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THE EFFECTS OF THERMAL CONSTRAINTS  
ON THE DAILY ACTIVITY OF  
CROTAPHYTUS COLLARIS

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By

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## CHAPTER I

### INTRODUCTION

Organisms have been physiologically classified according to the sources of heat available to them, e.g. poikilothermic (cold-blooded), and homeothermic (warm-blooded). These older terms, however, have limited application in modern thermal biology and can be misleading. Many "cold-blooded" animals maintain body temperatures ( $T_b$ ) equal to or greater than those in birds and mammals (Cowles and Bogert 1944; Porter 1972; Avery 1979; Pough and Gans 1982; Spellerberg 1982). Careful maintenance of internal  $T_b$  over air temperature ( $T_a$ ) by "cold-blooded" animals also occurs. This is accomplished by various behavioral mechanisms such as basking, shuttling between shade and sunlight (Hammel et al. 1969; Spellerberg 1972) and moving into and out of water (Lillywhite 1970).

The terms used in modern thermal biology to distinguish organisms based on thermal requirements are ectothermic and endothermic, emphasizing the source of body heat. Endotherms are animals utilizing internal sources of heat generated from metabolic processes to maintain a constant  $T_b$ . Because the heat source of endothermic animals is internal and the heat is dispersed outward, some form of



body insulation must be present. Insulation can be in the form of hair, feathers, blubber, etc. Ectotherms rely on external sources of heat, such as direct solar radiation, hot rocks or bark, or hot springs and geysers to maintain  $T_b$  within a narrow range. Ectotherms may be further classified as either thigmothermic or heliothermic. Heliothermic ectotherms rely on basking for their thermoregulation and thigmothermic ectotherms receive the majority of their heat from the ambient air or water and contact with warm surfaces (Porter 1972; Avery 1979; Pough and Gans 1982; Spellerberg 1982).

The role of thermoregulatory behavior in ectotherms is important in the regulation of metabolism and other chemical processes. All chemical processes proceed at a rate that is dependent upon the  $T_b$  of the organism. Metabolic rates increase from the lowest level that can be tolerated to the upper lethal limits. The increase in metabolic rate is an exponential function of  $T_b$ . A  $10^\circ\text{C}$  rise in temperature approximately doubles the metabolic rate (Porter 1972). Diurnal lizards maintain  $T_b$  well above  $T_a$  in order for physiological functions to proceed normally (Cowles and Bogert 1944; Vial 1975). Thermoregulation at higher  $T_b$  within a given species' thermal range may increase digestive efficiency (Lillywhite et al. 1973), as demonstrated in Sceloporus occidentalis and Cnemidophorus tigris (Harwood 1979). An increase in  $T_b$  results in increased oxygen consumption, heart rate, breathing rate, and evaporative

water loss in Gerrhonotus multicarinatus (Dawson and Templeton 1966). The cave-spring dwelling salamander, Eurycea neotenes, when subjected to temperatures greater than those to which it was acclimated, exhibited acute metabolic compensation with regard to oxygen consumption in order to maintain metabolic homeostasis (McAllister and Fitzpatrick 1989).

$T_b$  must be maintained within narrow limits or the functioning of certain enzyme systems can cease (Goin et al. 1978), resulting in physiological impairment or death. Increased  $T_b$  above preferred thermal levels in lizards can result in testicular tissue damage, muscle tissue damage, and denaturation of certain enzymes. On the other hand, when  $T_b$  is low, digestion and egestion of food and antibody production may cease (Dawson 1975). Lizards, however, may deliberately raise their  $T_b$  for protection against infection. After inoculation with a fever-producing bacteria, Dipsosaurus dorsalis raised its  $T_b$  above 30°C by behavioral means, resulting in a "fever" that afforded protection against bacterial infection (Bernheim and Kluger 1976).

Careful thermoregulation is not without costs, however. In determining optimal thermoregulatory behaviors for lizards, both costs and benefits must be taken into consideration. For example, optimal temperatures for physiological processes may be ecologically maladaptive. Costs associated with competition, risk of predation, and

reduced availability of optimal thermal habitats may outweigh the benefits of careful thermoregulation (Huey and Slatkin 1976; Huey 1982). Some lizards occur in thermally diverse habitats and experience a wide variation in  $T_b$  (eurythermic). These lizards have a greater tolerance to extreme  $T_b$  than lizards occurring in less diverse habitats. However, the temperature dependence of metabolic processes imposes limits on the range of  $T_b$  suitable for certain activities. Therefore, the range and variance of  $T_b$  distribution can be considered a compromise between the ecological advantages of eurythermy and the limitations imposed by the optimal temperature ranges of thermochemical processes (Soulé 1963). Eurythermality in Gerrhonotus coeruleus apparently is a result of the lizard behaviorally regulating to different  $T_b$ , depending upon the environmentally determined cost of thermoregulation (Campbell 1985).

My study analyzes the effects of thermal constraints on the daily activity of the collared lizard, Crotaphytus collaris, through the use of physical (copper) models of collared lizards. The equilibrium temperature of these models is the  $T_b$  experienced by the collared lizard in the same microhabitat, position, and orientation. By measuring the activity temperature range of collared lizards, I can compare these temperatures to model temperatures and use the models to predict daily activity of collared lizards. I assume that the activity of collared lizards is constrained



to times when thermal environments allow lizards to maintain a  $T_b$  that is optimal for metabolic processes. The questions I address are as follows:

1. Do copper models predict different uses of microhabitat by different sex/age groups?
2. Were lizards active at the same hours as the models predicted? If not, why?

## CHAPTER II

### LITERATURE REVIEW

#### Thermal Biology

In order to fully understand the role of thermoregulatory behavior in modern thermal biology, it is necessary to become familiar with the terminology currently used in this field as well as thermoregulatory mechanisms used by organisms. This section reviews the vocabulary of modern thermal biology, behavioral and physiological mechanisms utilized by ectotherms in thermoregulation and temperature control, and the effect of  $T_b$  on performance.

#### Vocabulary of Modern Thermal Biology

The following terms and definitions are a compilation from Goin et al. (1978), Avery (1979), Pough and Gans (1982), and Spellerberg (1982).

Activity Temperature Range is the  $T_b$  at which an animal in its natural setting performs its daily routine.

Mean Activity Temperature is the arithmetic average of the  $T_b$  of animals within their activity temperature range.

Critical Thermal Maximum (CTMax) is the  $T_b$  above which

metabolic and physiological processes cease to function normally. In lizards, CTMax is measured by panting and convulsions. CTMax depends on the season and other ecological factors.

Critical Thermal Minimum (CTMin) is the  $T_b$  below which metabolic and physiological processes cease to function normally. In lizards, CTMin is measured by the inability of the individual to right itself. CTMin depends on the season and other ecological factors.

Eurythermal refers to organisms that experience a wide variation in  $T_b$ .

Stenothermal refers to organisms that tolerate a narrow range of  $T_b$ .

Selected Body Temperature Range is the range of  $T_b$ 's that an ectotherm maintains in laboratory conditions when it is exposed to a thermal gradient.

Mean Selected Temperature is the average  $T_b$  measured from an ectotherm exposed to a laboratory thermal gradient.

Eccritic, Preferred, and Voluntary Temperatures are synonymous but Pough and Gans (1982) suggest that "preferred" has an anthropomorphic meaning and should be avoided.



### Behavioral Mechanisms

Behavioral mechanisms used by ectotherms in thermoregulation may provide a range of  $T_b$  greater than the range in  $T_b$  that results from physiological adjustments (Bartholomew 1982; Christian et al. 1984; Stevenson 1985). Such behavioral mechanisms include shuttling, orientation, postural changes, and times of seasonal and daily activity (Table 1). The most important are times of seasonal and daily activity and selection of microhabitat (Avery 1979; Stevenson 1985).

Nonrandom use of habitat by shuttling between sun and shade has been observed in several species of lizards from the Kalahari desert (Huey and Pianka 1977) and in Leiocephalus schreibersi (Marcellini and Jenssen 1989). Uta stansburiana and Sceloporus undulatus seek sunlit microhabitats in early morning and late afternoon even though the majority of microhabitats available are in the shade. Conversely during midday, the majority of these lizards are found in the shade when a greater proportion of microhabitats are in the sun (Waldschmidt 1980). The land iguana Conolophus pallidus chooses a cliff face for basking during the cool season on the Galapagos in order to elevate its  $T_b$ . During the cool season the land iguana's  $T_b$  is 4°C lower than in the hot season. During the hot season the land iguana opts for a plateau for basking. However during the late afternoon, when temperatures drop, lizards can be

found on the cliff face, which stays warmer, and the lizards thus lengthen their activity period up to an hour (Christian et al. 1983). Under thermal conditions that vary seasonally, land iguanas choose different sleeping sites (Christian et al. 1984). In the coolest season, adult land iguanas choose sleeping sites that are warmer than the coolest sites available. This may be because the coolest season is a time when environmental conditions mitigate against rapid warm-up in the mornings, so lizards may regulate nighttime  $T_b$  so that it is easier to warm up to preferred daytime  $T_b$ . Conversely, in the warmest season, adult iguanas choose the coolest sleeping sites available. This results in voluntary hypothermia, which can be advantageous in energy conservation and in avoiding detrimental effects associated with maintenance of a constant  $T_b$  throughout the day and night. Avoiding extreme  $T_a$  is not the only criterion however for microhabitat selection in land iguanas. Hatchling land iguanas maintain a  $T_b$  between 32°C and 40°C in open areas to maximize sprint rates in order to avoid predation by hawks (Christian and Tracy 1981).

Amphibians also select suitable microhabitats for thermoregulation. The bullfrog, Rana catesbeiana, spends most of the day avoiding the hot temperatures of the pond by moving onto the bank and thermoregulating by behavioral means. The bullfrog will utilize artificial sources of shade to lower its  $T_b$  and may even reenter the water,



shuttling from the high temperatures of the upper surfaces to the cooler depths of the water (Lillywhite 1970). Individuals of the green toad, Bufo debilis, faced with the opposite necessity to retain heat, were found grouped with other green toads and in crevices in order to heat up. These toads also burrow their hindquarters into the moist substrate for maximum absorption of heat and water and thus minimize the area exposed to wind which could result in convective heat loss (Seymour 1972).

