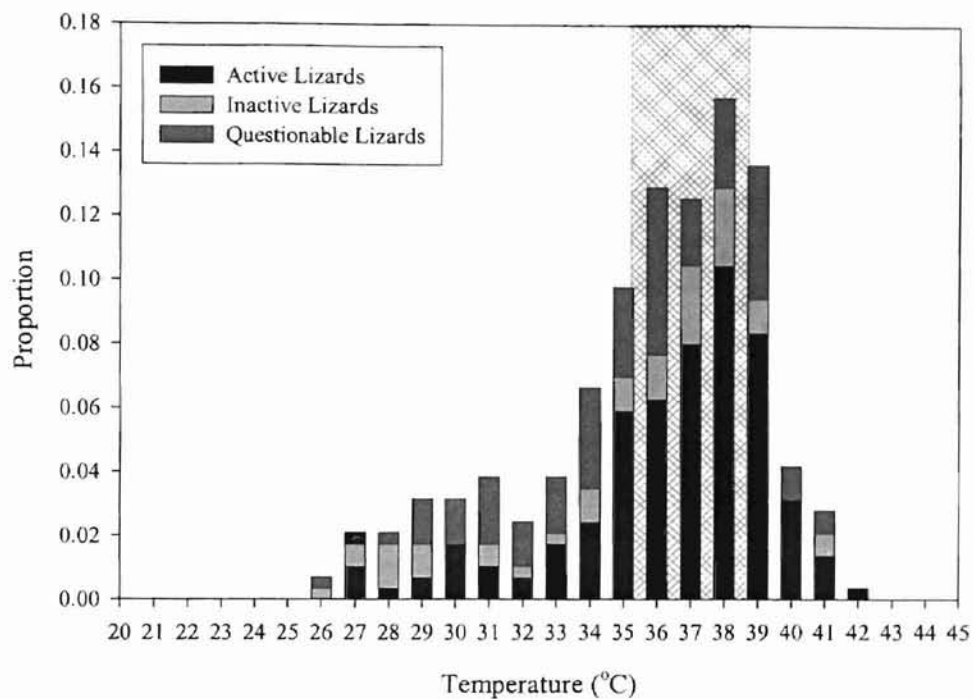
Figure 2. A histogram of body temperatures of all lizards caught during the study period. Active, inactive, and lizards of uncertain-activity are denoted accordingly. The shaded area indicates T_{sel} as indicated above. Note in all histograms, bins contain temperatures ≤ the indicated temperature (e.g. the bin for 30°C includes temperatures from 29.01-30.00°C).
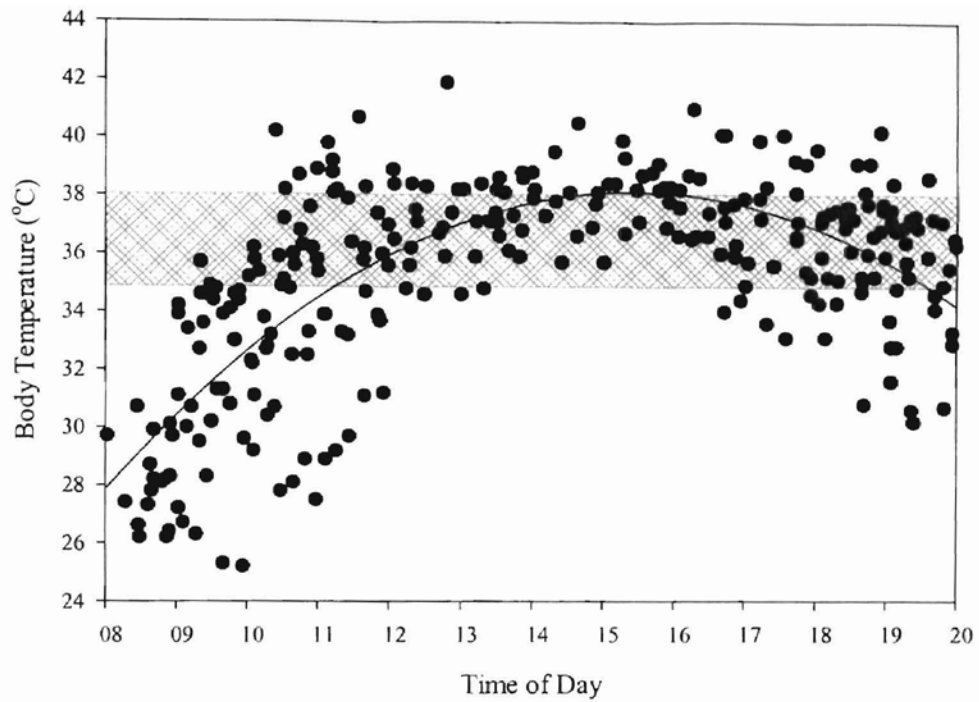
Figure 3. The relationship of body temperature and time of day for all lizard captures (active, inactive, and questionable-activity). The solid line indicates the best-fit quadratic curve (see equation 1 in the text). The shaded area indicates T_{sel}.
