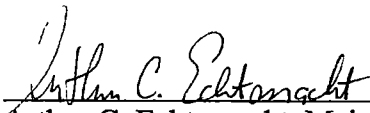
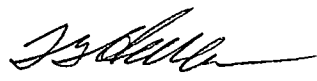


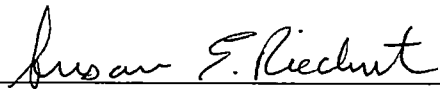
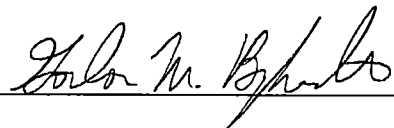
To the Graduate Council.

I am submitting herewith a thesis written by David Christopher Bishop entitled "Aspects of the winter behavioral ecology of *Anolis carolinensis* at the northern limit of its range." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

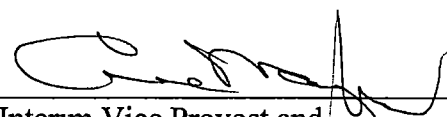

Arthur C. Echternacht, Major Professor


Thomas G. Hallam, Department Head

We have read this thesis and
recommend its acceptance:

Accepted for the council


Interim Vice Provost and
Dean of The Graduate School

Aspects of the winter behavioral ecology of *Anolis*
carolinensis at the northern limit of its range

A Thesis
Presented for the
Master of Science Degree
The University of Tennessee, Knoxville

David Christopher Bishop
December 2000

DEDICATION

To my parents, who have supported me in everything I have ever done

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ABSTRACT

The green anole (*Anolis carolinensis*, Sauria: Polychrotidae) is the only native member of the neotropical genus in the United States and can be found as far north as North Carolina and Tennessee. This thesis describes a two-year field study on the winter behavioral ecology of a northern population of green anoles in Tennessee. Green anoles remain active throughout the entire winter in Tennessee, a rare behavior for reptiles at this latitude. In the population used in this study, *A. carolinensis* shift habitats during the winter to a south-facing bluff where they seek refuge in rock crevices at night and during cloudy days. The crevices provide thermal protection from air temperatures that routinely drop below freezing. There are not enough crevices for all lizards to be solitary; however, *A. carolinensis* often aggregate even when unoccupied crevices are available nearby. Aggregations do not seem to provide any thermal benefits to the lizards. Lizards emerge from the crevices when the sun illuminates their section of the bluff. The emergence order of lizards from a crevice was nonrandom, some lizards consistently emerged earlier than others. Position in the emergence sequence was determined by the depth of the lizard within the crevice with shallow lizards emerging first. Lizards remain close to the same group of crevices throughout the entire winter season and often return to the same section of the bluff the following winter season. The winter sex ratio of the lizards on the bluff was male-biased during both seasons. Although appetite appears to be reduced in the winter, individuals were observed to eat throughout the winter season. There was significant growth in snout-vent length during

both winter seasons and significant growth in mass during the second season. Males had higher growth rates than females.

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PART I

GENERAL INTRODUCTION

Temperate-zone reptiles must be able to survive the low winter temperatures that occur at higher latitudes. The response of most temperate reptiles is to become dormant during the coldest part of the year. Winter dormancy can be found in all reptilian orders and may be viewed as an adaptive strategy for reducing costs when there are few benefits in remaining active (Hainsworth and Wolf 1978). The duration of winter inactivity in reptiles depends on the costs and benefits of being active and the severity of the climate. Reptiles may be continuous hibernators or be active periodically during the winter; and even within a species, the different sexes and age groups may vary in their amount of winter activity (see Gregory 1982 for an overview)

The main factor that regulates winter dormancy in reptiles is probably temperature (Case 1976), but food supply, photoperiod, and biological rhythms may also influence the onset and duration of hibernation (see Gregory 1982 for an overview). When temperatures begin to drop, reptiles often shift habitats to suitable overwintering sites. Winter habitat shifts have been found in turtles (Woodbury and Hardy 1948, Ernst 1976), lizards (Ruby 1977, Boykin and Zucker 1993) and snakes (Fitch 1963, 1965). Those individuals that survive may return to the same overwintering site that proved successful in previous years (Carpenter 1957, Worthington and Sabath 1966, Weintraub 1968, Brown and Parker 1976).

Choosing a suitable overwintering site is crucial for a reptile at higher latitudes. The greatest threat during the winter is freezing temperatures (Carpenter 1953, Lowe et al. 1971), but flooding of retreat sites and predation also cause mortality to overwintering reptiles (see Gregory 1982). Reptiles are not passive in their selection of retreat sites; refugia may be chosen using physical characteristics such as height, width, orientation,

depth and moisture (see Part II) Even after a winter retreat site is chosen, an individual may move to a different refuge altogether during the winter season or take advantage of the range of temperatures that are available within the refuge by shifting positions (Huey et al. 1989)

Reptiles often form aggregations in the winter, even if they are highly territorial during the breeding season Winter aggregations have been found in turtles (Woodbury and Hardy 1948, Felger et al. 1976), lizards (Vitt 1974, Ruby 1977), and snakes (Noble and Clausen 1936, Galligan and Dunson 1979). If a territorial species is confined to a limited amount of space, dominance hierarchies may form (Hunsaker and Burrage 1969, Brattstrom 1974) However, hierarchies are rare in winter aggregations since the dominance drive in most temperate reptiles is probably suppressed after the breeding season (Berry 1974) It would be wasteful to expend any excess energy in dominance-related disputes unless there is some limited resource that is worth fighting for such as food or basking and retreat spots. According to Gregory (1982), reptiles may form winter aggregations for at least three reasons. 1) there are a limited number of overwintering sites which forces animals to aggregate, 2) there may be thermal benefits in huddling together, 3) mating opportunities may be enhanced upon emergence from hibernation

Reptiles that do not hibernate must be able to maintain their energy and water budget to survive the winter season. If a reptile remains active during the winter without feeding, it may lose considerable weight (Wharton 1966). In addition, winter-active reptiles are more at risk to predators than inactive ones, and their escape ability may be impaired by the low temperatures (Huey and Bennett 1987) However, being active

provides opportunities for growth and temperature regulation (Huey 1982) that may be very valuable for individuals trying to reach reproductive size.

There are few winter field studies of the behavior of temperate zone reptiles. The present study is an investigation of the winter activity of the green anole (*Anolis carolinensis*, Sauria: Polychrotidae) in Tennessee. The population studied is near the northern range limit of the species, a boundary thought to be set by low winter temperatures (Gordon 1956). The green anole is the only reptile at the study location that is not dormant during the winter. Individuals can be seen basking on sunny winter days, even when temperatures are below freezing. Winter activity may be adaptive for *A. carolinensis* or possibly be the result of a phylogenetic constraint on the neotropical genus (Jenssen et al 1996). The present study focuses on the winter behavior of *A. carolinensis* rather than the physiology associated with winter activity.

In the population used for this study, *A. carolinensis* shift habitats prior to the winter season to a south-facing rocky bluff where they seek refuge in crevices at night and during cloudy days (Gatten et al 1988, personal observations). In part II of this thesis, I describe the thermal properties of the crevices and the behavior of the lizards in relationship to the crevices. Body temperatures of lizards were recorded prior to emergence from the crevices to determine if there were temperature differences between lizards with different masses and to see if lizards could maintain body temperatures independent of crevice temperatures. The emergence order of the lizards from several crevices was observed to determine if an individual's position in the emergence sequence was random, and if it was not, what factors influenced emergence position. Also, light intensity, and air, crevice, and rock face temperatures were recorded to identify the major

physical cues that trigger emergence from the crevices. Finally, the last section of Part II describes the winter and seasonal movements of the lizards. Movements were monitored to determine if lizards remain at the same crevice throughout the entire winter season and to see if individuals return to the same crevices the following winter season. Part III describes the winter sex ratio, size distribution, and growth of the lizards found on the bluff.

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PART II

EMERGENCE AND MOVEMENTS OF WINTER-AGGREGATED
GREEN ANOLES (*Anolis carolinensis*, SAURIA: POLYCHROTIDAE)
AND THE THERMAL PROPERTIES OF THEIR CREVICES IN
TENNESSEE

INTRODUCTION

Reptiles that live in temperate regions have two options during the winter. They either become dormant or acclimate (Ragland et al. 1981, Jenssen et al. 1996). Those individuals that cannot maintain adequate body temperatures must hibernate (Gregory 1982). Many lizards are able to acclimate to colder temperatures and are active on sunny winter days (Miller 1951, Gordon 1956, Worthington and Sabbath 1966, Weintraub 1968, Goldberg 1972, Ballinger and Congdon 1981, Rugiero 1995, Blazquez and Ortega-Rubio 1996). Winter activity in lizards may increase growth (Crenshaw 1955, Miller 1951, Ruby 1977, Ballinger and Congdon 1981), decrease gestation time (Ruby 1977), or be the result of a phylogenetic constraint (Jenssen et al. 1996).

Reptiles that are solitary or territorial during the breeding season often aggregate in the winter. Winter aggregations may form for a variety of reasons but are often attributed to insufficient over-wintering sites or for thermoregulatory purposes (see Elfström and Zucker 1999 for an overview). Winter aggregations occur in snakes (Vitt 1974a, Brown et al. 1974, Prior and Weatherhead 1996), turtles (Woodbury and Hardy 1948, Patterson 1971) and lizards. Winter aggregations of hibernating and active lizards have been found in *Anolis carolinensis* (Polychrotidae: Hamilton 1948, Neil 1948, Gordon 1956), *Eumeces fasciatus* (Scincidae: Hamilton 1948), *Eumeces septentrionalis* (Scott and Sheldahl 1937), *Gerrhonotus coeruleus* (Anguidae: Vitt 1973), *Podarcis muralis* (Lacertidae: Rugiero 1995), *Sceloporus grammicus* (Phrynosomatidae: Axtell and Axtell 1970), *Sceloporus jarrovi* (Burns 1970, Tinkle and Hadley 1973, Ruby 1977, 1978, Congdon et al. 1979, Marler and Moore 1988), *Sceloporus occidentalis* (Gray and Stroud 1979), *Sceloporus orcutti* (Weintraub 1968), *Urosaurus ornatus*

(Phrynosomatidae: Worthington and Sabbath 1966, Vitt 1974b, Boykin and Zucker 1993, Elfström and Zucker 1999), and *Xantusia vigilis* (Xantusiidae: Miller 1951, Zweifel and Lowe 1966).

The green anole (*Anolis carolinensis*) is the northern-most member of its neotropical genus (Williams 1969) and can be found as far north as North Carolina and Tennessee (Conant and Collins 1991). The northern boundary of the species range appears to be limited by low temperatures (Gordon 1956, Wilson and Echternacht 1987). Low winter temperatures are common in Tennessee, but *A. carolinensis* do not hibernate. In the population used for this study, *A. carolinensis* are found in winter aggregations on a south-facing bluff where they seek refuge in crevices at night and during cloudy weather. The winter behavior of aggregated *A. carolinensis* has not been previously studied. I investigated the thermal properties of the crevices, lizard body temperatures within the crevices, the cues that influence lizard emergence from the crevices, emergence behavior, and winter and seasonal movements.

METHODS

Site Description. - The study site is located on the Little Tennessee River in Monroe County, Tennessee. A south-facing bluff is located about 15-20 m from the river. There is a narrow strip of vegetation along the edge of the river separated from another at the base of the bluff by an old railroad bed. Deciduous trees dominate the area. The common species are: black locust (*Robinia pseudoacacia*), hackberry (*Celtis occidentalis*), redbud (*Cercis canadensis*), ash (*Fraxinus* spp.), oak (*Quercus* spp.), black walnut (*Juglans nigra*), sycamore (*Platanus occidentalis*) and box elder (*Acer negundo*).