Behavioral thermoregulation has also been found in turtles. Pseudemys scripta living in a nuclear reactor reservoir utilizes two types of basking for thermoregulatory purposes. Near the reactor the thermal effluents can raise the water temperature by as much as 9°C. Turtles found in this area maintained  $T_b$  by aquatic basking: floating in the warm surface water with the carapace just under the water exposed to the sun. Aquatic basking serves as a fine-tuning mechanism for maintaining a relatively constant, high body temperature. Through such basking the turtles can elevate  $T_b$  1-3°C above water temperature. In other areas of the reservoir turtles thermoregulate by conventional basking: sitting on land or some object out of the water exposed to the sun (Spotila et al. 1984). The Egyptian tortoise, Testudo kleinmanni, can be found under shrubs during daily periods of inactivity. But during seasonal periods of inactivity T. kleinmanni utilizes rodent burrows. By using shrubs for shade and protection during its active season, T.

kleinmanni can maintain a higher  $T_b$  than it could if it used burrows and this may allow for longer periods of daily activity (Geffen and Mendelssohn 1989).

While selection of microhabitat affords the greatest change in  $T_b$ , both orientation and postural adjustments are important too. Many ectotherms will lay prostrate on the substrate in early morning and late afternoon in order to maximize heat gain via conduction. During midday as  $T_a$  increases, ectotherms often assume an elevated posture which increases the surface area exposed to the wind and thus maximizes convective heat loss (Muth 1977a; Muth 1977b). A change from prostrate to elevated position results in a significantly lower rate of heat gain for the zebra-tailed lizard, Callisaurus draconoides (Muth 1977a).

Changes in orientation to the sun may also effect the  $T_b$  of ectotherms. The magnitude of the effect is equivocal, however. For a given posture, a change in orientation accounts for only about a  $1^\circ\text{C}$  difference in  $T_b$  of the zebra-tailed lizard, Callisaurus draconoides (Muth 1977b). But in the African rainbow lizard, Agama agama, a change in orientation reduces daily energy requirements by 11-18%. When this lizard changes orientation from perpendicular to the sun to orientation toward the sun, the  $T_b$  of the lizard is reduced. As a result, energy (food) requirements are reduced because of a decrease in metabolic rate and evaporative heat loss at this lower  $T_b$  (Porter and James 1979).



In full sun, A. agama reduces the amount of surface area exposed to sun by assuming a straight vertical posture parallel to the sun during midday (James and Porter 1979). This was accomplished by clinging to the side of a ledge or building, allowing the body to hang downward. Conversely both Uta stansburiana and Sceloporus undulatus maintain orientations perpendicular to the sun in the early morning hours in order to maximize thermal input (Waldschmidt 1980).

Studies of orientational responses by lizards, however, should include the measurement of three angular deviations of the sun from the body of the lizard (Muth 1977b). These are the relative solar azimuth angle (RAZ), the solar zenith angle (Z), and the relative zenith angle (RZ). RAZ is the horizontal angle of the sun ( $0^{\circ}$  -  $180^{\circ}$ ) relative to the head and frontal plane of the head. If RAZ is  $90^{\circ}$  the lizard is perpendicular to the sun. Conversely, if RAZ is  $0^{\circ}$  the lizard is parallel to the sun. Z is the angular deviation of the sun from the vertical ( $0^{\circ}$  -  $90^{\circ}$ ). In many instances, however, a lizard may be sitting on a sloping surface such as a rock or a tree. In this case it is important to use also RZ, which is the deviation of the sun from a perpendicular to the sagittal plane of the lizard. In other words, if the back of the lizard is perpendicular to the sun, RZ is  $0^{\circ}$  and if the head and frontal plane are parallel to the sun, RZ is  $90^{\circ}$ . It is important to distinguish between Z and RZ since changes in posture and orientation have a large effect on  $T_b$  in lizards (Muth 1977b;

Waldschmidt 1980).

Although behavioral thermoregulation is uncommon in tropical and temperate zone salamanders (Feder and Lynch 1982), Feder (1982) reported that some neotropical salamanders demonstrate behavioral thermoregulation when placed in a substrate thermal gradient in the laboratory. Feder suggests that the limited thermal diversity in the salamanders' microhabitats and their hydric requirements may moderate active thermoregulation.

#### Physiological Mechanisms

Possible physiological mechanisms used in the control of  $T_b$  include evaporative cooling via cutaneous losses, panting, salivation or urination; heat production through muscle activity or resting metabolism; control of blood flow via vascular shunts, cardiac shunts, counter-current systems, or vasodilation and vasoconstriction; and change in reflectance of the integument (Table 1) (Bartholomew 1982; Bradshaw 1986; Patterson and Davies 1989). Through physiological control of  $T_b$  lizards may be able to extend the amount of time they can remain active during the day (Bradshaw 1986).

Rates of heating and cooling in ectotherms are tied to body size. The large surface to volume area of small animals causes  $T_b$  to change so rapidly that any physiological control or adjustment of  $T_b$  is negligible. Therefore the physiological control of  $T_b$  may be



functionally more important in larger ectotherms than in smaller ones (Bradshaw 1986).

In general, lizards heat at a faster rate than they cool. This is in part a result of the control of periperal blood flow within the lizard. Vasodilation within the peripheral tissues allows for an increase in blood flow throughout the body and an increase in the amount of heat absorbed at the peripheral regions. Vasoconstriction reduces the amount of heat lost to the external environment while also reducing the amount of heat absorbed (Avery 1979; Spellerberg 1982; Bradshaw 1986). Therefore, when heating up, lizards, via vasodilation, increase heat uptake. However, when cooling down, if  $T_b$  is lower than  $T_a$ , lizards minimize heat gain through vasoconstriction. Conversely, if  $T_a$  is lower than  $T_b$ , lizards can cool down faster via vasodilation.

Lizards may also maintain regional heterothermy within the body. This is accomplished via cardiac shunts, vasomotor activity, counter-current vascular systems, and local evaporative cooling (Bartholomew 1982). According to Cowles (1958), the evolution of vascular blood shunting arose in the amphibia to serve respiratory needs and in the reptilia blood shunting allowed for heat absorption and dispersal throughout the body.

In the collared lizard, Crotaphytus collaris, evaporative cooling accounts for only about a quarter of resting heat production from 32°C to 40°C. At 44°C,

evaporative cooling results in the dissipation of about 1.3 times the resting heat production. This enhanced heat loss is attributed to panting which begins at 42.5°C (Dawson and Templeton 1963). The chuckwalla, Sauromalus obesus, will begin panting at a  $T_b$  of 42-46°C (Templeton 1967). Water evaporated through panting can dissipate all body heat produced as well as a small amount gained from the environment (Templeton 1967).

Bradshaw (1986), however, maintains that the amount of heat dissipated through panting amounts to no more than 50% of the metabolic heat produced and suggests that the short term advantages of heat lost through panting would be outweighed in the long run by the complications resulting in water loss through evaporative cooling. These studies on effects of evaporative cooling, however, have been confined to the laboratory and actual studies on long term effects are scarce.

Reflectance and color change have also been studied in relation to physiological control of  $T_b$ . Internal pigmentation may aid in the regulation of  $T_b$ . Internal pigmentation blocks ultraviolet wavelengths from 1875-3100 Å (Hunsaker II and Johnson 1959). Studies have suggested that when  $T_b$  is below the selected range, reptiles darken their skin, which facilitates heat absorption and increases heat transfer. As  $T_b$  rises, blanching of the skin may occur which reduces radiant heat absorption. However, when reflectance is enhanced, peripheral circulation necessarily



also increases, which results in increased absorption of heat into the body. Thus, the effectiveness of reflectance as a physiological control of  $T_b$  is compromised (Bartholomew 1982).

Studies of the importance of physiological control of  $T_b$  in reptiles have been limited to the laboratory. Results of these studies suggest that physiological mechanisms do play a role in temperature control. However, the effects may be negligible in small ectotherms when compared to behavioral mechanisms of thermoregulation. Firth and Turner (1982) suggest a relationship between sensory, neural, and hormonal modalities and the thermal biology of reptiles. Both behavioral and physiological mechanisms have a sensory, neural, and hormonal basis. It would therefore be imprudent to ignore possible physiological mechanisms when studying the thermal biology of a species. An animal that is thermoregulating by behavioral mechanisms maintains its  $T_b$  within a narrow range at times when  $T_a$  is less than  $T_b$  and at times when  $T_a$  is greater than  $T_b$ . Temperature control in both situations is partly accomplished by physiological mechanisms (Bartholomew 1982). Without physiological fine-tuning, reptiles would be less efficient while thermoregulating behaviorally.

#### Effects of Temperature on Performance

Thermal dependence of certain biochemical and physiological reactions has been established in ectotherms

1(Spotila et al. 1972; Crowley 1987). Recent studies have tested the thermal dependence of certain whole animal behaviors. Sprint speed in the lizard Uta stansburiana is dependent on  $T_b$  (Waldschmidt and Tracy 1983). However, recent studies suggest that burst speed and distance running are not as dependent on  $T_b$  as other physiological processes (Bennett 1980; Huey and Hertz 1984; Huey and Dunham 1987). While sprint speeds do increase as  $T_b$  increases, changes are not statistically different. At temperatures above and below optimal temperature for maximal speed, sprint speed is lower (Waldschmidt and Tracy 1983). Many of the maximal performances observed in laboratory studies are effected at a  $T_b$  that is not observed in these animals in the field (Bennett 1980). In two closely related genera of lizards, Agama and Stellio, which differ in thermal biology and geographic location, there was no geographic or interspecific variation in maximum velocity, optimal temperature, optimal temperature range, or thermal performance breadth for sprint speeds between the two genera nor among different populations of Stellio. Field data taken for these two genera indicate that the lizards are active at a  $T_b$  at which sprint speeds are not optimal (Hertz et al. 1983).

In the gopher snake, Pituophis catenifer affinis, strike velocity and successful prey capture increased from 18°C to 27°C but there was no significant increase in either of the two behaviors between 27°C and 33°C (Greenwald 1974).