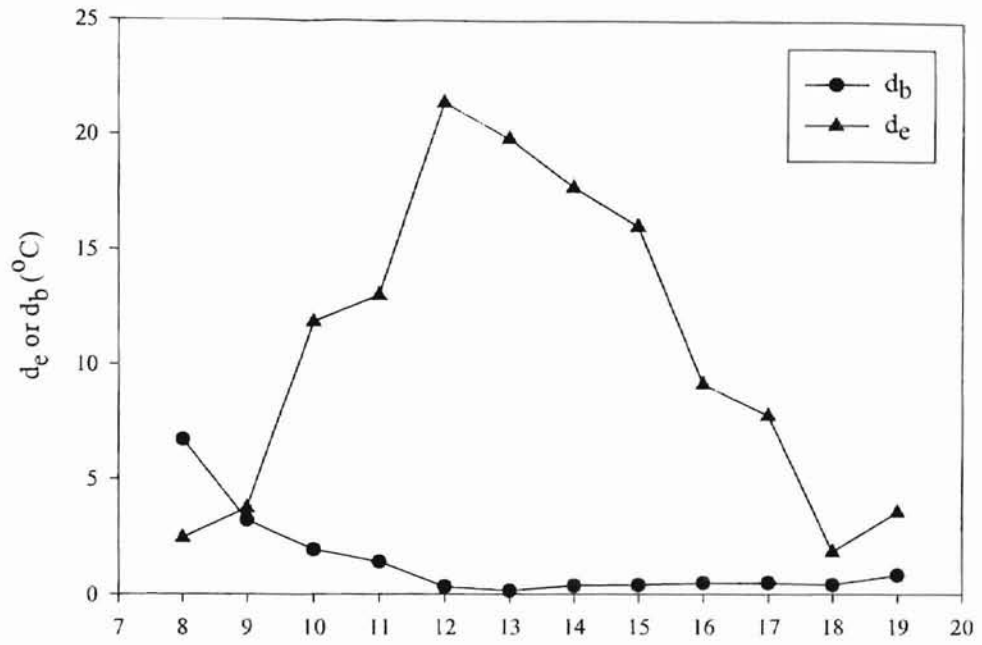
Figure 4. Hourly deviation of body temperature (•) and operative temperature (▲) from the preferred temperature range. Note data are pooled over the study period into hours of day to represent one day.
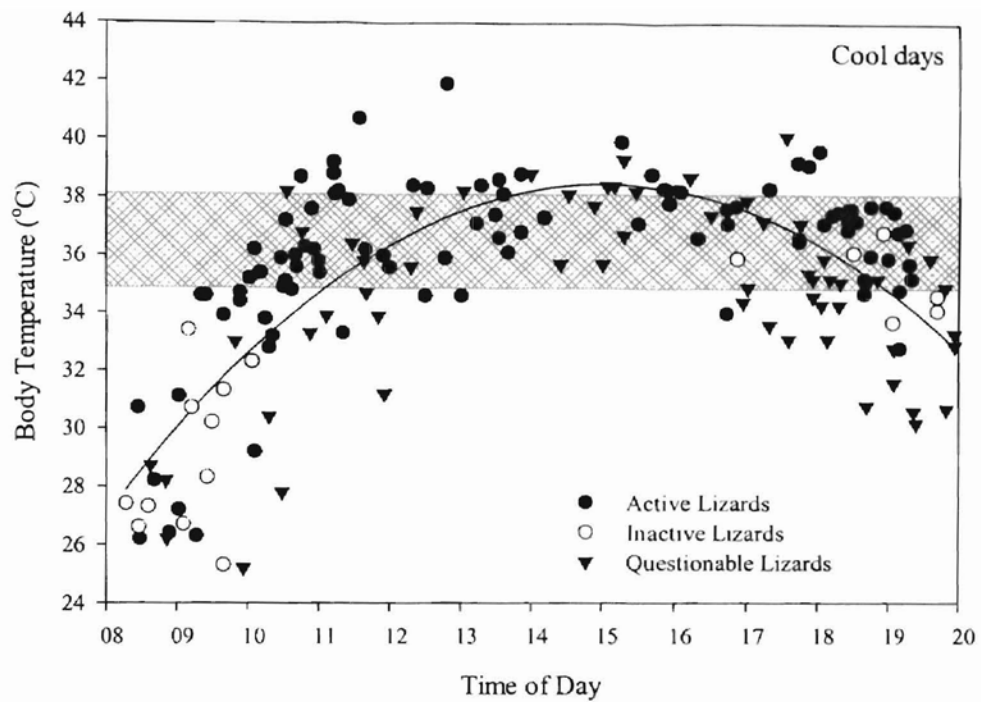
Figure 5. The relationship of body temperature and time of day for cool days. All data are included (active, inactive, and questionable). The solid line indicates the best-fit quadratic curve (see equations 2 and 3 in the text). The shaded areas indicate T_{sel}.
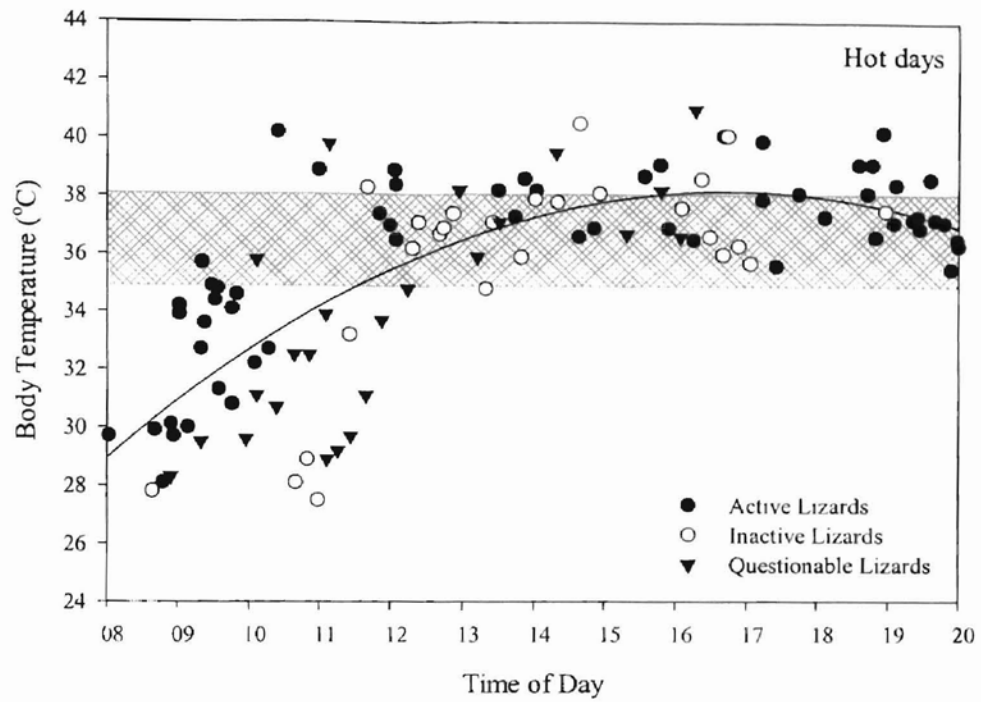
Figure 6. The relationship of body temperature and time of day for hot days. All data are included (active, inactive, and questionable). The solid line indicates the best-fit quadratic curve (see equations 2 and 3 in the text). The shaded areas indicate T_{sel}.
