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Ecology of Sceloporus Consobrinus Populations in Two Thermally Different Habitats

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ECOLOGY OF *SCELOPORUS CONSOBRINUS* POPULATIONS
IN TWO THERMALLY DIFFERENT HABITATS

By

ALYSSA N. BANGS

Submitted to the Faculty of the Graduate College of
Arkansas Tech University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE IN FISHERIES AND WILDLIFE SCIENCE
December 2016

ECOLOGY OF *SCELOPORUS CONSOBRINUS* POPULATIONS
IN TWO THERMALLY DIFFERENT HABITATS

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ABSTRACT

Life history traits in ectotherms are tied to environmental temperature, and many species exhibit morphological and behavioral differences in thermally different habitats. Although these differences are generally attributed to differences in thermal regimes between habitats, most prior research on this topic has been performed across latitudinal or altitudinal gradients. Consequently, I wanted to determine if differences in morphology and behavior are also present among populations of *Sceloporus consobrinus* that inhabit thermally different habitats at the same latitude and elevation.

In this study, I chose sites that fit one of two habitat types: warmer open rocky habitat and cooler, more vegetated forested habitat. Throughout 2013 and 2014, I monitored temperature in the two habitats to verify that they differed in thermal regime. Between April –July 2013 and 2014, I captured 267 individuals and collected data on morphology, thermoregulatory behavior, microhabitat use, and predation. I filmed 98 lizards and quantified behavior to determine if lizards in different thermal environments differed in rates of thermoregulatory and non-thermoregulatory behaviors. I also monitored and compared activity throughout the year in both habitats to determine if differences existed and were associated with thermal differences between the habitats.

Although the rocky habitat was warmer throughout the year, I found no difference in snout-to-vent lengths (SVL) or weights of lizards in the two habitat types. Similarly, I found little difference in rate of thermoregulatory behaviors in lizards between the two habitats, although there was a difference in the time of day lizards were active. Body temperature of active lizards was also similar between the two habitats. These results suggest that morphological differences found in previous studies for populations in

thermally different habitats may be due to a combination of other factors associated with differences in latitude or elevation.

Keywords: Thermal ecology, *Sceloporus consobrinus*, Thermoregulation, Morphology, Population activity

Table of Contents

	Page
ACKNOWLEDGEMENTS	v
ABSTRACT	vi
LIST OF TABLES	x
LIST OF FIGURES	xi
INTRODUCTION	1
METHODS	9
Study Organism	9
Study Area	9
Habitat Temperature Profiles	10
Capture and Morphology	11
Body Temperature and Thermoregulation	12
Population Activity	14
Lizard Behavior	15
RESULTS	17
Temperature	17
Morphology	19
Microhabitat	21
Population Daily Activity	22
Lizard Behavior	23
DISCUSSION	25
Temperature	25
Morphology	25

Thermoregulation	27
Predation.....	31
LITERATURE CITED	36
TABLES	49
FIGURES.....	55

List of Tables

Table 1. Average substrate temperature ($^{\circ}\text{C}$) \pm SE in both habitat types for one week each month April to November 2013	49
Table 2. Average daily minimum and maximum temperatures ($^{\circ}\text{C}$) for both habitat types for one week each month April - November 2013. Bolded p-values are significant.....	50
Table 3. Average body temperature (T_b) for lizards engaged in 7 behaviors at time of capture. BROS (body resting on substrate), FLEPOS (front legs extended, pelvis on substrate), and ALEBNTS (all legs extended, body not touching substrate) are thermoregulatory positions	51
Table 4. Average body temperature (T_b) in degrees Celsius and sample size (n) for lizards captured on 7 substrates in 2013 and 2014	51
Table 5. Proportion of lizards captured in each age class for habitat, sex, and year	52
Table 6. Comparison of rates of common lizard activities in number of times activity was performed per minute for rocky and forested habitats ($n=98$). BROS (body resting on substrate), FLEPOS (front legs extended, pelvis on substrate), and ALEBNTS (all legs extended, body not touching substrate) are thermoregulatory positions	53
Table 7. Comparison of rates of common lizard activities in number of times activity was performed per minute for rocky and forested habitats ($n=98$). BROS (body resting on substrate), FLEPOS (front legs extended, pelvis on substrate), and ALEBNTS (all legs extended, body not touching substrate) are thermoregulatory positions	54