These snakes fed most often at 33°C.

In amphibians, Londos and Brooks (1988) observed that the locomotory performance of Bufo woodhousei woodhousei depended on the acclimation temperature to which it was subjected, but different performance measures were optimal at different temperatures. Toads acclimated to 20°C had a greater mean jump frequency than toads acclimated to 30°C and the former had greater mean and longest jump lengths than the latter.

Future studies are necessary to determine the actual effect of temperature on these locomotory and behavioral performances. Both laboratory and field studies must be conducted. Thermal dependence observed in the laboratory within a certain range of  $T_b$  may not reflect ecologically relevant temperatures for a certain species.

#### Operative Environmental Temperatures

Body temperatures are a function of ambient temperature, radiant temperature, and air movement. Biologists have tried to characterize an environment by a single measure which conveys a description of what the environment means to a certain organism. This measure is a representation of the  $T_b$  of an organism which takes into account the interaction between the effects of ambient temperature, radiant temperature, and air movement on the organism.

Two such indices that have been proposed are the

standard operative temperature ( $T_{es}$ ) and the operative environmental temperature ( $T_e$ ).  $T_{es}$  is equivalent to the environmental temperature at which a warm body (such as a human or animal) loses heat at a standard cooling rate (Gagge 1940).  $T_{es}$  is an index of sensible heat flow to the environment and may be used as the independent variable for plotting thermoregulatory responses to complex thermal environments (Bakken 1980).  $T_e$  is defined as the equilibrium temperature of an inanimate object of zero heat capacity with the same size, shape, and radiative properties as the animal under study and exposed to the same microclimate (Bakken and Gates 1975).

$T_e$  can be measured directly by placing physical models of an organism in the environment. The equilibrium temperature of these models is the temperature experienced by an organism in the same microhabitat, position, and orientation.  $T_e$  can also be measured by using steady - state energy balance equations (Porter and Tracy 1983). Both methods measure the same  $T_e$ .

#### Use of Physical Models in the Field

Physical models can be used directly in the measurement of  $T_e$ . These physical models are actual models of the animal under study. For reptiles, amphibians, and other small ectotherms, thin hollow metal casts of the animal can be made (Bakken and Gates 1975).  $T_e$  is measured from the interior of the model with a copper-constantan thermocouple



and electronic thermometer.

Metal casts can also be made for endotherms but it is necessary to duplicate the radiative properties of the integument, either fur or feathers. This can be done by painting the cast or covering the cast with the integument of the animal. It is imperative that the heat capacity of the organism be duplicated. In order for the heat capacity of the entire organism to be duplicated the heat capacity per unit volume of the organism must be replicated.

For small animals that live close to the ground, slight variation in shade, skin color, substrate, exposure to sun, wind velocity, and  $T_a$  can affect the  $T_e$  of the model. When using models to predict environmental temperatures of animals, it may be useful to place them in several habitats under various environmental conditions in order to obtain a range of  $T_e$  that is available to the animal (Bakken and Gates 1975).

Few studies have been conducted using these models as indices of thermoregulatory responses, but they have shown that models can be used to predict activity periods of certain animals (Bakken 1980; Bakken et al. 1981; Crawford et al. 1983; Peterson 1987; Grant and Dunham 1988; Adolph 1990).

Electrically heated taxidermic mounts of the American Goldfinch were used to study the thermal significance of nocturnal winter roost selection (Bakken et al. 1981). These "environmental temperature thermometers", by

simulating the goldfinch's effect on air movement in the roost, were able to quickly integrate effects of wind, solar radiation, and air temperature and measure the  $T_{es}$  of the roost.

Hollow copper models of Pseudemys scripta have been used to predict basking behavior of turtles (Crawford et al. 1983). Body size of the models was found to have no direct relationship with  $T_e$ . The medium sized models consistently measured the highest temperature, and the shape difference between the models accounted for only a small difference in temperature.

Copper models of the desert lizard, Sceloporus merriami, were used to study thermally imposed time constraints on lizard activity (Grant and Dunham 1988). Even more important than range of available  $T_e$  to an animal was the spatial distribution of these temperatures in an animal's home range. While many areas in a home range may yield  $T_e$  conducive to lizard activity, the distribution of these patches may be such that it is too costly in terms of metabolic energy and potential predation to move from one patch to another.

Polyvinylchloride (PVC) models were used to describe how  $T_e$  varies with substrate and sunlight level and predict which microhabitats are more suitable for providing preferred  $T_b$  for Sceloporus occidentalis and S. graciosus (Adolph 1990). Models demonstrated that an orientation perpendicular to the sun can increase  $T_b$  by  $10^\circ$  to  $15^\circ\text{C}$ .  $T_e$



was highest on the ground, intermediate on logs, and lowest on trees. Microhabitat use by the lizards reflected model predictions in that lizards found at high altitudes were perched on the logs and ground, basked in the sun, and maintained an orientation perpendicular to the sun frequently. Those lizards found on the desert floor frequently used trees as perch sites to escape extremely high  $T_a$ .

Use of  $T_e$  to assess the range of  $T_b$  available to organisms in certain environments is useful for answering questions about their thermal biology and geographic distribution. However, the entire range of physiological states (e.g. body temperature, hydration level) that theoretically could be achieved may never actually be attained by the animal because of certain morphological, physiological, and behavioral adaptations (Tracy 1982).

#### Eastern Collared Lizard

The Eastern Collared Lizard, (Crotaphytus collaris collaris), is a member of the Iguanid family. Collared lizards can be recognized by an incomplete conspicuous black and white collar around the neck. All collared lizards have large heads and powerful jaws. Male lizards are brightly colored having yellow, green, brown or blue coloration. The dorsum is speckled with light spots and in younger males, dark crossbands. Females are similar in coloration but less brilliant (Conant 1975).

The range of the collared lizard extends from southern Missouri through northern Arkansas and west to northern and central Texas (Behler and King 1979). In Oklahoma, collared lizards can be found statewide but tend to avoid the Coastal Plain. Large populations are found in the Arbuckle and Wichita mountains (Webb 1970). Their habitat consists of hardwood forests and rocky, hilly, semiarid regions. They are abundant on limestone ledges and rock piles because these areas allow for ideal basking sites and numerous hiding areas (Behler and King 1979). Because collared lizards are sit-and-wait predators, they avoid areas of high dense vegetation in order to maximize their range of view for potential prey. However, they will run into grassy areas to move from perch site to perch site or to catch insects (Fitch 1956). Arboreal behavior in the Western Collared Lizard (Crotaphytus collaris baileyi) has been observed, suggesting that desert dwelling lizards may become arboreal to escape high ground temperatures (Clark 1974).

Activity temperature ranges of the collared lizard measured previously were 35.5°C to 37.0°C (Brattstrom 1965) and 20.7°C to 43.3°C (Fitch 1956). Through thermoregulatory behavior, collared lizards tend to keep their  $T_b$  near the optimum, 37.0°C to 41.0°C, even though this may impose severe limitations on their activities (Fitch 1956).

Collared lizards will pant when subjected to high temperatures (Fitch 1956). An adult male collared lizard was constrained in direct sunlight on a sunny day when  $T_a$



measured 34.0°C. The  $T_b$  of the lizard rose to 45.0°C. During this period, the lizard showed discomfort by panting and struggling to escape. The threshold for panting in collared lizards is recorded as 42.5°C to 43.0°C (Templeton and Dawson 1963). At 44.0°C, evaporative cooling in collared lizards accounts for the dissipation of about 1.3 times the heat produced (Dawson and Templeton 1963).

## CHAPTER III

### DESCRIPTION OF STUDY AREA

I conducted field work in Payne Co., Oklahoma, from June through early September, 1989. Annual rainfall for 1989 was 928.1 mm. Summer rainfall was slightly higher than usual for the Stillwater area. Table 2 shows the total amount of rainfall for each month in 1989. Daily temperatures in the summer were lower than normal in Stillwater. Table 3 shows the maximum, minimum, and overall mean temperatures for each month in 1989.

The study site was the western slope of the Lake Carl Blackwell Dam, 11 km west of Stillwater. The western slope of the dam is approximately 10,800 m<sup>2</sup> in area and is composed mainly of piled rocks and exposed concrete. The site is also characterized by trees and herbaceous plants that grow among the rocks on the dam. Common trees in this area were cottonwood (Populus deltoides), black willow (Salix nigra), western hackberry (Celtis reticulata), and rough-leaved hackberry (C. occidentalis). Common shrubs found were grape (Vitis spp.), smooth sumac (Rhus glabra), buckbrush (Symphoricarpos orbiculatus), and buttonbush (Cephalanthus occidentalis). Common herbaceous plants included Bermuda grass (Cynodon dactylon), Johnson grass

(Sorghum halapense), American germanander (Teucrium canadense), Carolina horse nettle (Solanum carolinense), Virginia wild rye (Elymus virginicus), wax goldenweed (Haplopappus ciliatus), Louisiana sagewort (Artemisia ludoviciana), Japanese brome (Bromus japonicus), and fleabane (Erigeron spp.) (Bontrager 1980).

## CHAPTER IV

### MATERIALS AND METHODS

#### Daily Observations

Collared lizards were captured by a thread noose at the end of a cane fishing pole. Lizards caught for the first time were marked permanently by toeclips. Each toe was numbered (Figure 1) and a unique combination of three clipped toes per lizard was used to identify each lizard. Only one toeclip per foot was allowed for each lizard and toes 15 and 20 were not clipped. To avoid regeneration, toes were clipped at the first knuckle.

In addition to toeclips, lizards were also marked with color codes using model airplane enamel. Each lizard was given a four spot color code using no more than two different colors. Paint was administered to the dorsal surface of the lizards using disposable syringes without needles. Lizards that could not be caught with a noose were identified by their color codes through binoculars. Paint was reapplied to the dorsum after epidermal molts which resulted in the loss of paint marks.

Individuals caught for the first time were weighed to the nearest gram using a Pesola spring scale. Measurements of size were taken: snout-vent length (SVL), head length,



head width, mouth gape, and tail length. Age class and sex were noted.