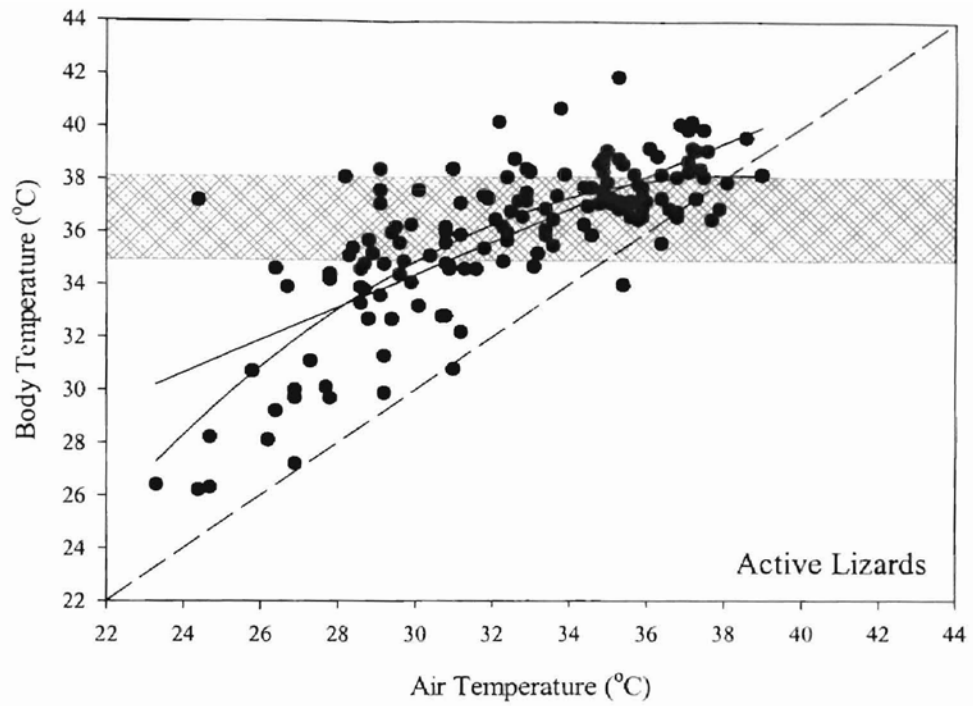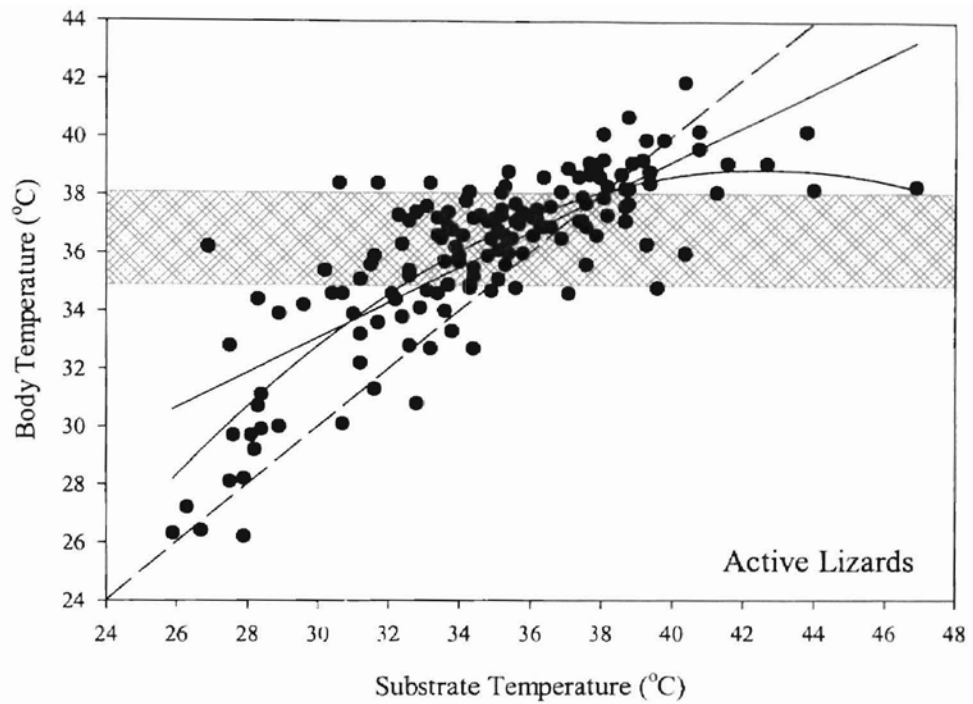
Figure 7. The relationship of body temperature and air temperature of active lizards. The solid lines represent linear and quadratic regressions (see equations 4 through 7 in the text). The shaded area indicates T_{sel}, and the dashed, diagonal line represents the isotherm.