List of Figures

Figure 1. Pattern of daily temperatures (°C) in the rocky and forested habitat for August 26, 2016 to September 7, 2016. The shaded area is the range of temperatures in which lizards are found active. This data is from one logger representative of the pattern seen in all summer data in each habitat.....	55
Figure 2. Core body temperature compared to ventral temperature for lizards in 2013 and 2014. Dotted line is the slope where body and ventral temperature are equal. Solid line is the trendline of the data; $R^2 = 0.570$, $P < 0.001$	56
Figure 3. Core body temperature compared to dorsal temperature for lizards in 2013 and 2014. Dotted line is the slope where body and ventral temperature are equal. Solid line is the trendline of the data; $R^2 = 0.668$, $P < 0.001$	56
Figure 4. Substrate temperature at initial capture location plotted against core body temperature at capture for the 2013 and 2014 field seasons. $R^2 = 0.204$	57
Figure 5. Air temperature at initial capture location plotted against core body temperature at time of capture for the combined 2013 and 2014 field seasons. $R^2 = 0.117$	57
Figure 6a and b. Percent of lizards in each age class in rocky and forest habitats for 2013 (a) and 2014 (b). * denotes significant difference between habitats for that age class. Juvenile is individuals with SVL >50 mm, Adult I consists of individuals with SVL 50-59.99 mm, and Adult II consists of individuals with SVL ≥ 60 mm.	58
Figure 7a and b. Percent of males and females in each age class for 2013 (a) and 2014 (b). * denotes significant difference between the sexes for that age class. Juvenile is individuals with SVL >50 mm, Adult I is individuals with SVL 50-59.99 mm, and Adult II is individuals with SVL ≥ 60 mm.	59

Figure 8. Unbroken tail length versus snout-to-vent length (SVL) for male ($R^2 = 0.7925$) and female ($R^2 = 0.801$) lizards.	60
Figure 9a and b. Substrate temperature at location of capture for lizards captured in each habitat in 2013 (a) and 2014 (b). Data include only the first capture site for any lizards that were captured more than once. Y-axis is percent of lizards caught in that habitat.....	61
Figure 10. Proportion of lizards observed of the total estimated population at each site compared to average substrate temperature for that transect during the summer season (April-June). Each point represents the proportion of the estimated population that was active at a site over the course of an hour for three forest and three rocky sites	62
Figure 11. Proportion of estimated site population observed active per hour of the day (daylight savings time) during the summer activity season (April-June) in the rocky habitat. Each point represents the proportion of the estimated population that was active at a site over the course of each hour for three sites.	63
Figure 12. Hourly air and substrate temperatures for the forest and rocky habitats over a 9-hour period in June. Data is averaged from 3 forest and 3 rocky sites, with 6 ibuttons per site. Error bars are standard error.....	64
Figure 13. Proportion of estimated site population observed active per hour of the day (daylight savings time) during the summer activity season (April-June) in the forest habitat. Each point represents the proportion of the estimated population that was active at a site over the course of each hour for three sites	65
Figure 14. Proportion of lizards observed of the total estimated population at each site compared to substrate temperature during fall and winter (October –February)	65

INTRODUCTION

The idea that local populations can adapt to environmental variation is a tenet of evolutionary biology (Otte and Endler 1989). These adaptations can result from phenotypic plasticity (Losos et al. 2000) or genetic differences (Niewiarowski and Roosenburg 1993), but populations of organisms occupying habitats that have different selective pressures often show life-history differences (Losos 1990a; Losos 1990b; Irschick et al. 2005; Buckley et al. 2010). This is especially true for ectotherms, as environmental temperature has a much larger effect on most aspects of their life history. Therefore, thermally distinct habitats should exert different selective pressures on ectotherms that could alter their life history (Jameson and Allison 1976; Adolph 1990; Grant and Dunham 1990; Beaupre 1995; Shine and Madsen 1996; Bashey and Dunham 1997; Sears 2005).