Data were collected daily from 0900 h to 2000 h, including color code, toe clip, date, time of day, habitat type,  $T_a$  taken in the shade 2 cm above the substrate with a Miller and Weber rapid-register thermometer,  $T_b$  (if lizards were captured) measured with a Miller and Weber rapid-register thermometer, orientation, posture, relative wind speed and sky conditions. Observed panting in the lizards was also recorded.

Three types of habitat were defined for this study: rock-sun, rock-shade, and rock-mosaic. Almost no other types of habitat were present on the site. Orientation was defined as either parallel to the sun or perpendicular to the sun. Posture was defined as either upright or adpressed to the substrate. Sky conditions at the time of lizard capture or observation was reported as either clear, partly cloudy, cloudy, or overcast.

#### Operative Environmental Temperatures

Copper models of collared lizards were constructed to measure  $T_e$ . Models were created from thin copper sheeting and were painted with gray enamel spray paint. These hollow models were equipped with copper-constantan thermocouples inside the body cavity.  $T_e$  was taken using an Omega Thermocouple Digital Thermometer HH-99A-T2.

Three sizes of copper models were used to reflect the

three age classes of lizards studied: hatchlings, juveniles, and adults. Each size was represented by two postures: upright and adpressed.

Twice a month, once at the beginning and once during the middle of the month, I placed the models in the study site at each hour of the day from 0900 h to 2000 h in each of the microhabitats available and  $T_e$  was measured. To allow adequate time to equilibrate, models were left in place for 3 minutes before  $T_e$  was measured. Upright models were placed parallel to the sun and adpressed models were placed perpendicular to the sun. This technique yielded minimum and maximum  $T_e$  and subsequently the minimum and maximum  $T_b$  a live lizard could attain in that particular microhabitat.

Concomitantly, I placed four 15 m tape measures in the study area and at each hour of the day the percentage of available microhabitat in sun-rock, shade-rock, and mosaic-rock was measured. This was done by measuring the amount of the tape in sun, shade, and mosaic and subsequently calculating the percentages.

## CHAPTER V

### RESULTS

I caught and marked thirty-one collared lizards: 8 adult males, 7 adult females, 4 juvenile males, 7 juvenile females, 3 hatchling males, and 2 hatchling females (Table 4). Adults were considered to be two years or older, juveniles to be one year old, and hatchlings in their first summer. Adults and juvenile lizards were separated on the basis of SVL and overall appearance, taking into account the time of year they were first caught. Average SVL for hatchlings was 44.6 mm, for juveniles, 81.5 mm, and for adults 95.9 mm (Table 5).

For the 31 lizards marked, the total number of sightings was 380. Of the 380 sightings, 340 (90%) were observations where lizards could be identified as hatchling, juvenile, or adult. Of these 340 cases, 180 (53%) of the observations were captures in which  $T_b$  was measured and 160 (47%) were observations where lizards were either not captured or capture occurred only after chasing the lizard, in which case  $T_b$  was not collected.

Collared lizards are difficult to catch because of their speed. Lizards became more wary of my presence on the dam. Nevertheless, some individuals were caught several



times a day. Repeated recaptures, plus the speed and enhanced wariness of the lizards, made capture of lizards increasingly more difficult as the season progressed.

#### Body Temperature

The range of  $T_b$  measured from active lizards was 26°C to 42°C with a mean of 37.6°C (Fig. 2).  $T_b$  between the sexes and among the different age classes was compared. No significant differences in  $T_b$  were found between the sexes in any age category (Tables 6, 7, and 8). Because there was no difference in  $T_b$  between the sexes, sexes were pooled in each age category and  $T_b$  was compared. Again, there was no significant difference in  $T_b$  among the three age classes (Table 9).

I performed ANCOVA to test the interaction between  $T_a$  and age and ( $T_a$  and sex) to see if the ages (or sexes) showed different linear relationships between  $T_b$  and  $T_a$ . Results were insignificant (ANCOVA -  $T_a$  \* Age:  $F = 2.82$ ,  $p > .05$ ; ANCOVA -  $T_a$  \* Sex:  $F = 2.97$ ,  $p > .05$ ). Because these results were insignificant, I then tested for overall differences in  $T_b$  at different  $T_a$  between the sexes and among the age classes. Results again were insignificant (Tables 10 and 11). The overall slope of  $T_b$  vs  $T_a$  from linear regression analysis of pooled data was 0.443.

### Lizard Activity

Each day of the study was grouped into a time period centered around the nearest day when  $T_e$  was measured. Thus, the season was partitioned into five periods: early June, mid June, early July, mid July, and early August (Fig. 3). Lizard activity depicted on the histograms represents the total number of lizards seen at each hour divided by the total number of lizards seen during that time period. Each individual was often counted more than once.

A somewhat bimodal distribution of lizard activity is seen in early June, early July, and early August. However, lizards tended to be active over all hours of the day even when availability of good microhabitat was reduced. Lizards active in the morning hours had an average  $T_b$  of  $34.6^\circ\text{C}$ , which is at the lower end of the activity temperature range for collared lizards. Lizards active in the afternoon hours were able to do so because of convective heat loss and evaporative heat loss via panting. Lizards seen in the hot afternoon hours were found on the rocks in full sunlight, sometimes panting.

There was no significant difference in the number of males and females or the number of individuals in each age class active at each hour of the day (Tables 12 and 13).

### Operative Environmental Temperatures

The range of  $T_b$  of active lizards was  $26^\circ\text{C}$  to  $42^\circ\text{C}$ . I



assumed that lizards in nature would not voluntarily overheat and the lower  $T_b$ 's measured were taken from lizards that had not yet equilibrated to preferred levels. Consequently, I defined the optimal range of  $T_b$  as 90% of the observed temperatures of the lizards starting from the highest  $T_b$  and working down. This range of optimal temperatures was 34°C to 42°C (Fig. 2). The copper model hourly temperatures were then compared to this optimal range and if either model (adpressed/perpendicular or upright/parallel) of a given size attained this temperature, the microhabitat was considered optimal. Percentage of optimal available microhabitat at each hour of the day was determined by data collected from the transects placed in the study site during the same hours.

A two-way ANOVA was performed on microhabitat availability for the different size classes at each hour for all bimonthly sampling periods pooled. There was no difference in the percentage of optimal available microhabitat among the size classes (Table 14). As expected, a significant difference in percentage of optimal available microhabitat among the hours was evident. Figure 4 represents the percentage of optimal microhabitat available as predicted by the copper models at each hour of the day during the different bimonthly periods that sampling took place. The percentages are an average of optimal available microhabitat for all three size classes of models combined. During early (0900 - 1000) and late (2000) hours



available optimal microhabitat is low.  $T_e$  measured at these hours indicates that lizards are not able to maintain  $T_b$  in their activity temperature range. In the mid-afternoon, temperatures become too extreme for the lizards. Therefore we see a bimodal distribution in the percent available microhabitat over the day. This is extremely noticeable in early July and early August, when the models predicted that lizards would be too hot at 1400 h, 1500 h, and 1600 h (Fig. 4).

Because there was no difference among the size classes, data from medium-sized copper lizards were used to compare the predicted activity of collared lizards with their observed activity. A goodness-of-fit test was performed for all data collected during each bimonthly sampling period to test the difference between the number of observed and expected lizards in optimal and suboptimal microhabitats at each hour of the day. Expected values were generated from the product of the proportion of optimal and suboptimal microhabitats against number of lizards active at a given hour. Selection of microhabitat is a nonrandom process (Table 15). At some hours in particular the process was markedly nonrandom. At 0900 h and 1000 h few lizards were expected in good microhabitat because of its reduced availability. However, many more lizards were observed than expected in this microhabitat then. At 1500 h more lizards were observed in suboptimal microhabitat than were predicted by random expectations. The lizards remained active in

microhabitats with high  $T_e$  as measured by the copper models. During the rest of the day, activity of collared lizards was generally as predicted from availability of optimal and suboptimal microhabitats.

## CHAPTER VI

### DISCUSSION

The summer of 1989 was rainier than most summers in north central Oklahoma. As a result, the vegetation on the study site grew to such a degree that large portions of the dam were covered by vines and grasses. Many of the rocky areas became unsuitable for successful basking. Consequently, sample size of marked lizards of this study was low.

Seasonal changes in activity of collared lizards also played a major role in the number of lizards seen. Breeding season for collared lizards in Douglas Co., Kansas, begins in late May and June (Fitch 1956). After eggs are laid, adults of both sexes are less evident than in the spring and early summer because territorial perches are abandoned and adults retreat to more sheltered spots or may even remain underground and inactive. At Lake Carl Blackwell adult brumation begins between 28 July and 11 August (Bontrager 1980).

Predators may also have reduced the number of lizards. Although hawks were seen flying overhead and snakes were sighted among the rocks, I believe their predatory impact was negligible. However, throughout the study a family of



minks was seen traversing the dam, and even though there is no evidence in the literature to lead one to believe that minks are a major predator of collared lizards, the minks seen on the dam were poking through the rocks and could very well have been successfully preying on collared lizards.

#### Body Temperature

The range of  $T_b$  measured from active collared lizards,  $26^{\circ}\text{C}$  to  $42^{\circ}\text{C}$ , coincides with the activity temperature range of collared lizards as measured by Fitch (1956) and Brattstrom (1965), or  $35.5^{\circ}\text{C}$  to  $37.0^{\circ}\text{C}$  and  $20.7^{\circ}\text{C}$  to  $43.3^{\circ}\text{C}$ , respectively.

No difference in  $T_b$  among age classes or between sexes was found. Fitch (1956) suggested that preferred temperatures may differ slightly between sexes. He noted that a disproportionately large number of  $T_b$  above  $40^{\circ}\text{C}$  were of females. However,  $T_b$  was not tested statistically and thus no sexual difference was conclusively shown.