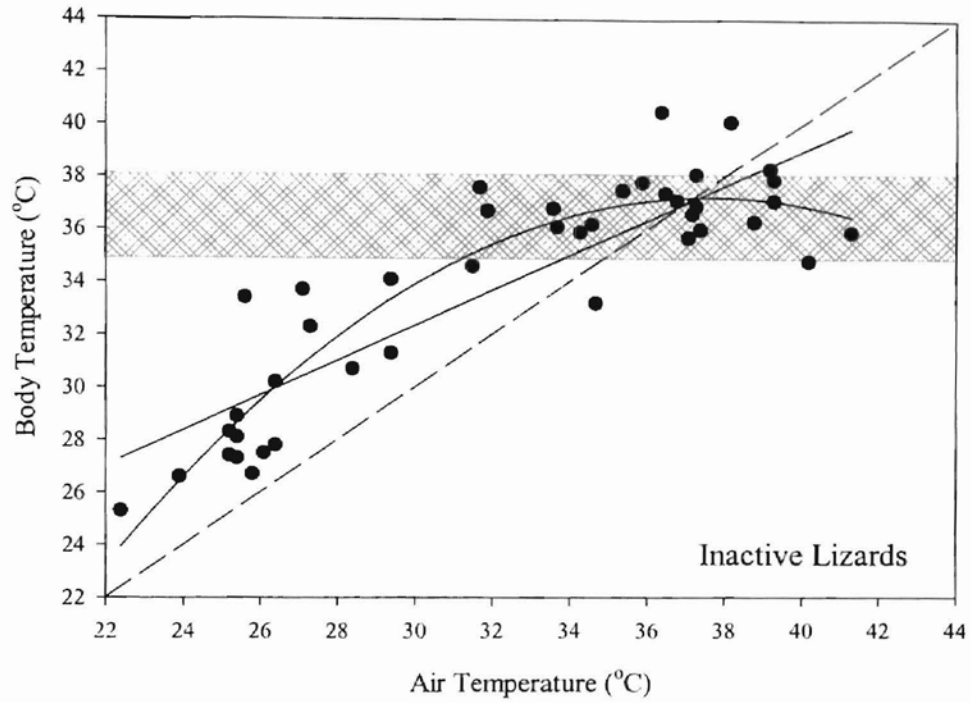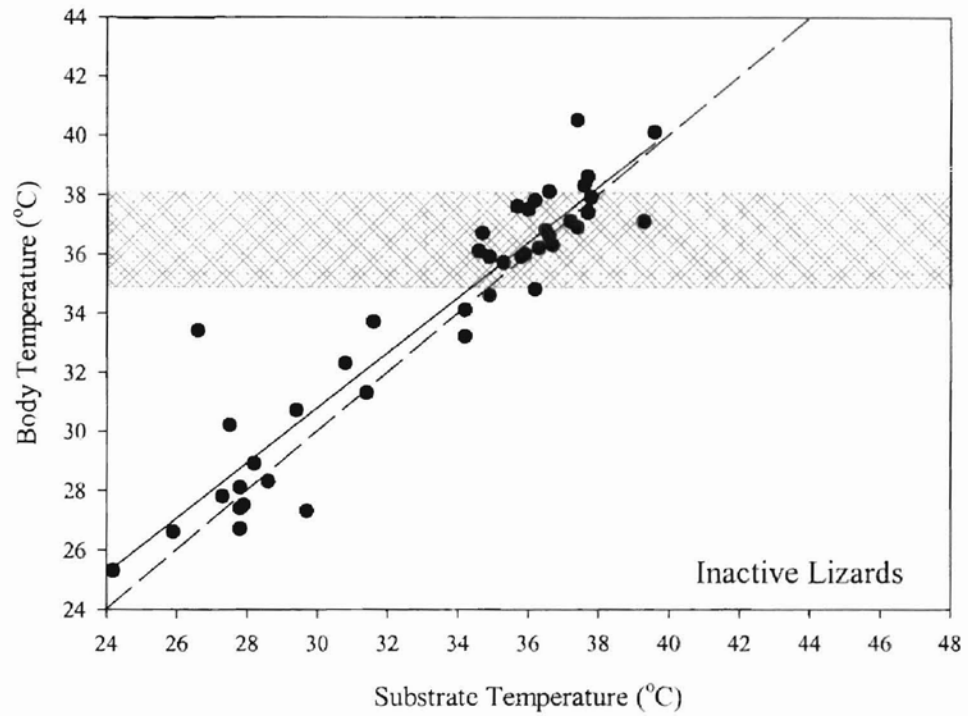
Figure 8. The relationship of body temperature and air temperature of inactive lizards. The solid lines represent linear and quadratic regressions (see equations 4 through 7 in the text). The shaded area indicates T_{sel}, and the dashed, diagonal line represents the isotherm.

Figure 9. The relationship of body temperature and substrate temperature of active lizards. The solid lines represent linear and quadratic regression (see equations 8 through 10 in the text). The shaded area indicates T_{sel}, and the dashed, diagonal line represents the isotherm.