There are a few eastern red cedars (*Juniperus virginiana*), and the dominant herbaceous vegetation is crown-beard (*Verbesina occidentalis*) and occasionally tickweed (*Verbesina virginica*) (Minesky 1999).

Subjects – *Anolis* is the largest lizard genus in the world with over 250 species found in the New World tropics and subtropics. The green anole (*Anolis carolinensis*) is the only member of the genus that is native to the continental United States (Conant and Collins 1991). *Anolis carolinensis* are small (under 75 mm snout-vent length), diurnal, arboreal lizards that are common in the southeast. During the spring and summer, male *A. carolinensis* spend much of their time displaying to other lizards and actively defending their territories. The aggressive activity decreases sharply after the breeding season (Gordon 1956, Jenssen et al. 1995, 1996) which allows for aggregations of lizards to form in the winter (Hamilton 1948, Neil 1948, Gordon 1956). The term hibernation has been used by several authors to describe the winter behavior of *A. carolinensis* (see Minesky 1999 for an overview), but winter activity has been documented (Neil 1948, Gordon 1956, Ragland et al. 1981, Gatten et al. 1988, Jenssen et al. 1996). Aggression resumes in the spring, and lizards begin to space themselves out and set up their breeding-season territories.

In the Monroe County, Tennessee population, *A. carolinensis* are found on trees and surrounding vegetation during the warmer months and begin moving to the rocky bluff in late October or early November where they usually stay until late March or early April (personal observations). Throughout the winter months (Dec - Feb) in Tennessee, lizards bask on sunny days on the sun-exposed rocky bluff and use the crevices for refuge. Crevices that contained *A. carolinensis* on at least three different days were

assigned a number and marked with red fingernail polish. Sixty-seven crevices were marked during this study and searched on each observation day. There were 70 observation days during the winter seasons of 1998-1999 and 1999-2000

The physical characteristics of occupied crevices (width at opening, length, and angle from the horizontal ground) were recorded to give the reader an idea of what the crevices look like. It was not the goal of the study to determine which physical characteristics of crevices were preferred by lizards. The depth of the majority of crevices could not be accurately measured due to the direction changes that occur within a crevice. No attempts were made to measure the height above the ground of high crevices. The lowest crevice observed is at ground level and the highest is estimated to be at least 20 m above ground level. Crevices are located at all heights in between. Lizards were observed at even higher positions on the bluff but were inaccessible for this study.

Capture of Lizards - Lizards were captured from November - March by hand or noose, toe-clipped and painted with a number using a silver paint pen (Pilot Silver Marker™). The shedding frequency decreases during the winter months, and lizards usually had to be painted only one time each winter. The sex of each lizard was determined on the basis of the presence (males) or absence (females) of post anal scales, and it was placed in a plastic bag and weighed to the nearest 0.5 g using a spring scale (Pesola™ 10 g). Its snout-vent length (SVL) and tail length were measured to the nearest 0.5 mm with a clear plastic ruler. Lizards were released at the point of capture immediately after measurements were taken.

Crevice Temperatures - Crevice temperatures were monitored in crevices 26 and seven. These crevices consistently had lizards present during both winter seasons and were located in an obscure part of the bluff that prevented potential vandals from finding the temperature equipment. To determine if crevices provide thermal benefits for overwintering lizards, a HOBO™ temperature data logger probe (Onset Computer Corp., Pocasset, MA, USA) was placed 10 cm inside a crevice (No 26) for 33 days (Jan 17 – Feb 19, 2000). Crevice 26 was occupied during both winter seasons. A Tidbit™ temperature data logger (Onset Computer Corp) was attached by Velcro™ to the rock face outside of the crevice opening. The internal temperature sensor in the Tidbit was less than 2 mm from the surface of the rock. Tidbits and HOBOS have been shown to produce temperatures similar to models for small lizards (Vitt and Sartorius 1999). Another Tidbit was used to measure air temperature in the shade 1m from the crevice. Temperatures were recorded at 15-min intervals.

Lizards may be found at various depths within a crevice. To determine the effects of depth on crevice temperature, three HOBO temperature probes were placed inside a crevice (No 7) at 10 cm, 20 cm and 30 cm, respectively. Rock face temperatures and air temperatures were recorded as described above. Temperatures were recorded at 15-min intervals for 19 days (Feb 24 – March 11, 2000).

Lizard Temperatures. – It is not possible to get cloacal temperatures without pulling lizards out of crevices. In order to determine if there was any difference between the skin and cloacal temperatures of anoles, a brief study was conducted prior to obtaining field data. Ten males and ten females were captured from the study site and

brought back to the laboratory. Lizards were fastened to wooden dowels with a rubber band, and copper-constantan thermocouples were inserted into the cloaca and taped to the dorsal skin of each individual. Lizards were placed in a dark climate-controlled room set at 9 °C for 1 hr prior to recording temperatures. Temperatures were obtained using a microprocessor thermometer (Omega Engineering, Inc., Stamford, Connecticut, USA, model HH-23). There was no significant difference between skin and cloacal temperatures for males (mean $\pm$ SE: skin = 9.7 ± 0.2 °C, cloacal = 9.7 ± 0.2 °C, t-test: $t_{18} = 4.734$, $P=0.873$) or females (mean $\pm$ SE skin = 9.3 ± 0.2 °C, cloacal = 9.2 ± 0.2 °C, Mann-Whitney U test: $U=41.50$, $N_1=10$, $N_2=10$, $P=0.515$)

Prior to the emergence of lizards from the crevices each morning, body temperatures of accessible individuals were obtained by pressing a temperature probe (Omega model HH-23) against each lizard's side. A flashlight was used to see into each crevice. Many crevices are oriented in a way that prevents access to, or even seeing, lizards that are deep in the crevice. The shaded air temperature 1 m from the crevice opening, and the substrate temperature within 1 cm of the lizard were also recorded. For those lizards that had multiple temperatures recorded during a season, the temperatures were averaged. Lizards that could not be identified were omitted from the body temperature analyses.

Emergence Cues - To determine if crevice temperature triggers lizard emergence, a HOBO temperature probe was placed 10 cm inside a crevice 1-2 hours before emergence to monitor any temperature changes within the crevice. Most lizards are found deeper than 10 cm within the crevice during typical winter weather, but I did not want to place the temperature probe too far in the crevice due to the possibility of

blocking the lizards within the crevice. A Tidbit was attached to the rock face with Velcro, and another Tidbit was suspended in the shade 1 m from the crevice opening and 1 m from the ground. Temperatures were recorded at 15-min intervals.

Light intensity (W/m^2) was monitored using a pyranometer (LI-COR Inc., Lincoln, Nebraska, USA, model PY 10882) attached to the rock face with Velcro. Light measurements were recorded in 15-min intervals with a LI-COR datalogger (model LI-1000). Lizard behavior did not seem to be influenced by the presence of the temperature and light data loggers. Three different crevices (23, 39, 43) were monitored on 13 randomly selected days between January 24, 1999 to March 18, 1999.

Emergence Order. - The order of emergence of lizards from a crevice was recorded to determine if emergence order is random and whether or not it is influenced by the size or sex of the individual. Crevices that contained at least three lizards were observed. During the 1998/1999 season, four crevices (19, 23, 39, 43) were observed, but only two (23, 39) consistently contained multiple lizards. Crevices 23 and 39 were close together (< 2 m), could be observed simultaneously, and were monitored during both 1998/1999 and 1999/2000 winter seasons.

A flashlight was used to search for lizards inside the crevices prior to their emergence. Numbers on individuals that could be seen in the crevices were recorded to see if lizards at shallower depths emerged earlier than lizards at greater depths. Most lizards within a given crevice could not be seen due to depth and orientation of the crevice.

The emergence of lizards was observed from a distance of 15-20 m with 10x binoculars. Lizard behavior did not seem to be influenced by my presence at this

distance The numbers written on the their sides could usually be seen unless the lizards were partially concealed within a crevice To make identification of partially concealed lizards easier, three dots were painted in various colors and patterns on the side of each individual's head with Testors™ model paint.

An index was created to rank each lizard by its position in the emergence sequence. The daily emergence index was calculated by dividing the individual's position in the emergence sequence by the number of lizards present that day. A mean emergence index was then calculated for each lizard that was seen five or more times. Values ranged from 0-1. A value of 1 indicates a lizard emerged last every day, and a value close to 0 indicates a lizard emerged close to first each day.

To determine if mass is correlated with emergence position, lizards in a crevice were first ranked by mass each day. A mass index was then calculated by dividing by the number of lizards with different masses present that day. A value of 1 indicates an individual is the heaviest lizard in the crevice that day, and a value close to 0 indicates an individual is the lightest lizard present. Observation days that included fewer than two lizards are omitted. Correlations between the daily emergence and mass indices were calculated.

Winter and Seasonal Movements. - To determine if lizards exhibit crevice fidelity during the winter season, I searched the study site on each observation day and noted the positions of each individual found. The number of the crevice that was occupied by each lizard was recorded. If an individual moved to a different crevice between sightings, the distance between the two crevices was recorded. Distances were estimated to the nearest

1 cm using a 15 m measuring tape. For those lizards seen at least five times between December 1st and the end of the winter season, the mean distance moved between crevices was calculated. This does not estimate the total amount of movement during the winter but provides an estimate of the amount of movement among crevices across sightings. For example, a lizard will have a mean movement distance of zero if it returns to the same crevice at night, even though it may have moved several meters during the day.

The winter season was determined to be over when lizards began moving from the rock crevices to the vegetation near the river. During the 1998/1999 season, lizards started to move the last week of March. In 1999/2000, warm temperatures arrived early (Table 2 1, Appendix), and lizards began to move during the last week of February and first week of March.

A 250 m transect was established along the base of the bluff to help detect movements. Stakes were hammered into the ground every 5 m. The rocks and the vegetation near the bluff and the river were searched for individuals during the spring and summer during both seasons to determine how far lizards move from their winter to summer range. During the 1999/2000 season, lizards were recaptured to determine if surviving individuals returned to the same crevices they inhabited the previous winter.

RESULTS

Crevice Physical Characteristics. – Out of 67 marked crevices, 58 were accessible for measurements. The majority of the crevices occupied were straight fissures; however, a few crevices were not, a characteristic that made measuring crevice

orientation (angle from the horizontal ground) difficult. Three crevices did not exist at the end of the 1999/2000 season (when crevice measurements were made) because of changing rock conditions. In addition, a few crevices were obstructed by woody vines that prevented accurate measurement of the crevices. Crevices had a mean width ($\pm$ SE) at the opening of 14.0 ± 0.9 mm (range = 4-35 mm) and a mean length of 257.5 ± 19.3 mm (range = 30-770 mm). The mean angle from the horizontal ground was $41.9 \pm 3.3^\circ$ (range = 6-87°).

Crevice Temperatures - Crevice temperatures do not vary as much as air or rock face temperatures (Fig. 2.1). Temperature sensors attached to the rock face heat up rapidly once the sun illuminates the bluff. Crevice temperatures lag behind the air and rock face temperatures and remain above freezing throughout the night (Table 2 2). Different crevices have different thermal properties. For example, temperatures were recorded in crevices 23 and 39 at 10 cm every 15 min for 49.5 h during March 17-19, 1999. Lizards occupied both crevices at that time. Crevice 23 had a mean ($\pm$ SE) temperature of 14.2 ± 0.26 °C (range=10.2-22.5 °C), and crevice 39 had a mean ($\pm$ SE) temperature of 15.2 ± 0.23 °C (range=7.83-20.6 °C). Even though the crevices are located less than two meters apart, they have significantly different temperatures (t-test: $t_{388}=-3.043$, $P=0.003$). Depth within a crevice also affects the range of temperatures that occur. Lizards at shallow depths experience a wider range of temperatures than those deeper within the crevice (Fig. 2.2). The temperature variances at the three depths (10, 20, 30 cm) are unequal (Levene's Test: $F_{2,4443}=275.73$, $P<0.0001$), and each depth is statistically different from the other two (Tukey's test. $P<0.05$). All crevice depths had

minimum temperatures above air and rock face minimum temperatures. In addition, all crevice depths experienced smaller temperature ranges than the air and rock face (Table 2.3).