Regression analysis of my data suggests that the relationship (slope) between  $T_b$  and  $T_a$  is not different for age class or sex. Furthermore, at a given  $T_a$  the  $T_b$  of any lizard, regardless of age or sex, is the same (regression lines are superimposed). The overall slope of  $T_b$  vs  $T_a$  (0.443) indicates that collared lizards are precise thermoregulators. Slopes close to zero indicate precise thermoregulation ( $T_b$  independent of  $T_a$ ) and slopes close to one indicate thermal conformity ( $T_b$  dependent on  $T_a$ ) (Huey

1982; Marcellini and Jenssen 1989). However, this method does have limitations. First, a lizard that thermoconforms while active (slope = 1) may still achieve low variation in  $T_b$  by restricting its activity to times and microhabitats that are thermally suitable (Hertz and Huey 1981). Second,  $T_a$  is only a convenient estimate of heat load imposed on lizards (Tracy 1982). Third, as  $T_a$  rises,  $T_b$  may rise above normal activity temperatures for the lizard, thereby curtailing the lizard's activity and restricting microhabitat use as the lizard becomes a thermal conformer (Huey 1982). To minimize interpretational errors, a second criterion based on the y-intercept has been proposed (Damme et al. 1987). For thermally conforming species the intercept should be close to zero with a slope close to one. However if the intercept is well above zero precise thermoregulation is occurring. For my data I calculated a y-intercept of 23.13 which is well above zero. Thus, careful evaluation of the  $T_b$  vs  $T_a$  regression showed the collared lizard to be a precise thermoregulator.

#### Operative Environmental Temperature and Daily Activity

Although the measurement of  $T_e$  allowed for predictions of collared lizard activity throughout most of the day, lizard activity recorded during midday hours did not coincide with copper lizard predictions.

Fitch (1956) found collared lizards active over a wide



range of  $T_a$ , from 13.5°C to 36°C. More than half of the observations however were at  $T_a$  within the range of 28°C to 33°C. He noted that by the time  $T_a$  had risen to the lizards' optimal  $T_b$  or near it (37°C or 38°C), the lizards sought shelter underground.  $T_a$  measured in this study ranged from 19.8°C to 40.2°C, suggesting that the collared lizards on the dam remained active under slightly more extreme conditions.

$T_e$  that predicted no activity ranged from 19.6°C to 25.0°C in the morning and 43.7°C to 49.9°C in midday. However, lizards were active throughout the day (including these times) and had  $T_b$  in both optimal and suboptimal microhabitats that ranged only from 26°C to 42°C. Therefore, active lizards in suboptimal microhabitats must have been able to maintain  $T_b$  in their activity temperature range by physiological and behavioral adjustments that the copper models could not account for.

Copper models were placed in approximately the same location on the dam during all model sampling days and they represented only two postures, upright/parallel and adpressed/perpendicular. While these postures/orientations should represent maximum and minimum  $T_b$ , location on the dam may increase the range of  $T_b$  available to the lizards. Muth (1977b) showed through computer simulations that a change in convective environment (i.e. perch height) is very important in determining a lizard's  $T_b$ . If a lizard climbs to a perch 50 cm high, even in the sun this enhanced elevation could



increase activity time by about four hours, allowing unimodal activity even in "worst case" environments. This is mainly due to decreased conduction and radiation from the hot substrate and increased convective loss via more wind. If the lizards of my study moved higher up the dam, they would not experience less radiation and conduction from the substrate, but they could show more convective heat loss.

In a separate experiment, I placed copper models on the top and bottom of the dam. Data were collected in accordance with sampling done on copper model sampling days. Analysis was performed to determine if there was a difference in percent available good microhabitat at each hour between the two locations on the dam. Because I had no replications for the bottom and top on the dam at each hour, I assumed no interaction term in the two-way ANOVA. Results suggest a slight difference in microhabitat availability at the two locations (Table 16), even though it was not a significant difference. Further scrutiny of my data, however, shows that both  $T_a$  and  $T_e$  measured during midafternoon hours at the bottom of the dam were lower than those measured in the same microhabitats at the top of the dam. Gusts of wind coming off the lake may have resulted in cooler microenvironments at the lower portion of the dam. I believe that lizard movement on the dam resulted from avoidance of cool air instead of avoidance of high  $T_a$  as previously thought. That is not to say, however, that lizards were not using some means of convective heat loss at

the top of the dam to maintain an optimal  $T_b$ .

It is quite evident that inanimate copper models are unable to account for physiological mechanisms that may be used in thermoregulatory behavior. Collared lizards were seen panting during the hot afternoons on the dam. Dawson and Templeton (1963) suggest that evaporative cooling dissipates considerable heat at high temperatures. Panting in the desert lizard, Sauromalus obesus, enables maintenance of a  $T_b$  about 4°C below ambient for several hours when exposed to 47°C air temperature (Bartholomew 1982).

Whatever the case, collared lizards were active at all hours of the day. Lizards were able to remain active by using both behavioral mechanisms and physiological adjustments. The ecological reason for this continuous activity is unknown and is a subject for further study. Some possible explanations are that adult female lizards needed to gain back the weight lost when their eggs were laid. Therefore remaining active all day allowed for more search time for prey. Juvenile males may have remained active because the dominant adult males had abandoned their territorial perches and were no longer a threat to the juveniles. This allowed for juveniles to find food and gain weight before entering their hibernacula, and perhaps to establish a territory for the next year.

As stated previously the threat of predators common to collared lizards was considered negligible except for the possibility of the minks seen on the dam. The cost of



remaining active in open areas on the dam may have been minimized by the lack of predators.

In conclusion, while using copper models or any other biophysical models as predictors of activity of certain organisms one must keep in mind that organisms, especially ectotherms, respond differently to certain environmental variables. Any particular set of environmental variables may correspond to a range of physiological states, which depend upon the effectiveness of morphological, physiological, and behavioral adaptations (Tracy 1982). When measuring ranges of physiological states, it is unreasonable to assume that the range of physiological states measured is realistically available to the organisms, or on the other hand, the models may not adequately measure the entire range of physiological states possible for an organism.



## BIBLIOGRAPHY

- Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two Sceloporus lizards. *Ecol.* 71(1):315-327.
- Avery, R. A. 1979. *Lizards - A Study in Thermoregulation.* University Park Press, Baltimore, MD. 56 pp.
- Bakken, G. S. 1980. The use of standard operative temperature in the study of the thermal energetics of birds. *Physiological Zoology* 53:108-119.
- Bakken, G. S., W. A. Buttemer, W. R. Dawson, and D. M. Gates. 1981. Heated taxidermic mounts: a means of measuring the standard operative temperature affecting small animals. *Ecology* 62(2):311-318.
- Bakken, G. S. and D. M. Gates. 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. Pages 255-290. In: *Perspectives of Biophysical Ecology*, D. M. Gates and R. B. Schmerl, eds. Springer-Verlag, New York, NY.
- Bartholomew, G. A. 1982. Physiological control of body temperature. Pages 167-211. In: *Biology of the Reptilia*. Vol 12, C. Gans and F. H. Pough, eds. Academic Press, New York, NY.
- Behler, J. L. and F. W. King. 1979. *The Audubon Society Field Guide to North American Reptiles and Amphibians.*

- Alfred A. Knopf, Inc., New York, NY. 743 pp.
- Bennett, A. F. 1980. The thermal dependence of lizard behavior. *Anim. Behav.* 28:752-762.
- Bernheim, H. A. and M. J. Kluger. 1976. Fever and antipyresis in the lizard, Dipsosaurus dorsalis. *Am. J. Physiol.* 231:198-203.
- Bontrager, S. K. 1980. Autecology of Crotaphytus collaris. M. S. Thesis, Oklahoma State Univ., Stillwater, OK. 151 pp.
- Bradshaw, S. D. and A. R. Main. 1968. Behavioral attitudes and regulation of temperature in Amphibolurus lizards. *J. Zool., Lond.* 154:193-221.
- Bradshaw, S. D. 1986. *Ecophysiology of Desert Reptiles*. Academic Press, Orlando, FL. 324 pp.
- Brattstrom, B. H. 1965. Body temperatures of reptiles. *Amer. Midl. Nat.* 73:376-422.
- Campbell, J. D. 1985. The influence of metabolic cost upon the level and precision of behavioral thermoregulation in an eurythermic lizard. *Comp. Biochem. Physiol.* 81(3):597-601.
- Christian, K. A. and C. R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling land iguanas to avoid predation during dispersal. *Oecologia* 49:218-223.
- Christian K., C. R. Tracy and W. P. Porter. 1983. Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (Conolophus pallidus). *Ecology*

64(3):463-468.

- \_\_\_\_\_. 1984. Physiological and ecological consequences of sleeping- site selection by the Galapagos land iguana (Conolophus pallidus). Ecology 65(3):752-758.
- Clark, W. H. 1974. Arboreal behavior of the Leopard lizard, Crotaphytus wislizenii in western Nevada. Trans. Kans. Acad. Sci. 77(1):68.
- Conant, R. 1975. A Field Guide to Reptiles and Amphibians of Eastern and Central North America. Houghton Mifflin Co., Boston MA. 429 pp.
- Cowles, R. B. 1958. Possible origin of dermal temperature regulation. Evolution 12:347-357.
- Cowles, R. B. and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Am. Mus. Nat. Hist. 83:261-296.
- Crawford, K. M., J. R. Spotila and E. A. Standora. 1983. Operative environmental temperatures and basking behavior of the turtle Pseudemys scripta. Ecology 64(5):989-999.
- Crowley, S. R. 1987. The effect of desiccation upon the preferred body temperature and activity level of the lizard Sceloporus undulatus. Copeia 1987(1):25-32.
- Damme, R. Van, B. Bauwens and R. F. Verheyen. 1987. Thermoregulatory responses to environmental seasonality by the lizard Lacerta vivipara. Herpetologica 43:405-415.
- Dawson, W. R. 1975. On the physiological significance of