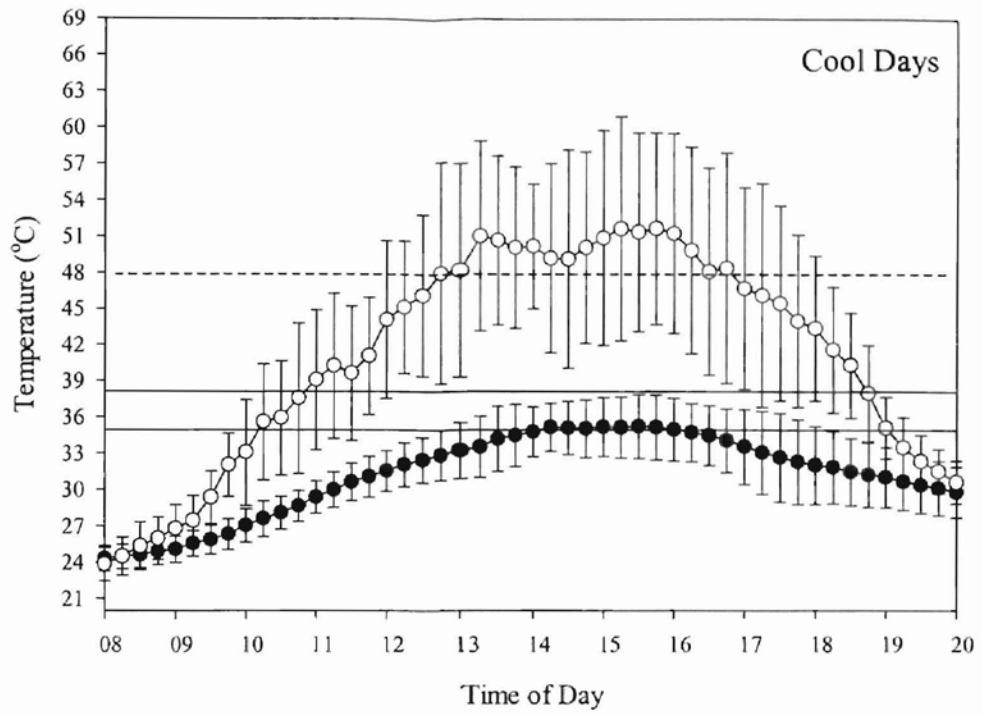
Figure 10. The relationship of body temperature and substrate temperature of inactive lizards. The solid lines represent linear and quadratic regression (see equations 8 through 10 in the text). The shaded area indicates T_{sel}, and the dashed, diagonal line represents the isotherm.

Figure 11. The daily variation of minimum ($\bullet$) and maximum ($\circ$) operative temperature models on cool days. The data represent mean temperatures at 15-min intervals with error bars of one standard deviation. The horizontal bars represent T_{sel}. The dashed line represents the critical thermal maximum (Prieto and Whitford 1971).
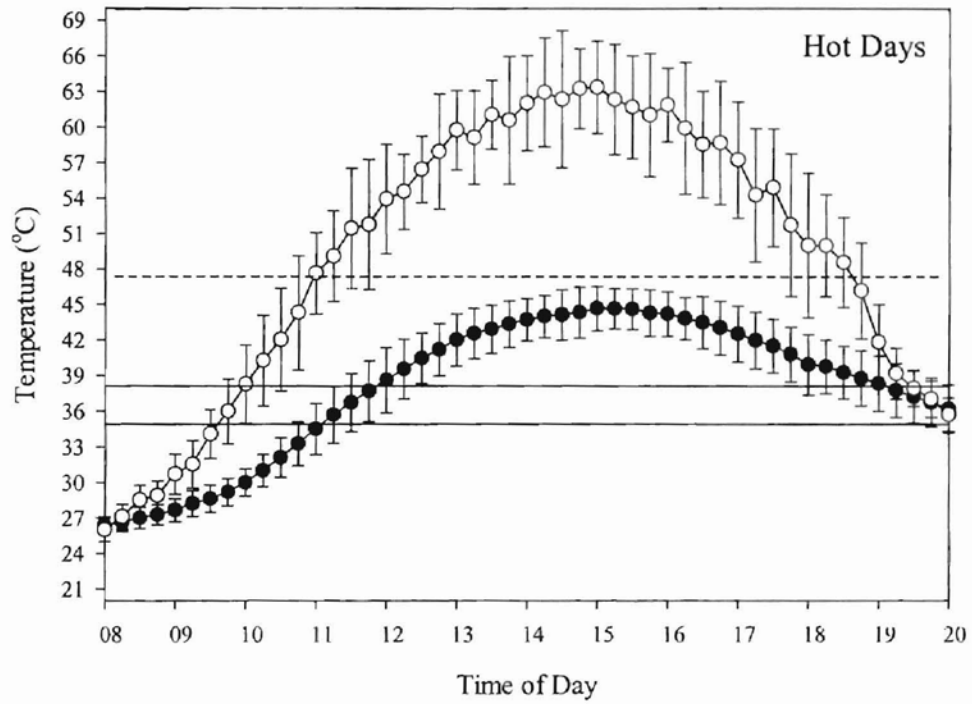
Figure 12. The daily variation of minimum (●) and maximum (○) operative temperature models on hot days. The data represent mean temperatures at 15-min intervals with error bars of one standard deviation. The horizontal bars represent T_{sel}. The dashed line represents the critical thermal maximum (Prieto and Whitford 1971).