Lizard Temperatures - During the 1998/1999 season, 78 surface body temperatures were recorded prior to emergence for 38 different lizards in 25 different crevices. There was no significant difference in male and female surface body temperatures (1998-1999: mean male temperature $\pm$ SE = 11.1 ± 0.5 °C, female = 10.4 ± 0.8 °C, t-test $t_{36} = 0.695$, $P=0.491$; 1999-2000: male = 11.9 ± 0.4 °C, female = 12.5 ± 0.5 °C $t_{58} = -0.818$, $P=0.417$) or in the differential between their body and crevice temperatures (1998-1999: mean male temperature differential $\pm$ SE = 0.2 ± 0.1 °C, female = 0.3 ± 0.2 °C, Mann-Whitney U test $U=152$, $N_1=25$, $N_2=13$, $P=0.746$, 1999-2000: male = $-2.3 \times 10^{-3} \pm 1.7 \times 10^{-2}$ °C, female = $1.2 \times 10^{-2} \pm 2.4 \times 10^{-2}$ °C, t-test $t_{58} = -0.458$, $P=0.648$) during either season, so males and females were combined. In 1998-1999, mean lizard temperature ($\pm$ SE) was 10.9 ± 0.45 °C, and mean crevice temperature at the point of the lizard was 10.6 ± 0.47 °C. During the 1999/2000 season, 94 temperatures were recorded for 60 different lizards in 27 different crevices. Mean lizard temperature was 12.0 ± 0.32 °C, and mean crevice temperature at the point of the lizard was 12.0 ± 0.32 °C. Lizard temperatures are highly correlated with crevice temperatures for both seasons ($P<0.001$, Fig.2.3). There was no significant difference between lizard and crevice temperatures during either season (t-test, 1998/1999: $t_{74} = -0.34$, $P=0.735$; 1999/2000: $t_{118} = -0.009$, $P=0.993$). The greater variation in temperatures during the 1998/1999 season is likely the result of two factors. The four temperatures with the

largest deviation from the regression line are the result of lizards being caught in shallow crevices on very cold mornings. At shallow depths, the low air temperature causes lizard body temperatures to drop below the crevice temperature. Also during the 1999/2000 season, my accuracy in using the temperature probe increased with experience. There is no significant correlation between lizard mass and the differential between lizard and crevice temperatures (Spearman rank correlation 1998/1999 $r_s = -0.023$, $N=38$, $P=0.889$; 1999/2000 $r_s = 0.015$, $N=60$, $P=0.907$)

Emergence Cues - The mean crevice temperature ($\pm$ SE) at the time of head emergence was 12.2 ± 0.7 °C (range 6.6-17.5 °C, $N=20$). The mean temperature 1 hr before head emergence was 10.4 ± 0.7 °C (range 5.0-15.6 °C). The mean change in temperature from 1 hr before head emergence to the temperature at head emergence was 1.9 ± 0.3 °C (range 0 - 4.6 °C)

Light appears to be the main factor that cues emergence. On typical winter days, lizards do not emerge from the crevices before the sun illuminates the crevice. On overcast winter days, lizards may never emerge. In addition, lizards that have already emerged may retreat during periods of prolonged cloudiness and emerge again when the sun is bright. Figure 2.4 illustrates an example of the emergence of lizards relative to light intensity and temperature.

Emergence Order - During the 1999/2000 season, fewer lizards stayed at the same crevice than in the 1998/1999 season, and all lizards vacated crevice 39 in 1999/2000 for several weeks for unknown reasons (Table 2.4). Mean emergence indices for lizards seen five or more times are listed in Table 2.5. During the 1999/2000 season,

only one lizard from crevice 39 was observed five or more times, so the crevice is omitted from the table. Mean emergence indices should converge around 0.5 if the emergence order is random. Some lizards consistently come out earlier or later than other lizards. Emergence position is correlated with mass in crevice 39 during the 1999/2000 season with smaller lizards coming out first (Table 2.6). There is no significant correlation between mass and emergence position for crevices 23 and 39 during the first season or for crevice 23 during the second season.

The key factor that seems to determine emergence position is the depth of the lizard within the crevice. The shallow lizard within a crevice was identified on 16 occasions (11 different lizards) during the 1999/2000 season. On each of these occasions, the shallow lizard was the first to poke its head out of the crevice every day and was the first to completely emerge 14 of the 16 times.

Winter and Seasonal Movements - The mean distance moved between crevices ($\pm$ SE) for all lizards seen five or more times was 0.86 ± 0.11 m/sighting in 1998/1999 (N=81) and 0.57 ± 0.06 m/sighting in 1999/2000 (N=93). Most lizards move very little during the winter (Figure 2.5). Males had a mean crevice movement rate of 0.95 ± 0.14 m/observation in 1998/1999 (N=54) and 0.58 ± 0.60 m/sighting in 1999/2000 (N=62). Females had a mean crevice movement rate of 0.68 ± 0.15 m/sighting in 1998/1999 (N=27) and 0.54 ± 0.65 m/sighting in 1999/2000 (N=31). There was no significant difference between mean crevice movements between males and females in either season (Mann-Whitney U test 1998/1999: $U=604$, $N_1=54$, $N_2=27$, $P=0.212$; 1999/2000: $U=894$, $N_1=62$, $N_2=31$, $P=0.582$). There was also no significant correlation between lizard SVL

and mean crevice movement in either season (Spearman rank correlation: 1998/1999: $r_s=0.060$, $N=81$, $P=0.592$, 1999/2000: $r_s=0.169$, $N=93$, $P=0.105$). The size or sex of the lizard does not influence how far it will move during the winter.

Lizards begin moving away from the bluff to the vegetation along the river in early spring when temperatures begin to warm. The lateral movements of the lizards along the 250 m transect established along the base of the bluff were followed during the spring and summer to determine if lizards remain in the same section of the bluff that they inhabit during the winter. During the spring and summer of 1999, 24 lizards were recaptured. Eighteen lizards (75%) were found directly across from or within 5 m of the bluff section where their winter crevice(s) were located. In the spring and summer of 2000, 52 lizards were recaptured with 45 (87%) lizards found directly across from or within 5 m of the bluff section where their winter crevice(s) were located. It appears that most lizards move straight out from the bluff to their spring and summer home ranges. The two greatest lateral distances moved were 40 m and 65 m made by two males in the summer of 1999.

During the 1999/2000 winter season, 42 lizards (31 males, 11 females) were recaptured that had been seen at a crevice in the 1998/1999 winter season. Twenty-nine of the 42 lizards (69%) returned to a crevice they had inhabited during the previous season. Five additional lizards (12%) returned to within 2 m of a crevice that they had inhabited in the 1998/1999 winter season. The remaining eight lizards (19%) were all within the same 20 m section of the bluff they had inhabited the previous winter. Males and females had similar return rates. Twenty-one of 31 males (68%) and eight of eleven females (73%) returned to a crevice they had inhabited in the previous season. Four of

the males (13%) and the remaining three females (27%) returned to within 5 m of a previously inhabited crevice. The other six males (19%) returned to within 20 m of a crevice they inhabited the previous winter season.

DISCUSSION

Ectotherms may regulate their body temperature during low temperatures by changing their physiology or behavior (Hertz 1981) *Anolis carolinensis* acclimate to colder temperatures (Ragland et al 1981, Gatten 1985, Wilson and Echternacht 1987, Gatten et al 1988), and those in Monroe County, Tennessee shift their habitats during the winter season to south facing rocky bluffs along the river *Anolis carolinensis* from Tennessee are more cold-tolerant than those from Georgia and Florida (Wilson and Echternacht 1987), but the winter habitat shift may increase their chances of survival in the northern part of their range

Winter habitat shifts to sun-exposed cliffs and hills are common in reptiles (Carpenter 1953, Vitt 1973, Ruby 1977, 1978, Christian and Tracy 1983, Boykin and Zucker 1993, Prior and Weatherhead 1996). Rocks are an important heat source late in the day (Scott 1978) and increase the amount of time that lizards can be active (Christian and Tracy 1983). In east Tennessee, the bluff rock temperatures are very close to air temperature before sunrise and rise rapidly once the sun illuminates the bluff. Crisp et al. (1979) found a similar pattern.

Rock crevices are often used by lizards for protection from weather and predators (Weintraub 1968, Burns 1970, Ruby 1977, Crisp et al. 1979, Grant 1990, Joshi 1991, Boykin and Zucker 1993, Schlesinger and Shine 1994, Ballinger et al 1995, Lemos-

Espinal et al. 1997, Lemos-Espinal et al. 1998). Seeking refuge within crevices is thermally beneficial for over-wintering *A. carolinensis* in Tennessee. Crevice temperatures are fairly consistent throughout the night and remain above freezing, while air and rock temperatures drop rapidly after sunset. Fence lizards (*Sceloporus undulatus*) and five-lined skinks (*Eumeces fasciatus*) have also been seen inside the crevices, but they were never observed to be active during the winter.

Choosing an unsuitable winter habitat may result in freezing to death for an ectotherm (Vitt 1974b, Gregory 1982), and it has been suggested that the ability to over-winter successfully may limit the northern range of a species (Rosen 1991). Previous studies have shown that crevices may be chosen based upon physical characteristics such as height, width, orientation, depth, and moisture (Weintraub 1968, Leavell 1972, Jackson 1988, Schlesinger and Shine 1994, Lemos-Espinal et al. 1998). In this study, no attempt was made to differentiate occupied and unoccupied crevices by physical characteristics. However, the entrances to most of the crevices that *A. carolinensis* occupy are less than 2 cm wide, a size that likely provides sufficient protection from weather conditions and predators. Within the range of crevice heights observed, there does not appear to be any preferences for any particular height above the ground. There does, however, appear to be a preference for drier crevices. During the 1999/2000 season, a crevice that was inhabited by several lizards during November was vacated after the inside of the crevice became wet. Lizards returned to the crevice in February after it had dried. In addition, the depth of crevice may also affect whether the crevice is inhabited or not. Several shallow crevices that had lizards present in the early part of the

winter season were usually avoided once temperatures remained consistently below freezing

Aggregations of touching ectotherms may be thermally beneficial to help reduce heat loss. Some snakes and fish form aggregations at low temperatures and will remain aggregated until the temperature rises (Breder and Nigrelli 1935, Aleksuik 1977). *Boa constrictor* (Boidae) cooled in touching aggregations cool slower than solitary individuals (Myres and Eells 1968), and marine iguanas (*Amblyrhynchus cristatus*: Iguanidae) that huddle together at night have higher body temperatures than solitary lizards (Boersma 1982). *Anolis carolinensis* are sometimes found touching within the crevice, but usually they are not. Body temperatures of *A. carolinensis* are very similar to crevice temperatures prior to emergence, and huddling together would not likely cause body temperatures to remain elevated for an extended period of time. Thus, winter aggregations do not seem to provide any thermal benefits for *A. carolinensis*.

If an animal is solitary, it usually means there is defense of the area (Davis 1958, Cooper et al. 1985, Ballinger et al. 1995). Crevices were usually occupied by more than one anole; only rarely was a crevice occupied by a solitary individual. Not all crevices that appear to be suitable are inhabited by *A. carolinensis* during the winter, which might reflect an active choice of the lizards. It is possible that certain characteristics of unoccupied crevices were undesirable and undetected by me; however, crevices that have been occupied may have lizards that vacate and join others in a nearby crevice. This may or may not be a permanent move and could be the result of changing crevice conditions or an attraction to crevices that contain other lizards.