- the preferred body temperature of reptiles. Pages 443-473. In: Ecological Studies 12: Perspectives of Biophysical Ecology, D. M. Gates and R. B. Schmerl, eds. Springer-Verlag, New York, NY.
- Dawson, W. R. and J. R. Templeton. 1963. Physiological responses to temperature in the lizard Crotaphytus collaris. Physiol. Zool. 36:219-236.
- \_\_\_\_\_. 1966. Physiological responses to temperature in the alligator lizard, Gerrhonotus multicarinatus. Ecology 47(5):759-765.
- Feder, M. E. 1982. Thermal ecology of neotropical lungless salamanders (Amphibia: Plethodontidae): environmental temperatures and behavioral responses. Ecology 63(6):1665-1674.
- Feder, M. E. and J. F. Lynch. 1982. Effects of latitude, season, elevation, and microhabitat on field body temperatures of neotropical and temperate zone salamanders. Ecology 63(6):1657-1664.
- Firth, B. T. and J. S. Turner. 1982. Sensory, neural, and hormonal aspects of thermoregulation. Pages 213-274. In: Biology of the Reptilia. Vol. 12, C. Gans and F. H. Pough, eds. Academic Press, New York, NY.
- Fitch, H. S. 1956. An ecological study of the collared lizard (Crotaphytus collaris). Univ. Kans. Publ. Mus. Nat. Hist. 8(3):213-274.
- Gagge A. P. 1940. Standard operative temperature, a generalized temperature scale applicable to direct and

- partional calorimetry. Amer. Jour. of Physio. 131:93-103.
- Geffen, E. and H. Mendelssohn. 1989. Activity patterns and thermoregulatory behavior of the Egyptian tortoise Testudo kleinmanni in Israel. J. Herpetol. 23(4):404-409.
- Goin, C. J., O. B. Goin and G. R. Zug. 1978. Introduction to Herpetology. W. H. Freeman and Co., New York, NY. 378 pp.
- Grant, B. W. and A. E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard Sceloporus merriami. Ecology 69(1):167-176.
- Greenwald, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. Copeia 1974(1):141-148.
- Hammel, H. T., F. T. Caldwell, Jr. and R. M. Abrams. 1967. Regulation of body temperature in the blue-tongued lizard. Science 1967:1260-1262.
- Harwood, R. H. 1979. The effect of temperature on the digestive efficiency of three species of lizards, Cnemidophorus tigris, Gerrhonotus multicarinatus and Sceloporus occidentalis. Comp. Biochem. Physiol. 63:417-433.
- Hertz, P. E. and R. B. Huey. 1981. Compensation for altitudinal changes in the thermal environment by some Anolis lizards on Hispaniola. Ecol. 62:515-521.
- Hertz, P. E., R. B. Huey and E. Nevo. 1983. Homage to



- Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evol.* 37(5):1075-1084.
- Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pages 25-91. In: *Biology of the Reptilia*. Vol. 12, C. Gans and F. H. Pough, eds. Academic Press, New York, N. Y.
- Huey, R. B. and A. E. Dunham. 1987. Repeatability of locomotor performance in natural populations of the lizard Sceloporus merriami. *Evol.* 41(5):1116-1120.
- Huey, R. B. and P. E. Hertz. 1984. Is a jack-of-all-temperatures a master of none? *Evol.* 38(2):441-444.
- Huey, R. B. and E. R. Pianka. 1977. Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecol.* 58:1066-1075.
- Huey, R. B. and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. *The Quarterly Review of Biology* 51(3):363-384.
- Hunsaker II, D. and C. Johnson. 1959. Internal pigmentation and ultraviolet transmission of the integument in amphibians and reptiles. *Copeia* 1959(4):311-315.
- James, F. C. and W. P. Porter. 1979. Behavior - microclimate relationships in the African rainbow lizard, Agama agama. *Copeia* 1979(4):585-593.
- Lillywhite, H. B. 1970. Behavioral temperature regulation in the bullfrog, Rana catesbeiana. *Copeia* 1970(1):158-168.



- Lillywhite, H. B., P. Licht and P. Chelgren. 1973. The role of behavioral thermoregulation in the growth energetics of the toad, Bufo boreas. Ecology 54(2):375-383.
- Londos, P. L. and R. J. Brooks. 1988. Effect of temperature acclimation on locomotory performance curves in the toad, Bufo woodhousei woodhousei. Copeia 1988(1):26-32.
- Marcellini, D. L. and T. A. Jenssen. 1989. Thermal ecology of the tropical iguanid lizard, Leiocephalus schreibersi. Am. Midl. Nat. 122:44-50.
- McAllister, C. T. and L. C. Fitzpatrick. 1989. The effect of thermal acclimation on oxygen consumption in the salamander, Eurycea neotenes. J. of Herp. 23(4):439-442.
- Muth, A. 1977a. Body temperatures and associated postures of the zebra-tailed lizard, Callisaurus draconoides. Copeia 1977(1):122-125.
- \_\_\_\_\_. 1977b. Thermoregulatory postures and orientation to the sun: a mechanistic evaluation for the zebra-tailed lizard, Callisaurus draconoides. Copeia 1977(4):710-720.
- Patterson, J. W. and P. M. C. Davies. 1989. A possible effect of climate on resting metabolic rate in lizards. Copeia 1989(3):719-723.
- Peterson, C. R. 1987. Daily variation in the body temperatures of free-ranging garter snakes. Ecology 68(1):160-169.

- Porter, K. R. 1972. Herpetology. W. B. Saunders Co., Philadelphia, PA. 524 pp.
- Porter, W. P. and F. C. James. 1979. Behavioral implications of mechanistic ecology II: the African rainbow lizard, Agama agama. Copeia 1979(4):594-619.
- Porter, W. P. and C. R. Tracy. 1983. Biophysical analysis of energetics, time-space utilization, and distributional limits. Pages 55-83. In: Lizard Ecology: Studies of a Model Organism. R. B. Huey, E. R. Pianka and T. W. Schoener, eds. Harvard Univ. Press, Cambridge, Mass.
- Pough, F. H. and C. Gans. 1982. The vocabulary of reptilian thermoregulation. Pages 17-23. In: Biology of the Reptilia. Vol. 12, C. Gans and F. H. Pough, eds. Academic Press, New York, NY.
- Seymour, R. S. 1972. Behavioral thermoregulation by juvenile green toads, Bufo debilis. Copeia 1972(3):572-575.
- Soule M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. Copeia 1963(1):107-115.
- Spellerberg, I. F. 1972. Thermal ecology of allopatric lizards (Sphenomorphus) in southeast Australia. I. The environment and lizard critical temperatures. Oecologia 9:371-383.
- \_\_\_\_\_. 1982. Biology of Reptiles: An Ecological Approach. Blackie, London, England. 158 pp.



- Spotila, J. R., R. E. Foley, J. P. Schubauer, R. D. Semlitsch, K. M. Crawford, E. A. Standora and J. W. Gibbons. 1984. Opportunistic behavioral thermoregulation of turtles, Pseudemys scripta, in response to microclimatology of a nuclear reactor cooling reservoir. *Herpetologica* 40(3):299-308.
- Spotila, J. R., O. H. Soule and D. M. Gates. 1972. The biophysical ecology of the alligator: heat energy budgets and climate spaces. *Ecology* 53(6):1094-1102.
- Stevenson, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *The Amer. Nat.* 126(3):362-386.
- Templeton, J. R. 1967. Panting and pulmonary inflation, two mutually exclusive responses in the chuckwalla, Sauromalus obesus. *Copeia* 1967(1):224-225.
- Templeton, J. R. and W. R. Dawson. 1963. Respiration in the lizard Crotaphytus collaris. *Physiol. Zool.* 36:104-121.
- Tracy, C. 1982. Biophysical modeling in reptilian physiology and ecology. Pages 275-321. In: *Biology of the Reptilia*. Vol. 12, C. Gans and F. H. Pough, eds. Academic Press, New York, NY.
- Vial, J. L. 1975. Thermal related activity in the mesoamerican lizard Gerrhonotus monticolus. *Brit. J. Herpetol.* 5(5):491-495.
- Waldschmidt, S. 1980. Orientation to the sun by the



iguanid lizards Uta stansburiana and Sceloporus undulatus: hourly and monthly variations. *Copeia* 1980(3):458-462.

Waldschmidt, S. and C. R. Tracy. 1983. Interactions between a lizard and its thermal environment: implications for sprint performance and space utilization in the lizard Uta stansburiana. *Ecology* 64(3):476-484.

Webb, R. G. 1970. Reptiles of Oklahoma. Univ. of OK Press, Norman, OK. 370 pp.

**APPENDIX**

TABLE 1. Estimates of the effects on  $T_b$  of different mechanisms used by terrestrial ectotherms for thermoregulation from Stevenson, 1985.

Mechanisms	Maximum Change in $T_b$ for a 1-kg Animal (°C)
<b>Behavior</b>	
Seasonal range of mean $T_b$	56
Daily range of $T_b$	55
Habitat choice	38
Selection of microhabitat	
Sun versus shade	28
Burrowing	45
Climbing	35
Animal Grouping	5
Postural adjustments	
Orientation to sun	18
Body-shape changes	5
Orientation to wind	1
Elevation off substrate	5
Conduction to substrate	10
<b>Physiology</b>	
Integument	
Shortwave absorptance	5
Heat production	
Resting metabolism	1
Muscle activity	3
Evaporative cooling	
Cutaneous losses	
Dry-skinned	1
Wet-skinned	20
Panting	5
Salivation	5
Urination	5
Cardiovascular system	
Control of blood flow	
Body-surface	6
Body-appendage	6



TABLE 2. Total 1989 rainfall (mm) for the vicinity of Stillwater, Oklahoma, from Oklahoma State University Department of Agronomy.

Month	Total	Greatest Amount On One Day
January	41.5	19.1
February	42.7	16.2
March	93.5	52.0
April	4.2	2.5
May	169.0	59.5
June	136.5	28.7
July	110.5	96.2
August	125.7	53.7
September	121.5	65.0
October	70.5	39.7
November	0.0	--
December	12.5	10.0

TABLE 3. Mean 1989 temperature ( $^{\circ}\text{C}$ ) for the vicinity of Stillwater, Oklahoma, from Oklahoma State University Department of Agronomy Weather Station.

Month	Mean Maximum	Mean Minimum	Overall
January	11.9	-3.9	4.0
February	4.2	-6.3	-1.0
March	16.6	2.1	9.3
April	22.2	9.3	15.8
May	26.2	13.9	20.0
June	28.7	17.2	22.9
July	31.7	20.2	25.9
August	31.5	20.3	25.9
September	26.6	13.5	20.0
October	24.4	9.6	17.0
November	17.5	2.3	9.9
December	4.6	-9.5	-2.4

TABLE 4. Numbers of subjects and sightings of Crotaphytus collaris.