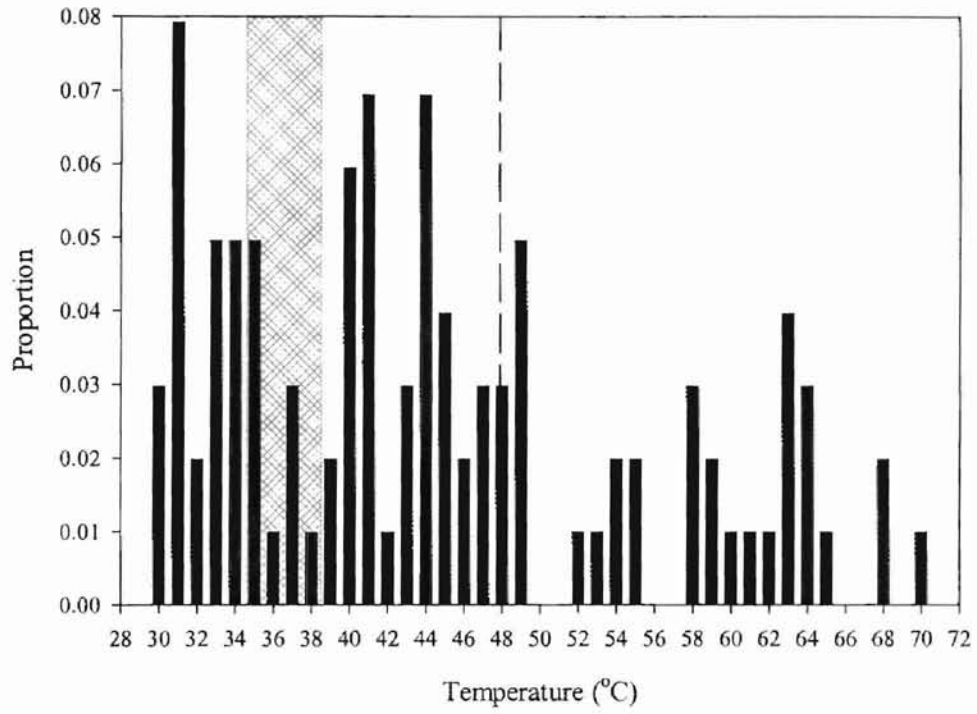
Figure 13. A histogram of all randomly placed operative temperature models during the study period. The single vertical gray bar indicates T_{sel} as indicated above. The dashed vertical line represents the critical thermal maximum (Prieto and Whitford 1971). Note in all histograms, bins contain temperatures $\leq$ the indicated temperature (e.g. the bin for $30^{\circ}C$ includes temperatures from $29.01\text{-}30.00^{\circ}C$).
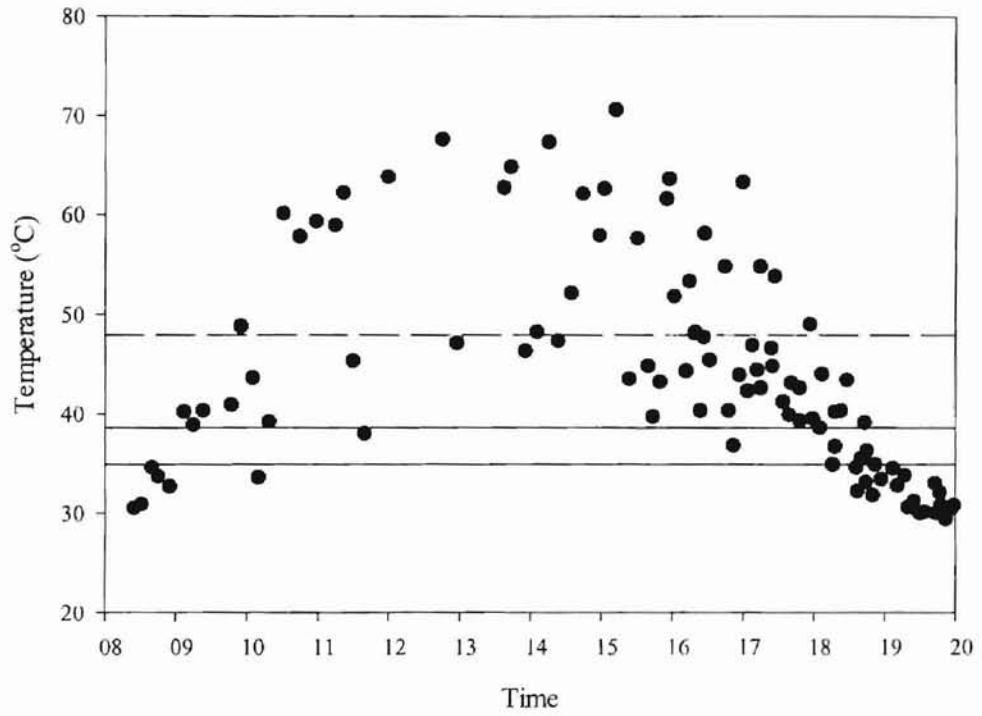
Figure 14. A scatter plot of operative temperatures of all randomly placed models over time of day. The horizontal bars represent T_{sel}. The dashed line represents the critical thermal maximum (Prieto and Whitford 1971).
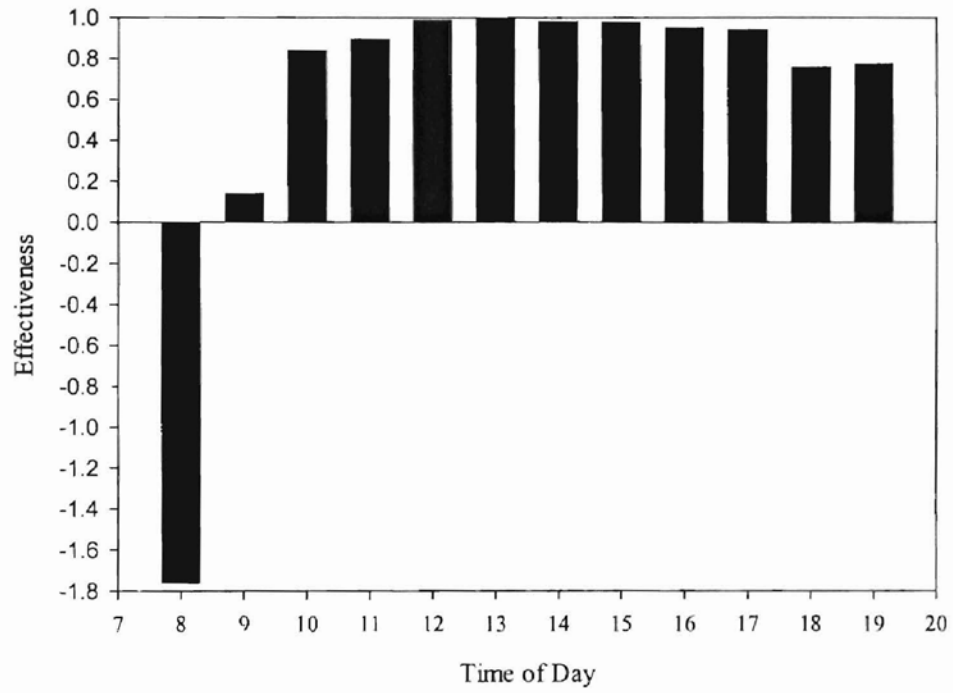
Figure 15. Hourly effectiveness of thermoregulation. Note data are pooled over the study period into hours of day to represent one day.