The sex and size distribution of reptiles within refugia is not always random (Carpenter 1953, Weintraub 1968, Brown et al. 1974, Lemos-Espinal et al. 1997). If there is segregation by size, it may be the result of the physical attributes of the refugia (Carpenter 1953, Weintraub 1968). Gordon (1956) reported that large male *A. carolinensis* space themselves out if hibernacula are not limited. In the present study, no consistent sex or size segregation was found for *A. carolinensis* within the crevices. However, one crevice consistently contained only small lizards, which was probably due to its narrow opening. Most crevices are large enough to allow all sizes of anoles to enter.

Anolis carolinensis emerge from crevices by first poking their head out and remaining there for several minutes with their body concealed within the crevice. Desert iguanas (Iguanidae: *Dipsosaurus dorsalis*) also emerge from their burrows in a similar manner which allows for body temperatures to be raised without being exposed to predators (Norris 1953, Dewitt 1967, Porter et al. 1973). After a few minutes, *A. carolinensis* will orient their bodies laterally within the crevice opening to expose an entire side to the sun. If the crevice is not long enough to permit sideways basking within the opening, the lizard typically emerges halfway out of the crevice while its hind legs and tail remain inside. Upon emergence, lizards may bask on the rock near the crevice, but often they will first bask in piles of dried leaves that heat up quickly and then move to the rocks after they have warmed.

The emergence of animals from refugia may be cued by light (Joshi 1991), temperature (Cowles 1941, Crenshaw 1955, Burns 1970) or biological rhythm (Heath 1962, Erkert 1982). *Anolis carolinensis* within a crevice orient their heads towards the

crevice opening which allows them to know when the sun has illuminated the crevice. On four occasions, lizards emerged 15-30 minutes before the sun illuminated the crevice, and on a few cloudy days, individuals were seen at the crevice opening at a time when they would normally emerge. This suggests that *A. carolinensis* may have a biological rhythm that helps regulate emergence, however, direct light levels are more important as indicated by the different emergence times depending on the amount of cloud coverage. Perhaps anoles sample the light intensity and air temperature to determine if it would be beneficial to emerge. Bats use light-sampling behavior prior to emergence from their roosts (Erkert 1982)

Gordon (1956) suggested that the emergence of *A. carolinensis* from winter refugia depends on air and substrate temperature. According to Gordon, air temperatures above 60° F (15.6 °C) will cause *A. carolinensis* in Louisiana to be active. The present study suggests there is no threshold crevice or air temperature that must be reached to cue emergence as long as the lizard is capable of moving. Temperatures vary on different days and within different crevices. Wilson and Echternacht (1987) found that *A. carolinensis* acclimated at 9 °C had a mean critical thermal minimum of 7.41 °C (range 5.8 - 9.1 °C) at which movement capability ceases. Crevices rarely dip below this temperature. Waiting for the crevice temperature to reach a minimum level before emergence would cause *A. carolinensis* to lose available activity time because of the lag between crevice temperatures and air or rock face temperatures (Fig. 2.4). *Anolis carolinensis* are active on sunny days even when the air temperature is below freezing. Although temperature may not be the main emergence cue, it does affect emergence.

Towards the end of the winter season, lizards often emerge prior to direct crevice illumination if the morning air temperature is warm.

Lizards will emerge and remain out of the crevices only if they can maintain their body temperatures within a preferential range. *Anolis carolinensis* will not emerge on overcast or windy days if the air temperature is low and will retreat back into the crevices if it becomes cloudy or windy. Failing to emerge or retreating during unfavorable conditions is common in lizards (Gordon 1956, Mayhew 1963, Burns 1970, Porter et al. 1973, Hertz and Huey 1981, Van Damme et al. 1987, Bauwens et al. 1990, Castilla and Bauwens 1991, Joshi 1991, Al-Johany 1995, Rugiero 1995) and helps protect them from being stranded away from their refugia due to low body temperatures.

It is disadvantageous for an ectotherm to emerge too early or too late. Emerging early may increase the time needed to raise body temperatures and cause greater exposure to predators (Avery and McArdle 1973). In addition, lower body temperatures decrease sprint speed and endurance and impair escape ability (Christian and Tracy 1981, Gatten 1985, Gatten et al. 1988, Huey and Bennett 1987, Castilla and Bauwens 1991). On two different occasions, I have seen *A. carolinensis* fall off of the rock face soon after emergence, which is probably the result of low body temperatures limiting their coordination. Emerging too late reduces available feeding and thermoregulatory opportunities (Avery and McArdle 1973, Christian and Tracy 1981).

The order of emergence of *A. carolinensis* within a crevice is nonrandom. Previous studies have shown that the emergence order from refugia may be influenced by sex (Korine et al. 1994), age/size (Mayhew 1963) or social rank (Quaranta and Evans 1949, Berry 1974, Brackin 1978). The sex of *A. carolinensis* does not determine an its

position in the emergence sequence. Mass was weakly correlated with emergence position for one crevice in 1998/1999 with small lizards emerging before large lizards. No other crevice observed in the 1998/1999 or 1999/2000 had a correlation between mass and emergence position. The reason for the weak correlation is unknown.

Small ectotherms may be expected to emerge before larger ones because of their higher heating rate (Cowles 1941, Claussen and Art 1981, Stevenson 1985). Berry and Turner (1986) found that small desert tortoises (*Gopherus agassizii* Testudinidae) emerged at lower air temperatures than large ones. However, small *A. carolinensis* within a crevice should not heat up faster than larger individuals since lizards begin to emerge before the crevice temperature rises significantly. Large ectotherms usually cool more slowly than small ones (Brattstrom 1973, Berry 1974, Claussen and Art 1981, Stevenson 1985) which might allow for larger individuals to emerge sooner if their body temperatures could be maintained throughout the retreat period. Due to their small size, *A. carolinensis* probably acclimate to the crevice temperature soon after they retreat which eliminates the possibility that larger lizards might emerge first because of higher body temperatures. *Anolis carolinensis* with different masses do not vary in body temperatures prior to emergence. The first lizard to poke its head out of the crevice will be the first to achieve a higher body temperature, and is usually the first to emerge completely

Social status might influence emergence position if there is some advantage in being the first or last lizard to emerge. If there is a correlation between size and emergence position, it may be difficult to differentiate whether the emergence order depends on social status or mass since dominance is often correlated with size in lizards

(Evans 1936, Greenberg and Noble 1944, Stamps 1984, Tokarz 1985) Social rank should not be assumed to affect emergence order unless there is evidence suggesting a social system exists. Hierarchies have been observed in territorial lizards that are confined to limited space (Evans 1936, Hunsaker and Burrage 1969, Brattstrom 1971, Pearson et al. 1976, Brackin 1978, Greenberg and Crews 1990). *Anolis carolinensis* do engage in some behaviors associated with dominance during the winter (dewlapping, headbobbing, chasing), but these behaviors are not nearly as common as they are in the breeding season (Jenssen et al. 1996, personal observations).

The most crucial winter resources for *A. carolinensis* are probably basking and retreat sites, but there is no shortage of available basking sites on the sun-exposed bluff, and crevice space is not limited. It would be wasteful to fight for a resource that is not in short supply (Marler 1956) The first lizards to emerge may have better feeding opportunities, but little time is spent foraging by *A. carolinensis* in the winter (Jenssen et al. 1996, personal observations) There would be little advantage in being the last to emerge unless the emergence position is a result of dominant lizards getting a better place within the crevice This would assume that the preferential spots are deeper within the crevice Greater crevice depths do have more stable temperatures and likely provide better protection from freezing and predators, but it is unlikely that social status influences emergence of *A. carolinensis* from winter retreats.

The depth that *A. carolinensis* occupies within a crevice has the greatest influence on emergence position. Shallow lizards within a crevice are the first to emerge. Others have made similar observations on other reptiles (Cowles 1941, Carpenter 1953). On warm nights, lizards do not retreat as far into the crevice, which allows them to emerge

sooner the following day. The fact that some individuals consistently emerge near the beginning or end of the sequence suggests that some lizards may have positions within the crevice that are used each time they retreat.

There is high crevice fidelity for *A. carolinensis* during the winter, with the majority of lizards moving less than 1 m from their last occupied crevice. Gordon (1956) and Gatten et al. (1988) indicated that *A. carolinensis* do not move much during the winter except in the vicinity of the overwintering retreats, and Jenssen et al. (1995, 1996) reported that movements are reduced during the post-breeding and winter season. Similarly, *Sceloporus jarrovi* usually remain within 0.5 m of their crevice during the winter (Ruby 1977).

The methods used in this study underestimate the total distance moved by the lizards throughout the day. Lizards often move away from their crevice once they have attained higher body temperatures and will usually return to the same crevice at night. If disturbed, lizards will retreat into a nearby crevice even if it is not one they normally inhabit. Some lizards remain at the same crevice over the entire winter while most alternate between several crevices in the same vicinity. Switching retreat sites during the winter has been found in tortoises (Woodbury and Hardy 1948, Wilson et al. 1999), snakes (Huey et al. 1989) and lizards (Worthington and Sabbath 1966).

Ruby (1977) found that *Sceloporus jarrovi* may move over 200 m to get to their overwintering site. *Anolis carolinensis* in Monroe County, Tennessee do not have to move large distances from their winter to summer habitat. The majority of lizards remain within 20 m of the bluff during the spring and summer. Most lizards move directly away from the bluff to the vegetation near the river rather than making large lateral movements

parallel to the bluff. The two male lizards that made lateral movements of 40 and 65 m were probably free-ranging males (Jenssen et al. 1995). Long movements may be underrepresented if lizards moved away from the observed area.

The permanent shift from the bluff to the surrounding vegetation is a gradual process that occurs over several weeks. *Anolis carolinensis* may move to the vegetation near the river on warm sunny days and return to their crevices at night. To determine if lizards would return to the same crevice if transplanted to the river vegetation in late winter, four lizards were moved to a tree about 20 m from their crevice on February 26, 2000. All four lizards were seen within three days at the same crevice from which they had been transplanted. The increase in air temperature, longer photoperiods, and increase in aggression likely cause lizards to begin to move to their breeding-season territories, but the overnight low air temperatures probably regulate the permanent habitat shift.

Many surviving *A. carolinensis* return to a crevice that they had used the previous winter. Returning to the same overwintering site each year may be the result of a shortage of available sites or the decision of the animal to return to a site that proved successful in the past (Gregory 1982). Those anoles that did not return to the same crevice were still found within 15 m of a crevice they had inhabited previously. It is unknown if individuals are choosing to return to a crevice they are familiar with or whether their return to the same location is due to their lack of movement away from that particular section of the bluff and river vegetation.

It is difficult to estimate winter mortality, but it is unlikely that many lizards die as the result of freezing once they make it to the bluff crevices. Not all lizards were recaptured after their initial marking, which may indicate mortality or movement to

crevices that were not observed. Over the course of the study, only three dead lizards and one skeleton were found. Two of the dead lizards were males with SVL's of 63 mm and 64 mm, and the female had a SVL of 57 mm. These mature lizards may have died of old age rather than environmental conditions. The sex and size of the skeleton was not determined. Snakes are probably the main predators for *A. carolinensis* during the spring and summer. During the winter, death due to predation is probably minimal with birds being the biggest threat during the daytime. *Anolis carolinensis* are dark brown throughout the entire winter in Tennessee and blend in very well with the leaves and dead vegetation scattered over parts of the bluff. The paint marks made lizards more conspicuous to me, but previous studies have shown that paint marking does not influence survival of other lizards (Jones and Ferguson 1980, Simon and Bissinger 1983). No predator attacks against *A. carolinensis* were observed during either winter season.