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	Numbers		Sightings
	Males	Females	
Hatchlings	3	2	44
Juveniles	4	7	96
Adults	8	7	200

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TABLE 5. Average mass (g) and average snout-vent length (mm) of Crotaphytus collaris subjects.

	Average Mass (g)		Average SVL (mm)	
	Males	Females	Males	Females
Hatchlings	4.3	2.5	46.0	42.5
Juveniles	28.0	22.0	83.3	80.4
Adults	44.6	30.7	99.6	91.7

TABLE 6. One-way ANOVA of hatchling male and female  $T_b$ .

Source	df	Mean Square	F	Probability
Between Sexes	1	1.04	0.40	0.57
Among Sexes	3	2.60		

TABLE 7. One-way ANOVA of juvenile male and female

 $T_b$ .

Source	df	Mean Square	F	Probability
Between Sexes	1	0.06	0.01	0.91
Among Sexes	79	4.95		



TABLE 8. One-way ANOVA of adult male and female  $T_b$ .

Source	df	Mean Square	F	Probability
Between Sexes	1	0.00	0.00	0.99
Among Sexes	92	7.54		

TABLE 9. One-way ANOVA of hatchling, juvenile, and adult  $T_b$ .

Source	df	Mean Square	F	Probability
Between Ages	2	1.29	0.21	0.81
Within Ages	177	6.18		

TABLE 10. Analysis of covariance of  $T_b$  of the three age classes of Crotaphytus collaris at different  $T_a$ .

Source	df	SS	F	Probability
Air temperature	1	500.76	148.65	< .0001
Age	2	2.23	0.33	.7188
Error	176	592.90		



TABLE 11. Analysis of covariance of  $T_b$  of the two sexes of Crotaphytus collaris at different  $T_a$ .

Source	df	SS	F	Probability
Air Temperature	1	500.76	149.86	< .0001
Sex	1	3.70	1.11	.2941
Error	177	591.43		

TABLE 12. Chi-square analysis for numbers of males and females active at each hour of the day.

HOURS	MALES		FEMALES	
	OBS	EXP	OBS	EXP
0900	8	7.05	7	7.95
1000	13	11.28	11	12.72
1100	15	15.51	18	17.49
1200	18	15.98	16	18.02
1300	20	17.39	17	19.61
1400	8	14.57	23	16.43
1500	12	14.10	18	15.90
1600	11	14.57	20	16.43
1700	14	11.75	11	13.25
1800	14	14.10	16	15.90
1900	14	10.34	8	11.66
2000	9	9.40	11	10.60

$$\chi^2 = 13.11, 11 \text{ df}, p = .2862$$

TABLE 13. Chi-square analysis for different age classes active at each hour of the day.

HOUR	HATCHLINGS & JUVENILES		ADULTS	
	OBS	EXP	OBS	EXP
0900	5	5.79	9	8.21
1000	9	8.69	12	12.31
1100	14	12.41	16	17.59
1200	9	12.82	22	18.18
1300	16	16.13	23	22.87
1400	13	12.82	18	18.18
1500	21	13.65	12	19.35
1600	16	15.31	21	21.69
1700	10	11.58	18	16.42
1800	12	14.48	23	20.52
1900	9	8.27	11	11.73
2000	5	7.03	12	9.97

$$\chi^2 = 11.51, 11 \text{ df}, p = .4019$$



TABLE 14. Two-way ANOVA of percent available microhabitat for small, medium, and large lizards for all hours of the day.

Source	df	Mean Square	F	Probability
Sizes	2	0.04	0.26	0.770
Hours	11	1.27	9.56	< 0.005
Interaction	22	0.06	0.40	0.990
Error	180	0.13		

TABLE 15. Goodness-of-fit for microhabitat selection by Crotaphytus collaris to random expectations drawn from copper models and transects defining availability of optimal and suboptimal microhabitats.

HOUR		N	OPTIMAL		SUBOPTIMAL	
			OBS	EXP	OBS	EXP
0900	*	16	5	1.16	11	14.85
1000	*	25	13	3.91	12	21.10
1100		34	17	15.74	17	18.26
1200		39	27	24.59	12	14.41
1300		43	30	30.06	13	12.93
1400		34	20	22.27	14	11.73
1500	*	35	20	28.09	15	6.91
1600		39	13	14.14	26	24.86
1700		30	16	18.22	14	11.78
1800		36	26	24.58	10	11.42
1900		23	13	11.82	10	11.18
2000		20	1	2.46	19	17.54

$\chi^2 = 54.49$ , 12 df,  $p < .005$

\* = Major contribution to  $\chi^2$

TABLE 16. Two-way ANOVA of percent available microhabitat on the upper and lower portion of the dam for all hours of the day.

Source	df	Mean Square	F	Probability
Position	1	0.02	3.53	0.083
Time	13	0.40	75.13	0.0001
Error	13	0.01		



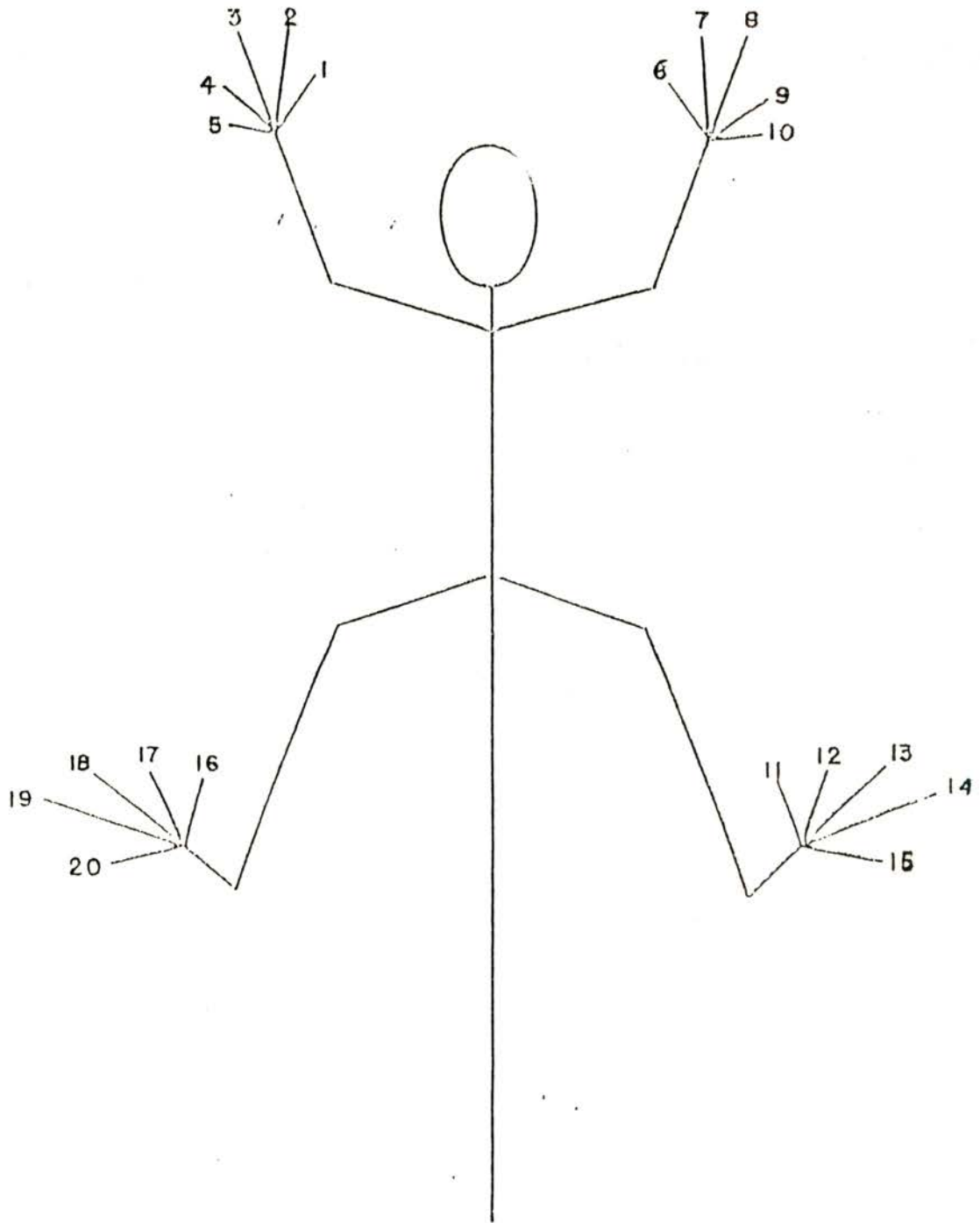


Figure 1. Numbering System Used for Toe-Clipping Lizards (Dorsal View)