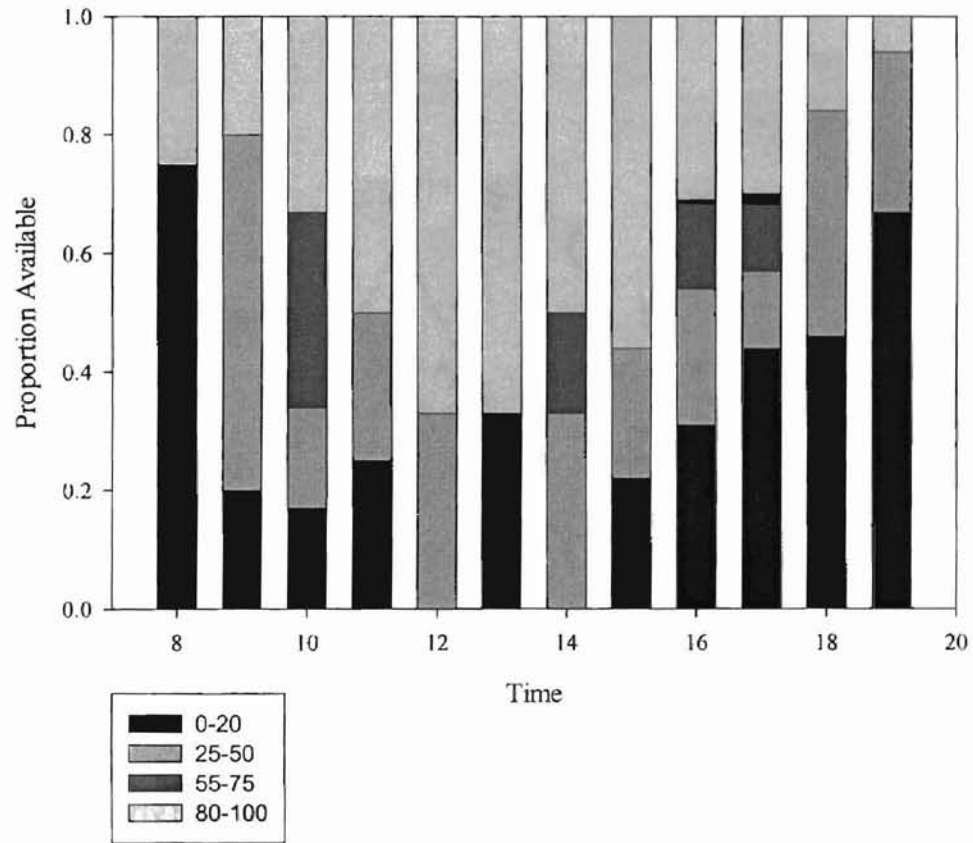
Figure 16. Hourly proportions of sun/shade microhabitats available to lizards over the day. Percent sun categories are indicated. Note 0-20% sun indicates lizards in relatively shady microhabitats; conversely 80-100% sun indicates lizards in relatively sunny microhabitats.
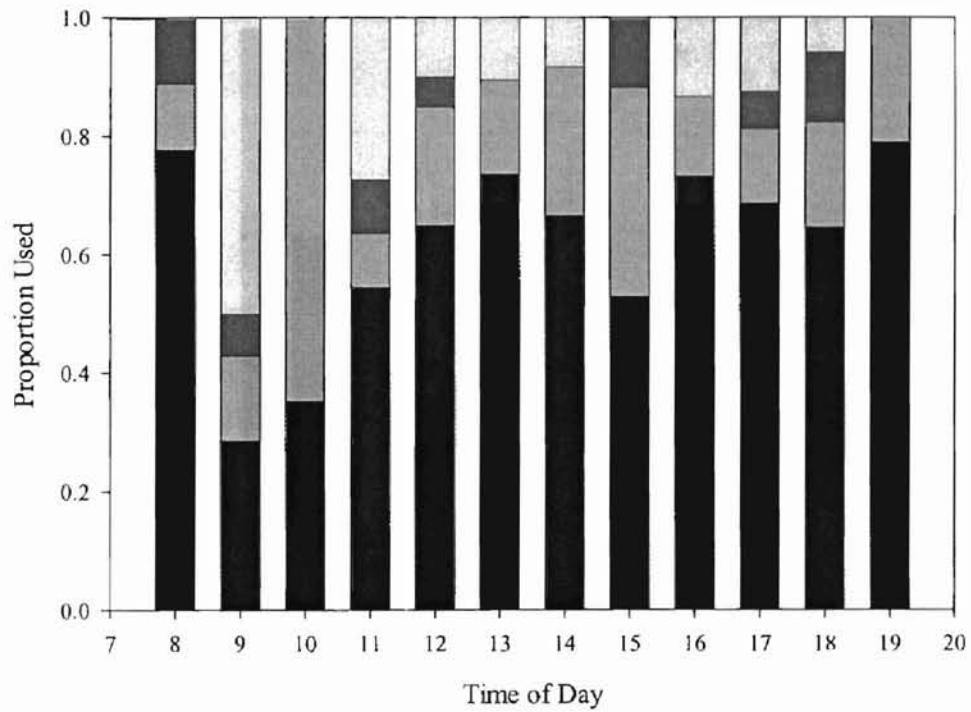
Figure 17. Hourly proportions of sun/shade microhabitats used by lizards over the day. Percent sun categories are indicated. Note 0-20% sun indicates lizards in relatively shady microhabitats; conversely 80-100% sun indicates lizards in relatively sunny microhabitats.