In summary, the winter habitat shift to the south-facing bluff likely increases the chances of survival for *A. carolinensis* in Tennessee. The crevices providing thermal benefits to lizards and probably protection from predators. Aggregations within crevices are likely the result of limited overwintering sites and possibly an attraction to crevices that contain other lizards. There does not appear to be any thermal benefits for aggregations within a crevice, and there is no predictable segregation based upon sex or size. Individuals may switch crevices during the winter but usually remain within the same vicinity throughout the winter. Many surviving lizards return to the same crevice the following winter. Depth appears to be the key factor that controls emergence order with shallow lizards emerging first. The emergence of lizards from a crevice is

controlled mainly by light intensity and is nonrandom, but more study is needed to understand why.

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APPENDIX

Table 2.1. Temperature comparisons for the 1998-1999 and 1999-2000 winter seasons. Temperatures (°C) were recorded at the McGhee-Tyson Airport in Knoxville (20 miles NE from study site). Data obtained from the United States National Oceanographic and Atmospheric Administration, Asheville, North Carolina

		Nov	Dec	Jan	Feb	Mar
Mean Maximum Temp.	1998-1999	15.8	11.4	11.8	12.2	13.1
	1999-2000	18.0	11.7	7.8	14.3	18.2
Maximum Recorded Temp.	1998-1999	23.3	23.3	23.3	23.3	21.7
	1999-2000	24.4	21.7	23.3	25.0	25.0
Mean Minimum Temp.	1998-1999	4.3	2.3	1.1	1.3	1.6
	1999-2000	5.0	-0.2	-1.7	1.3	5.4
Minimum Recorded Temp.	1998-1999	-2.2	-5.0	-9.4	-8.3	-3.9
	1999-2000	-2.8	-8.3	-10.6	-7.8	-2.2
Number of Days below 0 °C	1998-1999	5	13	13	13	14
	1999-2000	8	19	20	13	4

Table 2.2. Temperatures (°C) for crevice 26 between Jan 17-Feb 19, 2000 in Monroe County, Tennessee. Rock face temperatures were recorded by a T1dbit™ sensor attached to the rock 10 cm from the crevice. Air temperatures were recorded by a shaded T1dbit 1 m from the crevice. Crevice temperatures were recorded by a Hobo™ temperature probe 10 cm inside the crevice

Location	Temperature Mean $\pm$ SE	Temperature Range	Variance
Air	5.74 $\pm$ 0.13	-8.76 – 27.63	54.75
Rock Face	7.92 $\pm$ 0.15	-6.73 – 36.24	74.55
Crevice (10 cm)	9.99 $\pm$ 0.08	1.84 – 22.28	18.17

Table 2.3. Temperatures (°C) at different crevice depths between Feb 24-Mar 11, 2000 in Monroe County, Tennessee. Crevice temperatures were recorded by three Hobo™ temperature probes placed at 10, 20 and 30 cm inside the crevice. Air and rock face temperatures were recorded as described in Table 2.2.

Location	Temperature Mean $\pm$ SE	Temperature Range	Variance
Air	15.94 $\pm$ 0.18	2.78 – 32.14	45.65
Rock Face	18.05 $\pm$ 0.22	5.13 – 42.94	72.19
10 cm	18.04 $\pm$ 0.09	11.79 – 27.66	12.44
20 cm	17.51 $\pm$ 0.07	12.54 – 25.00	6.51
30 cm	17.31 $\pm$ 0.05	13.82 – 22.19	3.58

Table 2.4. Number of *Anolis carolinensis* present at each crevice where emergence order was observed. All observations were made between Dec-Mar in Monroe County, Tennessee.

Year	Crevice Number	Number of observations	Number of Lizards			Number Seen 5 or More Times	Number Seen Less Than 5 Times
			Mean	Range			
1998-1999	39	12	4.92	2 - 9	4	12	12
1998-1999	23	14	5.93	3 - 8	6	9	9
1999-2000	39	8	3.63	2 - 8	1	11	11
1999-2000	23	11	4.27	3 - 6	3	12	12

Table 2.5 Emergence indices for *Anolis carolinensis* seen five or more times. Daily emergence indices are calculated by dividing an individual's position in the emergence sequence by the number of lizards present that day. A mean emergence index is calculated for each lizard. A mean emergence index close to 0 indicates a lizard emerged close to first each day. All observations were made between Dec-Mar in Monroe County, Tennessee.

Year	Crevice	Lizard ID	Sex	SVL (mm)	Mass (g)	Number of observations	Mean Emergence Index
1998-1999	39	29	F	53	3.4	9	0.35
		3	M	48	3.1	7	0.69
		79	F	38	1.5	7	0.70
		37	F	41	1.5	8	0.88
1998-1999	23	62	M	51	3.2	12	0.22
		36	M	56	3.9	12	0.45
		72	M	45	2.3	10	0.53
		76	M	54	4.1	12	0.71
		89	M	42	2.2	8	0.82
		118	F	54	3.9	11	0.90
1999-2000	23	290	M	48	2.7	7	0.40
		206	M	61	5.2	5	0.43
		77	M	62	5.4	6	0.74

Table 2.6 Correlation between daily emergence index and mass index to determine if mass influences lizard emergence position. A positive correlation indicates that smaller lizards emerge earlier than larger lizards. All observations were made between Dec-Mar in Monroe County, Tennessee.

Year	Crevice	N	r_s	P
1998-1999	39	57	0.353	0.007
1998-1999	23	82	0.015	0.896
1999-2000	39	27	-0.047	0.818
1999-2000	23	44	0.064	0.681

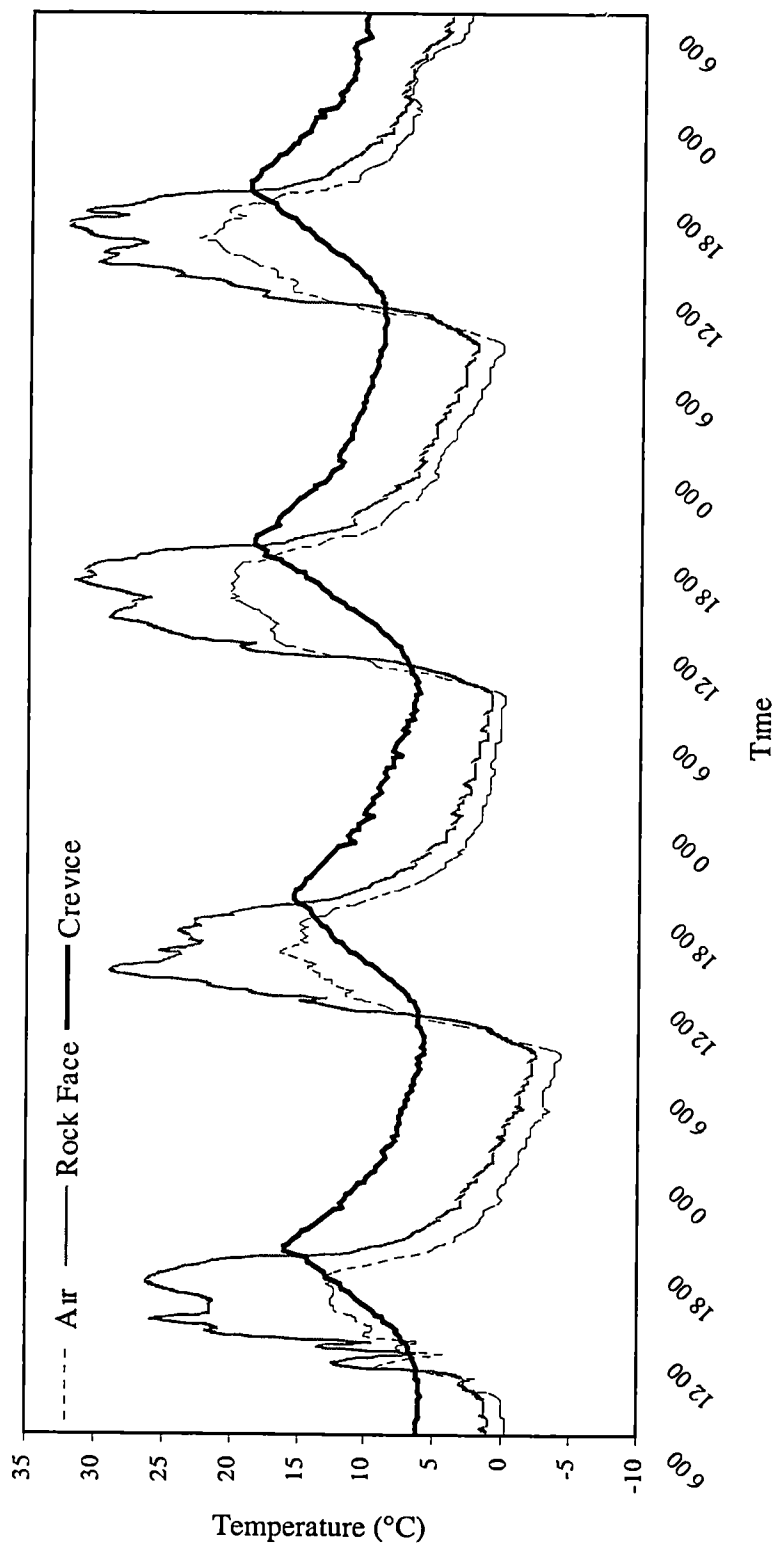


Figure 2.1. Temperatures ($^{\circ}\text{C}$) of crevice 26 between Feb 5-9, 2000 in Monroe County, Tennessee. Rock face temperatures were recorded by a TidbitTM sensor attached to the rock 10 cm from the crevice. Air temperatures were recorded by a shaded Tidbit sensor 1 m from the crevice. Crevice temperatures were recorded by a HoboTM temperature probe 10 cm inside the crevice.

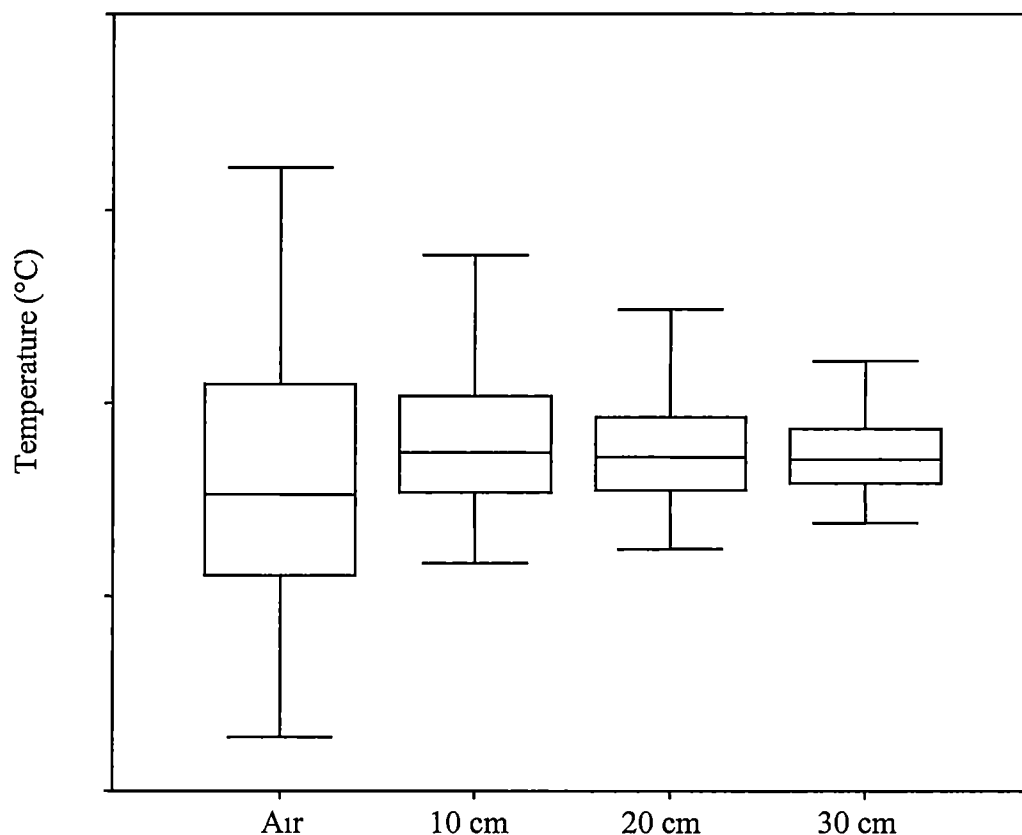


Figure 2.2. The effect of depth on temperature range of crevice seven between Feb 24 – Mar 11, 2000 in Monroe County, Tennessee. Crevice temperatures were recorded by Hobo™ probes placed at different depths (10, 20, 30 cm) within the crevice. Air temperatures were recorded by a shaded Tidbit™ sensor 1 m from the crevice. Box plots display interquartile range. The middle line is the median. The whiskers indicate the range of values.