## BODY TEMPERATURE FREQUENCY

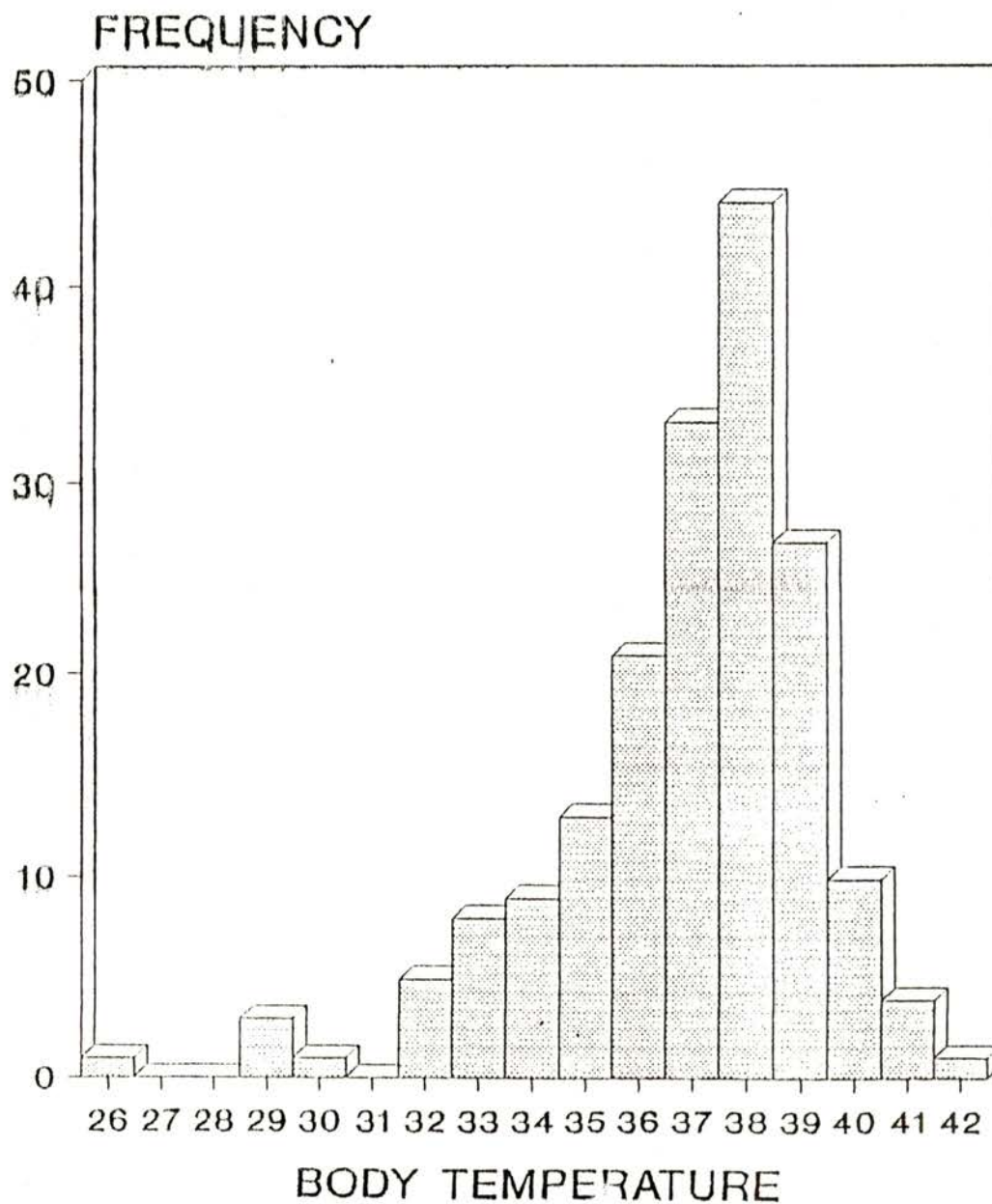


Figure 2. Frequency of Field Body Temperatures Measured from Crotaphytus collaris

# ACTIVITY OVER THE DAY

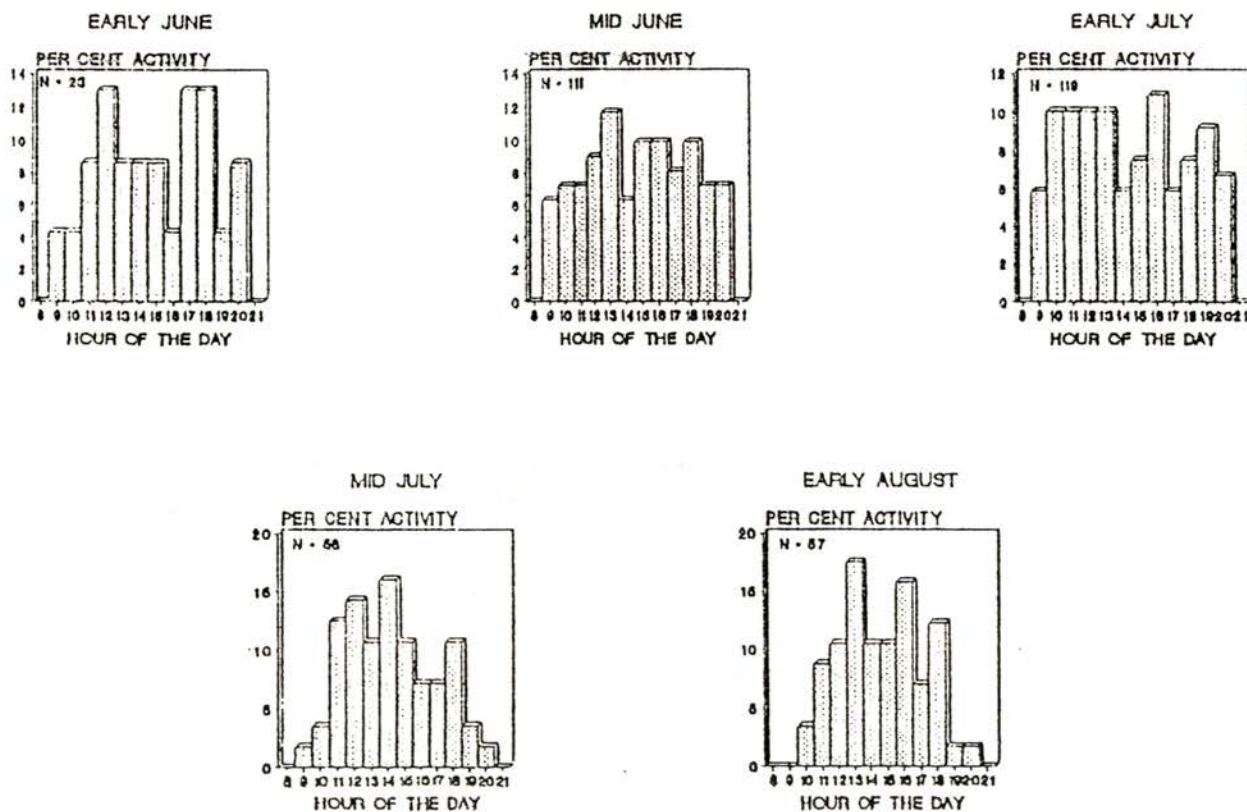


Figure 3. Percentage of *Crotaphytus collaris* Active Throughout the Day During the Five Major Sampling Periods



# MICROHABITAT AVAILABILITY OVER THE DAY

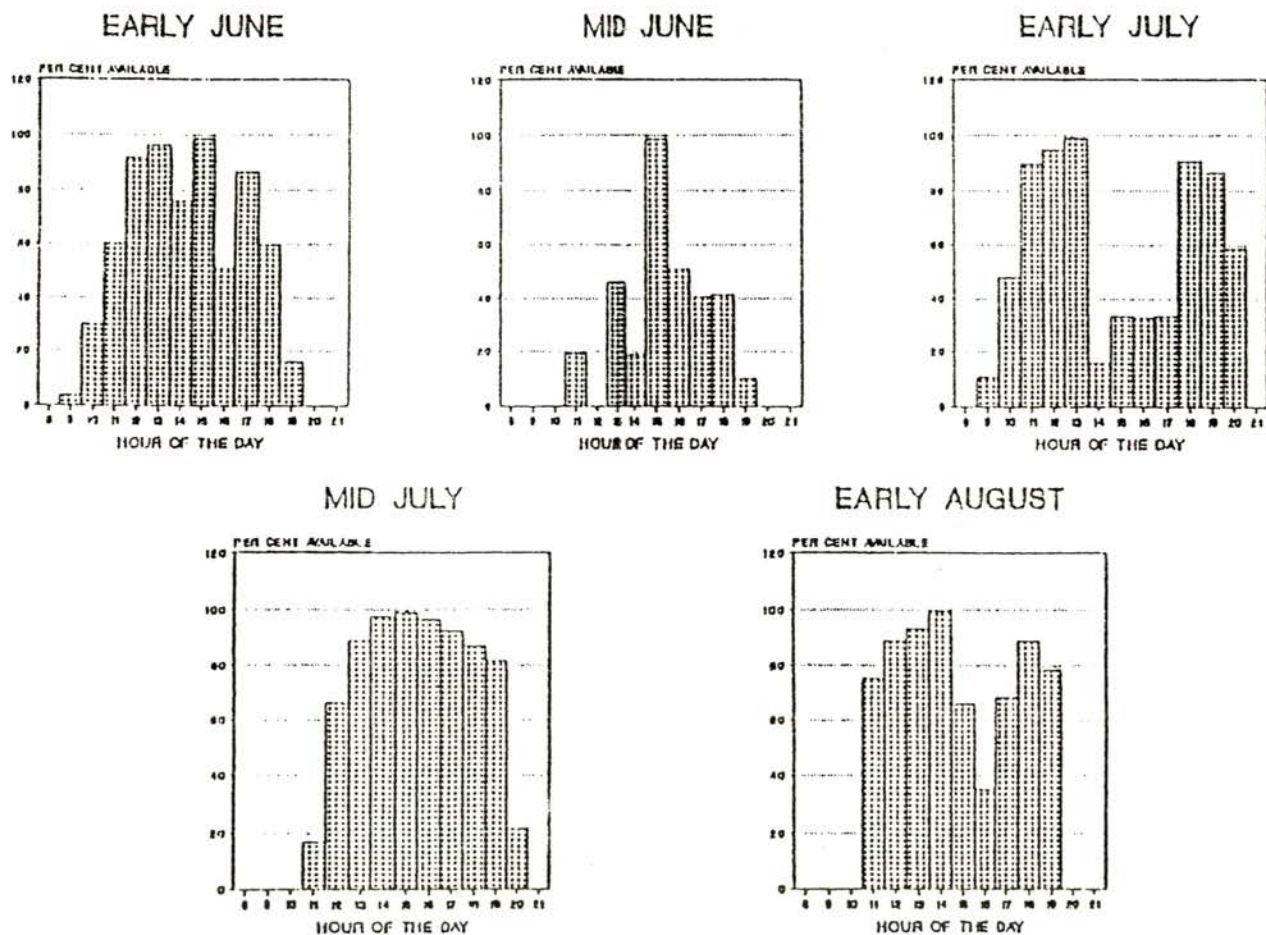


Figure 4. Percentage of Microhabitat Available to Crotaphytus collaris Throughout the Day, as Measured by Copper Models

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