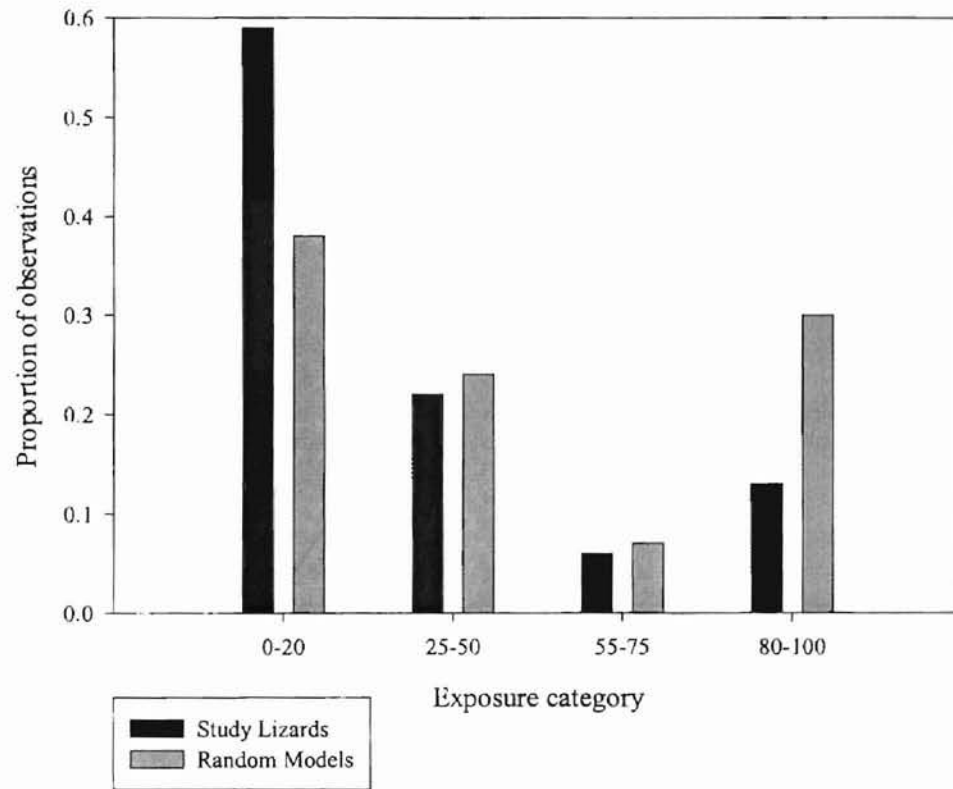
Figure 18. The proportion of study lizards and randomly placed models observed in each sun exposure category.
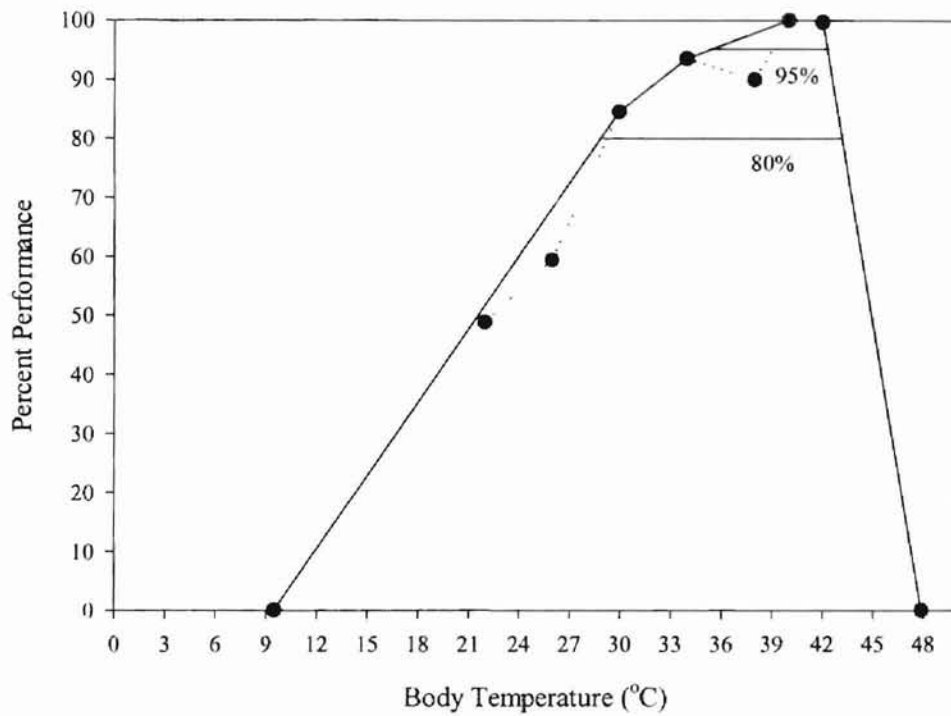
Figure 19. The performance curve: the relationship between sprint speed and body temperature. Solid lines indicate the convex-up performance curve used for calculations. Note the CT min (9.5°C) and CT max (47.9°C) were based on Prieto and Whitford's (1971) observations. Body temperatures over which lizards could run at 80 and 95% of their maximum speed are also indicated.

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