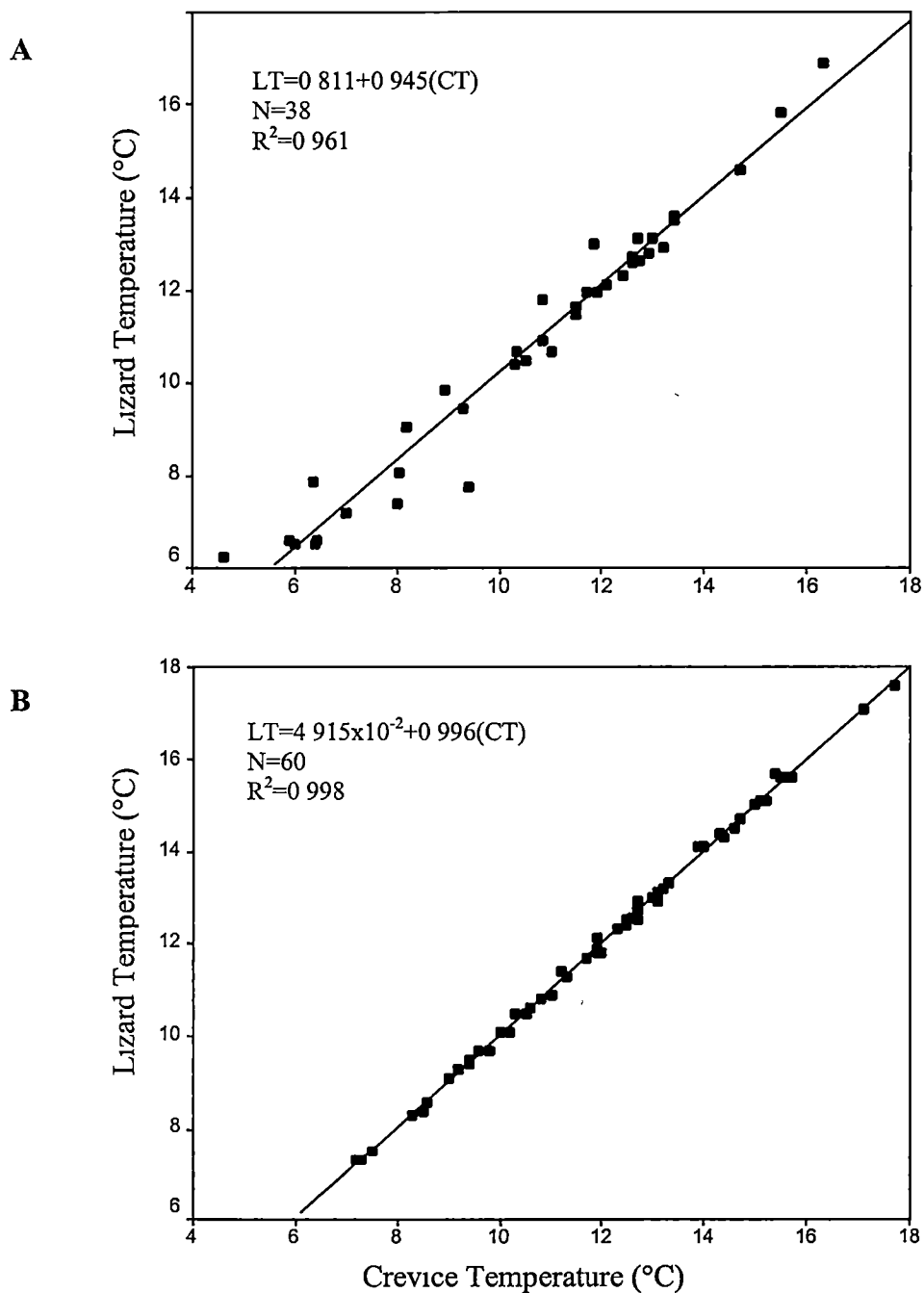


Figure 2.3 The relationship between *Anolis carolinensis* temperature (LT) and crevice temperature (CT) prior to emergence for (A) 1998/1999 and (B) 1999/2000 in Monroe County, Tennessee. Lizard temperatures were recorded by pressing a temperature probe against the side of the lizard inside the crevice. Crevice substrate temperatures were recorded within 1 cm of the lizard. All temperatures were recorded between December and March

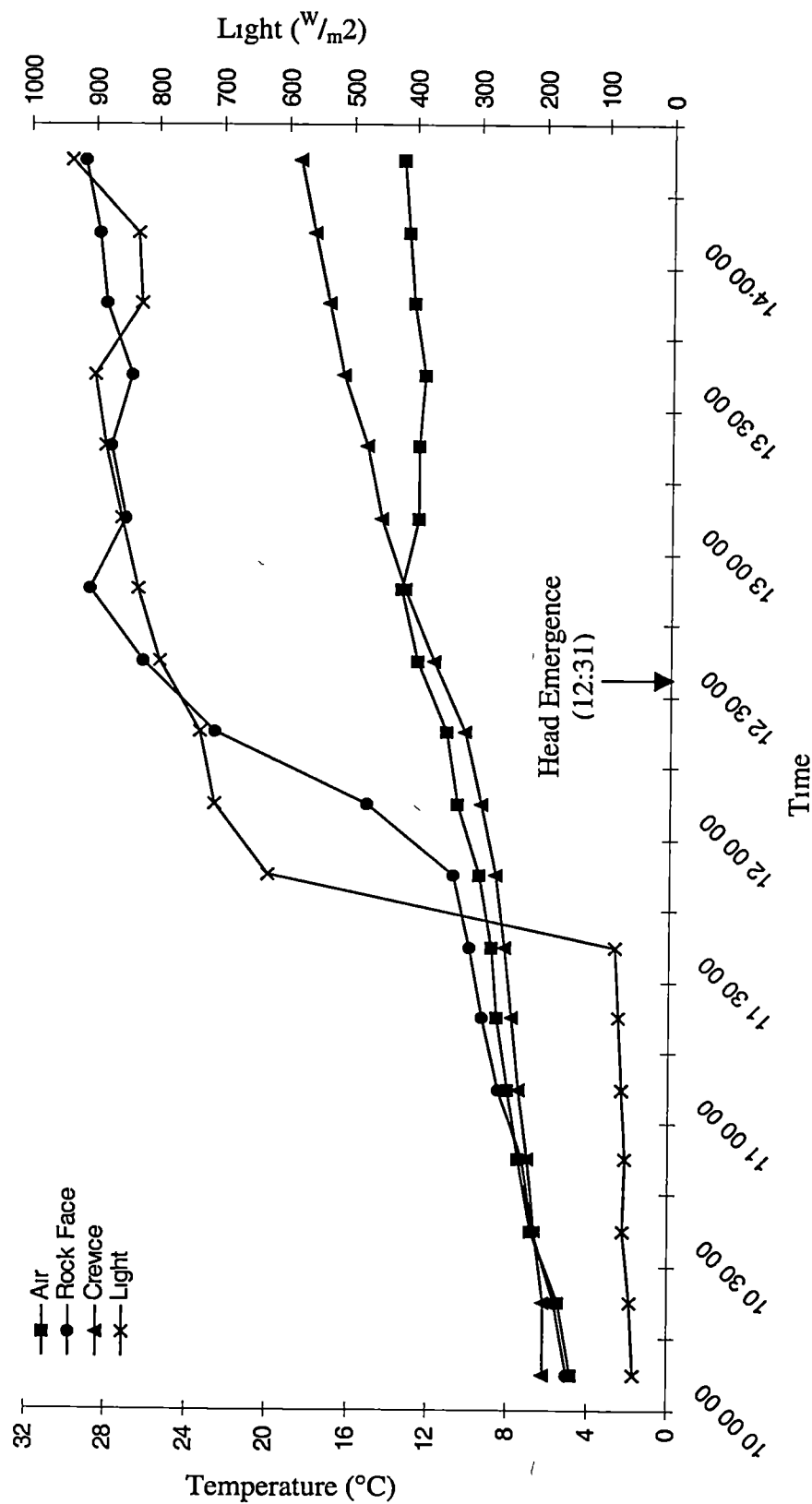


Figure 2.4. Relationship between light intensity, air temperature, rock face temperature, crevice temperature and emergence of *Anolis carolinensis* from crevice 39 on March 12, 1999 in Monroe County, Tennessee. Light intensity was recorded with a LI-CORTM sensor attached to the rock 1 cm from the crevice. Rock face temperatures were recorded by a TidbitTM attached to the rock 1 cm from the crevice. Air temperatures were recorded by a shaded TidbitTM 1 m from the crevice. Crevice temperatures were recorded by a HoboTM temperature probe 10 cm inside the crevice.

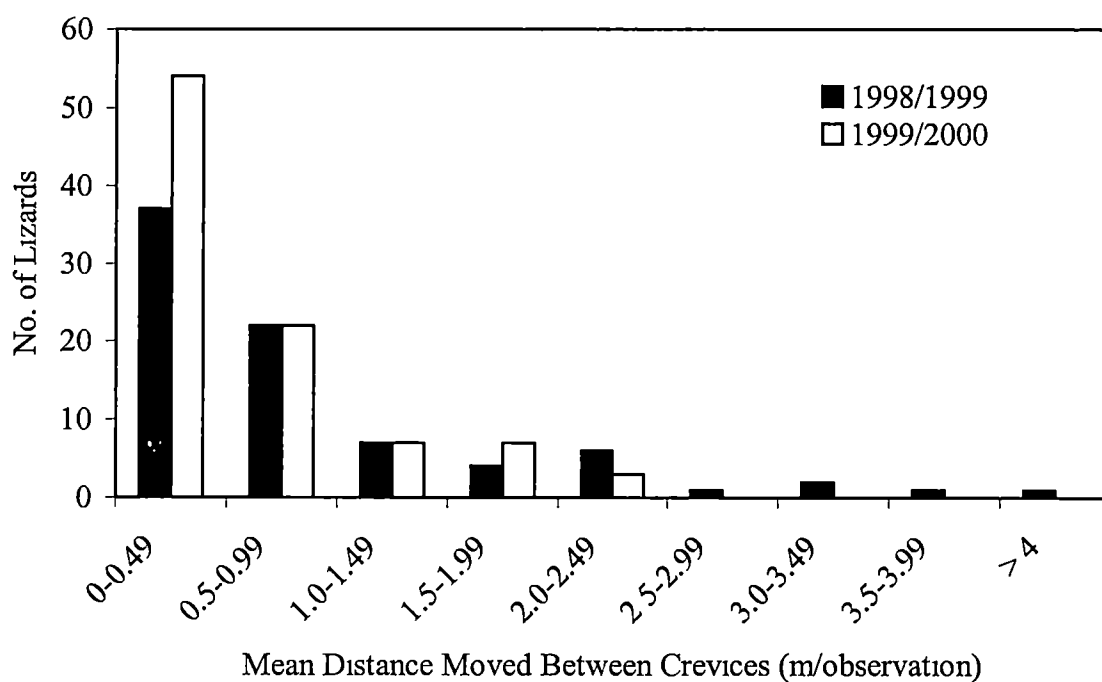


Figure 2.5. Mean distances moved between crevices by *Anolis carolinensis* during the 1998/1999 and 1999/2000 winter seasons in Monroe County, Tennessee. Lizards seen less than five times are omitted.