Body size is an important trait that is affected by differences in temperature regimes (Tinkle and Dunham 1986; Adolph and Porter 1993; Niewiarowski and Roosenburg 1993; Angilletta et al. 2004). Investigators that compare lizard morphology between thermally different habitats invariably find that body size differs between such habitats (ex., Tinkle and Dunham 1986; Adolph and Porter 1993; Niewiarowski and Roosenburg 1993; Angilletta et al. 2004). While many squamates are smaller in colder environments (reviewed in Ashton and Feldman 2003), *S. consobrinus* is larger in colder environments as compared to populations in warmer environments, potentially because a larger body size allows for better thermoregulation in cold environments (Bergmann 1847; Angilletta et al. 2004; Meiri et al. 2004; Olalla-Tarraga et al. 2006). Colder environments can also delay reproductive maturation of *Sceloporus* lizards up to 10 -12

months when compared to populations in warmer, lower latitudes (Atkinson 1996; Angilletta et al. 2004). Such a delay in maturation can shift allocation of resources away from reproduction towards growth, which would result in increased body size (Angilletta et al. 2004; Du et al. 2012). Lizards in colder environments may also survive better because of restricted activity periods (reviewed in Adolph and Porter 1993).

Sceloporus as a genus has been shown to be evolutionarily conservative in mean active body temperature across environmental conditions regardless of species or subspecies (Bogert 1949; Brattstrom 1965; Gillis 1991). This preferred body temperature range has been found to correspond with temperatures that optimize a number of physiological processes (Bennett 1980; Adolph 1990), including maximum sprint speed and endurance (Marsh and Bennett 1986; Pinch and Claussen 2003), digestive performance and metabolism (Angilletta 2001; Angilletta et al. 2002), respiration (Sears 2005), and prey capture and handling efficiency (Van Damme et al. 1992). Above and below this optimal temperature range, physiological processes are reduced (Bennett 1980).

Temperature regulation in *Sceloporus* is achieved through a combination of behavior and physiology (Bartholomew and Tucker 1963; Grigg et al. 1979; Dzialowski and O'Connor 2001; Seebacher and Grigg 2001; Seebacher and Franklin 2005). In reptiles, cardiovascular adjustments are vital to maintaining body temperature. Altering cardiac output and distribution of blood within the body can allow reptiles to control rates of heating and cooling when they move between microhabitats, which could reduce the amount of time devoted to behavioral thermoregulation (Bartholomew and Tucker 1963; Bartholomew 1982; Seebacher and Grigg 2001; Seebacher and Franklin 2005). Elevation

of heart rate and vasodilation in peripheral anatomy increases heat transfer between a lizard and its environment (Bartholomew and Tucker 1963; Grigg et al. 1979; O'Connor 1999; Seebacher 2000; Dzialowski and O'Connor 2004; Seebacher and Franklin 2005); which is useful for lizards attempting to thermoconform to the environmental temperature. Reptiles decrease heart rates and vasoconstrict their peripheral blood vessels to minimize heat transfer (Grigg et al. 1979; Seebacher and Grigg 2001; Seebacher and Franklin 2005), which will allow lizards to maintain body temperatures that are warmer or cooler than the surrounding environment. Behavioral thermoregulation involves changing basking duration and posture (Adolph 1990), changing activity periods (Grant and Dunham 1988; Adolph and Porter 1993), and shuttling between relatively warm and cool microhabitats (Huey et al. 1989; Adolph 1990; Shine and Madsen 1996; Asbury and Adolph 2007).