PART III

WINTER GROWTH, SEX RATIO AND BODY SIZES OF A NORTHERN
POPULATION OF *Anolis carolinensis* (SAURIA: POYCHROTIDAE)

INTRODUCTION

Reptiles that inhabit temperate areas and are active during the winter must be able to maintain their energy requirements to survive. This may be accomplished by relying on stored fat or by feeding throughout the year. If winter fat reserves and feeding opportunities are limited, a reptile will enter a dormant period that requires minimal energetic costs (Congdon et al. 1979, Jenssen et al. 1996). Reptiles that are able to remain active during the winter have the opportunity to grow faster and mature earlier than those that are dormant during part of the year (see Adolph and Porter 1993), but being active in the winter may be challenging to an ectotherm. It is more difficult for ectotherms to catch fast-moving prey when temperatures are low (Avery et al. 1982), and once a prey item is caught, digestion rate may be inhibited by the cold (Diefenbach 1975, Windell and Sarokon 1976). If digestion rate is severely reduced, food may even putrify in the gut (Scott et al. 1995).

The green anole (*Anolis carolinensis*) is the northern-most member of its neotropical genus (Williams 1969) and can be found as far north as North Carolina and Tennessee (Conant and Collins 1991). Although the energetic penalty for winter activity likely increases with latitude (Jenssen et al. 1996), green anoles do not hibernate. Lizards can be seen basking on sunny winter days (Covington and Covington 1991, Jenssen et al. 1996) even when air temperatures are below freezing (personal observations). During the fall season, individuals store fat that is utilized throughout the winter (Dessauer 1953, 1955a, b). The appetite of *A. carolinensis* decreases during the winter and appears to be stimulated by long photoperiods rather than high temperatures (Dessauer 1955b, Fox and Dessauer 1957). The purpose of this field study is to determine if there is any winter

growth in an *A. carolinensis* population that is near the northern range limit for the species. In addition, the sex ratios and size classes are reported for two winter seasons.

METHODS

The study was conducted during the winter seasons of 1998/1999 and 1999/2000 on the Little Tennessee River in Monroe County, Tennessee. A south-facing bluff is located about 15-20 m from the river. There is a narrow strip of vegetation along the edge of the river separated from another at the base of the bluff by an old railroad bed. Lizards shift their habitat from the river vegetation to the bluff during the winter where they seek refuge in the rock crevices. For a more detailed description of the study site and the winter behavior of the lizards, see Part II.

Lizards were captured from November - March by hand or noose, toe-clipped and painted with a number using a silver paint pen (Pilot Silver Marker™). The shedding frequency decreases during the winter months, and individuals usually had to be painted only one time each winter. The sex of each lizard was determined, and it was placed in a plastic bag and weighed to the nearest 0.5 g using a spring scale (Pesola™ 10g). Its snout-vent length (SVL) and tail length were measured to the nearest 0.5 mm with a clear plastic ruler. Lizards were released at the point of capture immediately after measurements were taken. Lizards were recaptured in March in both seasons to determine if there was any winter growth. Growth rates are calculated by dividing the total change in SVL and mass for each individual by the number of days between the

initial capture and recapture date. Growth rates are compared between the different sexes and sizes.

RESULTS

Four hundred and thirty-seven different anoles were marked between November and March of 1998/1999 and 1999/2000. Forty-four lizards that had been marked in 1998/1999 were recaptured during the 1999/2000 season (males=31, females=13). During the 1998/1999 season, 145 males and 95 females were marked. The male:female ratio (1.53) was significantly different from a 1:1 ratio (Chi square goodness of fit test, $\chi^2 = 10.42$, $P < 0.01$) in 1998/1999. In 1999/2000, 166 males and 73 females were marked. The 1999/2000 male:female ratio (2.27) was also significantly different from a 1:1 ratio (Chi square goodness of fit test, $\chi^2 = 36.19$, $P < 0.001$).

Table 3.1 (Appendix) gives the mean SVL and mass for males and females during both winter seasons. There was no significant seasonal difference in mean SVL or mass for males (Mann-Whitney U test, SVL: $U = 11569$, $N_1 = 145$, $N_2 = 166$, $P = 0.556$; mass: $U = 11773$, $N_1 = 145$, $N_2 = 166$, $P = 0.740$) or females (Mann-Whitney U test, SVL: $U = 3200.5$, $N_1 = 95$, $N_2 = 73$, $P = 0.392$, mass: $U = 3349.5$, $N_1 = 95$, $N_2 = 73$, $P = 0.705$). Table 3.2 gives the number and percentage of males in females in each SVL size class during both seasons.

The average number of days of growth for each lizard between the initial and final measurements was 88.7 during the 1998/1999 season and 83.4 during 1999/2000. There was significant growth in SVL during both winter seasons (1998/1999: paired t-

test, $t_{61} = -6.869$, $P < 0.001$; 1999/2000. Wilcoxon signed-ranks test, $T = 2232.5$, $N = 104$, $P < 0.001$), but only the 1999/2000 season had significant growth in mass (1998/1999: Wilcoxon signed-ranks test, $T = 69$, $N = 62$, $P = 0.485$; 1999/2000: $T = 1908.5$, $N = 104$, $P < 0.001$). Original SVL and SVL growth rate are correlated in 1999/2000 (Spearman rank correlation: $r_s = -0.398$, $N = 104$, $P < 0.001$), with smaller lizards growing faster than larger ones, but not in 1998/1999 ($r_s = -0.247$, $N = 62$, $P = 0.053$). There was no correlation between original mass and mass growth rate either season (1998/1999: $r_s = 0.056$, $N = 62$, $P = 0.664$, 1999/2000: $r_s = -0.006$, $N = 104$, $P = 0.949$).

Growth rates for both winter seasons are summarized in Table 3.3. There was a higher mean growth rate in 1999/2000 than in 1998/1999 for SVL (Mann-Whitney U Test: $U = 1485$, $N_1 = 62$, $N_2 = 104$, $P < 0.001$) and mass (Mann-Whitney U Test: $U = 1659.5$, $N_1 = 62$, $N_2 = 104$, $P < 0.001$). Males had a higher SVL growth rate than females for both seasons (Mann-Whitney U test 1998/1999: $U = 230$, $N_1 = 47$, $N_2 = 15$, $P = 0.037$, 1999/2000: $U = 824$, $N_1 = 73$, $N_2 = 31$, $P = 0.029$). Males also had a higher mass growth rate than females in 1999/2000 (Mann-Whitney U test: $U = 548.5$, $N_1 = 73$, $N_2 = 31$, $P < 0.001$), but not in 1998/1999 (Mann-Whitney U test: $U = 253$, $N_1 = 47$, $N_2 = 15$, $P = 0.10$).

DISCUSSION

In the population used for this study, the majority of *A. carolinensis* shift habitats in the winter to a south-facing bluff where they seek refuge in the rock crevices (see Part II). Both sexes are found in the same crevices, however, the sex ratio was male-biased during both winter seasons. Jenssen et al. (1995) found that the April-November sex ratio of a South Carolina *A. carolinensis* population was not significantly different from

1:1. Ruby (1984) also found that the Feb-Aug sex ratio of a Louisiana population did not differ from 1:1. During the breeding season, the behavior of males often makes them more visible (Jenssen et al 1995) which may bias the sex ratio, but this is unlikely during the winter. Displays are minimal in the winter and rarely bring attention to a lizard. In the present study, no other behavioral differences were detected between males and females that would bias the sex ratio such as females not emerging as frequently or choosing basking positions in less exposed areas. If the true sex ratio of the population is not significantly different from 1:1, it would mean that many of the females do not make the habitat shift to the south-facing bluff during the winter and seek refuge elsewhere.

It is difficult to differentiate age groups based on SVL, but there are likely three age classes present in the crevices of the rocky bluff. The young of the year which are entering their first winter season, the yearlings which are entering their second winter season, and the final age group that are over two years old and are entering their third or more winter season. The yearling age group comprises the majority of the lizards on the bluff and the young of the year the least numerous.

Anolis carolinensis hatchlings range from 19-27 mm SVL and begin appearing in July in Tennessee (see Minesky 1999). Hamlett (1952) reported that hatchlings in New Orleans attain a SVL of 35-40 mm prior to winter, and Fox and Dessauer (1958) suggested that males could obtain a SVL of 45-50 mm before their first winter. Gordon (1956) reported that the maximum SVL attained by a male hatchling prior to its first winter season in Louisiana was 49 mm whereas the maximum female was 38 mm. In this study, 4.1% and 7.8% of the male lizards and 20% and 23.3% of the female lizards found on the bluff had SVL's under 40 mm at the beginning of the 1998/1999 and 1999/2000

winter seasons, respectively. If it is assumed that males can grow to a maximum length of 45 mm before winter, 18.6% and 25.3% of male lizards would fall in this category in 1998/1999 and 1999/2000, respectively. Many juveniles seek refuge under leaf litter and fallen tree limbs which makes finding them more difficult and causes their numbers to be underrepresented.

There is some confusion over when *A. carolinensis* become sexually mature. The minimum SVL needed for sexual maturity for Louisiana males has been set at 45 mm (Gordon 1956), 55 mm (Fox and Dessauer 1958), and 60 mm (Hamlett 1952). The smallest Florida male that King (1966) found with enlarged vas deferens had a SVL of 51 mm. Louisiana females may become mature after reaching a SVL of 45-48 mm (Cagle 1948, Hamlett 1952, Gordon 1956). Andrews (1985) reported that all South Carolina females in her study that were 49 mm SVL or greater (N=16) laid eggs while only 2 of 7 between 45-49 mm did. King (1966) found a female with enlarged eggs at 41 mm SVL in Florida, and Michael (1972) set the minimum body size at 45-50 mm in Texas. Tennessee females have been found with oviducal eggs at 48 mm, and eggs have been palpated in some females as small as 44 mm (see Minesky 1999).

If 45 mm is used as the minimum SVL needed to be sexually mature for both sexes, 81.4% and 74.7% of males and 45.3% and 46.6% of females would be sexually mature in the 1998/1999 and 1999/2000 season, respectively. This is likely an overestimation of those lizards that actually will reproduce in the early spring due to the wide variability in size at sexual maturity and the fact that dominant male lizards have the majority of mating opportunities. According to Michael (1972), a male must be at least

60 mm SVL to become dominant in the field. In 1998/1999, 16.6% of the males had a SVL of 60 mm or greater, and 29.5% of the males did in 1999/2000.

Feeding events were rare for *A. carolinensis*, but were observed in all winter months during both seasons. Gordon (1956) also observed winter-feeding, and Hamilton (1948) found a spider leg in the stomach of one lizard during the winter. Winter appetite seems to be minimal in the field. Ants, spiders, and small beetles were observed on several occasions to walk directly in front of a basking individual with no reaction from the lizard. Prey availability may limit the winter growth of a lizard (Crenshaw 1955, Andrews 1982). However, the winter habitat shift of *A. carolinensis* not only provides thermal protection for the lizards (see Part II) but also allows arthropods to be active on the bluff throughout the winter.

There was significant growth in SVL for both seasons, but only the 1999/2000 season had significant growth in mass. In addition, lizards had a greater growth rate in 1999/2000 than in 1998/1999. This seasonal difference may be due to the earlier onset of warmer temperatures in 1999/2000 (Table 2.1). There is a large variability in the growth rates of individual lizards. Bradshaw (1971) noted that individual growth rates of *Amphibolurus* (Agamidae) vary and that this may lead to different survivorship probabilities. Assuming larger eggs are adaptive in northern populations of *A. carolinensis*, it would be beneficial for females to grow during the winter since female body size is correlated with egg size in Tennessee (Michaud and Echternacht 1995). Winter growth would be beneficial to males because larger males are more successful at settling territorial disputes and establishing breeding territories during the spring and summer (see Jensen et al. 1995).

Males grow more than females during the winter. Gordon (1956) also found this sexual growth difference in the spring and summer, and Michael (1972) assumed this to be true since hatchlings of both sexes are the same size whereas adult males are larger than females. Schoener and Schoener (1978) found that males in other *Anolis* lizards grow faster than similarly sized females, and Ruby and Dunham (1984) described a similar pattern in *Sceloporus jarrovi* (Phrynosomatidae). Smaller *A. carolinensis* grew more than larger lizards in 1999/2000 but not in 1998/1999. Fox and Dessauer (1958) found that smaller captive *A. carolinensis* grew faster than larger ones. Juvenile lizards of other species often grow faster than adults during the cold season and are usually more active on warm winter days, a behavioral difference that gives them more feeding opportunities (Crenshaw 1955, Weintraub 1968, Ruby 1977). There were no obvious differences in activity times between adult and juvenile *A. carolinensis* that would enable juveniles to have more feeding opportunities; however, this was not investigated thoroughly and there may be differences that were undiscovered.

In summary, *A. carolinensis* grow during the winter. Lizards increased in length during both seasons and mass during the second season, and males grew at a greater rate than females. Further study is needed to determine if juvenile growth rates are higher than adults during the winter. The average SVL for males and females remained the same over both seasons although there was variability in the number of individuals in each size category. The sex ratio on the bluff during the winter is male biased, but it is unknown whether this reflects the true sex ratio of the population or is due to the inability to find all of the females.

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APPENDIX

Table 3.1. Mean snout-vent length (SVL) and mass for male and female *Anolis carolinensis* during the 1998-1999 and 1999-2000 winter seasons. All lizards were captured between Nov-Mar in Monroe County, Tennessee

Year	Sex	N	Mean SVL ± SE (mm)	SVL Range (mm)	Mean Mass ± SE (g)	Mass Range (g)
1998-1999	Males	145	50.7 ± 0.7	37.0 – 66.0	3.3 ± 0.1	1.1 – 6.5
	Females	95	45.2 ± 0.6	35.0 – 57.0	2.3 ± 8.1x10 ⁻²	1.0 – 3.9
1999-2000	Males	166	51.1 ± 0.7	35.5 – 67.0	3.4 ± 0.1	1.2 – 6.4
	Females	73	45.8 ± 0.8	32.0 – 58.0	2.3 ± 9.5x10 ⁻²	0.9 – 4.3

Table 3.2. Number and percentage of male and female *Anolis carolinensis* in each size (snout-vent length SVL) class during the 1998/1999 and 1999/2000 winter seasons. Lizards were captured between Nov-Mar in Monroe County, Tennessee.

SVL	30-34 mm	35-39 mm	40-44 mm	45-49 mm	50-54 mm	55-59 mm	60-64 mm	65-69 mm	Totals
	1998-1999								
Males	0 0%	6 4.1%	21 14.5%	41 28.3%	44 30.3%	9 6.2%	23 15.9%	1 0.7%	145 100%
Females	0 0%	19 20.0%	33 34.7%	13 13.7%	24 25.3%	6 6.3%	0 0%	0 0%	95 100%
	1999-2000								
Males	0 0%	13 7.8%	29 17.5%	44 26.5%	24 14.5%	7 4.2%	46 27.7%	3 1.8%	166 100%
Females	1 1.4%	16 21.9%	22 30.1%	3 4.1%	24 32.9%	7 9.6%	0 0%	0 0%	73 100%

Table 3.3. Winter growth rates of *Anolis carolinensis* in Monroe County, Tennessee All lizards were captured between Nov-Mar in 1998/1999 and 1999/2000 Growth rates are calculated by dividing the total change in mass and snout-vent length (SVL) by the number of days between captures.

Year	Sex	N	Mean SVL Growth Rate (mm/day)	SE	Range of SVL Growth Rates (mm/day)	Mean Mass Growth Rate (g/day)	SE	Range of Mass Growth Rates (g/day)
1998/1999	Males	47	1.36×10^{-2}	2.76×10^{-3}	0 - 0.11	1.21×10^{-4}	5.01×10^{-4}	$-8.33 \times 10^{-3} - 6.03 \times 10^{-3}$
	Females	15	4.53×10^{-3}	1.65×10^{-3}	$0 - 1.72 \times 10^{-2}$	-1.53×10^{-3}	1.25×10^{-3}	$-1.11 \times 10^{-2} - 6.06 \times 10^{-3}$
	Both	62	1.14×10^{-2}	2.18×10^{-3}	0 - 0.11	-2.78×10^{-4}	4.87×10^{-4}	$-1.11 \times 10^{-2} - 6.06 \times 10^{-3}$
1999/2000	Males	73	3.13×10^{-2}	2.93×10^{-3}	0 - 0.12	4.21×10^{-3}	1.28×10^{-3}	$-6.92 \times 10^{-2} - 4.74 \times 10^{-2}$
	Females	31	1.99×10^{-2}	2.98×10^{-3}	$0 - 7.27 \times 10^{-2}$	1.10×10^{-3}	5.13×10^{-4}	$-4.76 \times 10^{-3} - 8.45 \times 10^{-3}$
	Both	104	2.79×10^{-2}	2.29×10^{-3}	0 - 0.12	3.20×10^{-3}	9.12×10^{-4}	$-6.92 \times 10^{-2} - 4.74 \times 10^{-2}$

PART IV

SUMMARY

Anolis carolinensis remain active during the winter throughout their range. In the northern population observed in this study, the majority of anoles shift habitats during the winter and aggregate on a south-facing rocky bluff along the Little Tennessee River. Crevices in the bluff provide refuge from predators and low temperatures at night and during cloudy days. Crevice temperatures are more stable than air and rock surface temperatures outside of the crevice and remain above freezing during the night. There are not enough crevices in the bluff for each lizard to be solitary; however, lizards are aggregated more than necessary and may leave previously occupied crevices temporarily or permanently to join other lizards in a nearby crevice. This crevice shift may be due to an attraction to crevices that contain other lizards or possibly the result of changing crevice conditions. There does not appear to be any thermal benefit for the aggregations since lizards are generally not touching each other within a crevice

The body temperatures of *A. carolinensis* within a crevice are not significantly different from the crevice temperature. Due to their small size, *A. carolinensis* cannot maintain elevated body temperatures once they are out of the sunlight, and they probably equilibrate to crevice temperatures soon after they retreat into a crevice. Crevices differ in temperatures, a characteristic that is likely important in crevice selection. There are also different thermal opportunities within a crevice that a lizard can utilize by shifting positions. Greater depths provide more stability against temperature fluctuations than shallow depths. Some lizards in shallow crevices have body temperatures that are below crevice temperatures. Normally, lizards are insulated from the air temperature in deep crevices; but in shallow crevices, the cool air temperature may lower a lizard's body

temperature below the crevice substrate temperature. Lizards usually avoid these shallow crevices once the temperatures remain consistently cold.

Lizards are dark brown the entire winter season. The first green lizards are seen in early spring when temperatures are warmer and individuals are spending greater amounts of time displaying in agonistic and courtship interactions. There is some displaying behavior of males and females during the winter, but it is minimal and probably has little affect on the social system of the aggregated lizards

Light intensity is the main factor that triggers the emergence of lizards from crevices. Lizards usually emerge soon after the sun has illuminated their section of the bluff. There is no minimum crevice temperature change that must occur or a threshold temperature that must be reached to trigger lizard emergence. Temperatures vary daily within a crevice and between different crevices, a property that makes temperature an inconsistent emergence cue. During rare periods of warm weather, lizards may emerge prior to crevice illumination. This early emergence behavior suggests that light intensity may be important only because lizards recognize that they can elevate their body temperatures when there is sufficient amount of sunlight. When air temperatures are high, less light intensity is needed to attain preferred body temperatures and lizards can emerge earlier or on cloudy days. On a few overcast days, lizards could be seen near the crevice opening even though air temperatures were low and there was no direct crevice illumination. Although individuals never emerged on cold, overcast days, this behavior suggests that a biological rhythm may be used to help cue emergence.

The emergence order of lizards from a crevice is nonrandom and depends on the individual's depth within the crevice. The shallowest lizard emerges first. Some lizards

consistently came out earlier than others, an indication that individuals may have preferred positions or depths within a crevice. The mass of the lizard has little influence on its emergence position since all individuals within a crevice have similar body temperatures prior to emergence and will not begin to warm until they emerge. Lizards emerge by first poking their head out of the crevice and remaining in that position for several minutes. If the crevice opening is large enough, a lizard may then orient its body laterally within a crevice until it has warmed enough to emerge completely. If space in the crevice opening is limited, a lizard will usually move the upper half of its body out of a crevice while the hind legs and tail remain inside. Several lizards may be going through this behavioral sequence simultaneously in larger crevices.

Once a lizard completely emerges from a crevice, it will move to a basking spot on the rocks or nearby vegetation. Lizards spend the majority of their time basking and may have preferred spots, but there is rarely active defense of any particular area. Lizards are very tolerant of each other and several individuals are often seen basking within a few centimeters of each other or even touching. When threatened, lizards will retreat quickly into a nearby crevice. The majority of individuals return to the same crevice each night or to another one that is close to it. Large movements to other crevices are rare during the winter, and the sex or size of the individual does not affect how far it is likely to move. Most lizards are familiar with several crevices within a meter or two of each other and may seek shelter in any of these crevices throughout the winter.

Feeding events are rare, but are seen in every month of the winter season. Although appetite is reduced during the winter, there was significant growth in snout-vent length (SVL) during both seasons. The second winter season also had significant

growth in mass. Males had higher growth rates than females, and smaller lizards grew faster than larger ones in 1999/2000 but not in 1998/1999. Growth rates were also higher in 1999/2000 than in 1998/1999, a difference that may be the result of warmer temperatures in 1999/2000.

The average SVL and mass for males and female was not significantly different between the seasons, but the percentage of lizards in each size category was. If SVL is used as the criteria for estimating age, the majority of the lizards found on the bluff are probably yearlings – lizards that are in their second winter season. The young of the year – those in their first winter season – are the least numerous. Due to their habit of hiding under leaf litter and fallen tree limbs, young of the year are more difficult to find than the other age groups.

Both males and females are found aggregated in the crevices and do not appear to have any behavioral differences in activity times. Despite this, more males were found on the bluff than females during both seasons. It is unknown whether this is a reflection of a true male-biased sex ratio of the population or an undetected behavioral difference between the sexes during the winter. It is most likely the latter.

In the early spring, lizards begin moving away from the bluff to the vegetation along the river during the day and returning to their crevices at night. These movements may last for several weeks. The lizards usually move to the same section of the river vegetation and often to the same tree. The habitat shift is not permanent until the low night temperatures remain warm enough for lizards to abandon their crevices. Most lizards move straight out from their crevices to the river vegetation and remain there throughout the spring and summer. There is little lateral movement along the base of the

bluff and the river Those lizards that survive to the following winter season will likely return to a familiar crevice they used in the previous winter.

VITA

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