Ectotherms are only active when at least some of the environment is between the critical minima and maxima; outside of this range of temperatures, individuals are sluggish or inactive (Cowles and Bogart 1944; Brattstrom 1965; Seebacher and Franklin 2005). Grant and Dunham (1988) and Tinkle (1967) found that the thermal environment restricted lizard activity to the times of day when the average available temperature among microhabitats was near the mean body temperature. This can be true in both cool and hot habitats; in very cool habitats, activity period is curtailed to the warmest part of the afternoon, while in very warm habitats, the surface temperatures are only cool enough for use in the morning and evening (Grant and Dunham 1988; Beaupre 1995; Sears and Angilletta 2004; Kearney et al. 2009). Reptiles in habitats that are very warm have been shown to have less time available for surface use, constrained body temperature, and

lower metabolic and growth rates when compared to populations of the same species in cooler habitats (Beaupre 1995). However, in habitats that do not reach temperatures above the optimal range, ectotherms in warmer habitats will exhibit a longer daily and seasonal activity period than ectotherms in cooler habitats (Sears and Angilletta 2004).

Temperature and structural differences between habitats may affect the ability of lizards to thermoregulate. Habitat structure plays a role in determining available thermal microhabitats, i.e., habitat patches that have distinct thermal characteristics (Anderson 2007). Different microhabitats give rise to different conditions available for ectothermic organisms (Blouin-Demers and Weatherhead 2002; Row and Blouin-Demers 2006). For example, a tree trunk and a fallen dead branch in the same habitat will provide different patterns and intensities of light. This variation in insolation allows for multiple different surface temperatures and opportunities for behavioral thermoregulation, as well as influencing crypticity. In an open, rocky habitat, radiant energy has two extremes: the surface of the rocks, which are almost constantly in full sun, and beneath the rocks, which are almost solely shaded. This in turn creates temperature extremes, as the surface of the rock gains heat much faster than the underside, which remains cooler. An open habitat also has fewer microhabitats to exploit in terms of prey availability and crypticity. Refuges are plentiful, but are limited to the colder microhabitat beneath rocks.

To maintain body temperatures within an optimal range, ectotherms must compensate for thermal variation among different habitats (Jameson and Allison 1976; Sears 2005). Variation in behavior among thermally different habitats will affect other life history traits (McGinnis 1970; Moermond 1979). Behavioral thermoregulation uses time that could be spent on other activities such as foraging and reproduction (Bennett

and Dawson 1976) as well as purposeful inactivity (Rose 1981). The extra time spent on behavioral thermoregulation causes a shift in predation risk (Rose 1981) and other life history factors (Bennett 1980; Dunham et al. 1989). If a lizard spends more time thermoregulating, it must either be active longer to complete necessary activities or reduce the time spent on foraging, reproduction, and inactivity. Increased activity is related to higher levels of predation (Huey and Pianka 1981; Rose 1981; Wilson 1991; Clobert et al. 2000), so lizards run the risk of mortality or loss of time from increased refuge use (Martin and Lopez 1999). Similarly, longer periods of activity and potentially reduced levels of foraging would cause a reduction in net energy available for growth, survival, and reproduction (Anderson and Karasov 1981; Huey and Pianka 1981; Du et al. 2012).

Sceloporus species easily autotomize their tails, usually in response to predation. Consequently, frequency of tail breaks is often used as an index of predation (Medel et al. 1988; Wilson 1991; Bateman and Fleming 2009). Since rocky and forested habitats are structurally different, they may support different predators, which may vary in predation efficiency upon lizards. Similarly, the expected difference in activity periods between populations in warm and cool environments will influence exposure to predation. If one habitat allows for more overall lizard activity, this may also lead to higher predation levels in that habitat. Consequently, I expected to find a difference in proportion of tail break and possibly length of tail lost in rocky and forested habitats. A difference in predation rate may also influence distribution of body size between the habitats; if predation pressure is higher on a certain size class, a higher proportion of this size class should get eaten, causing the overall body size distribution to shift.

Most studies that have investigated influence of thermal environment study populations spread across an elevation or latitudinal gradient (Jameson and Allison 1976; Adolph 1990; Grant and Dunham 1990; Beaupre 1995; Shine and Madsen 1996; Bashey and Dunham 1997; Sears 2005). Two published studies compared lizard morphology and thermoregulation between habitats at similar elevation and latitude but with dissimilar structure and thermal profiles; both compared populations in an open, warmer habitat and a cooler, vegetated habitat (Gillis 1991; Irschick et al. 2005). Irschick et al. (2005) evaluated habitat use, escape behavior and morphology in anoles (*Anolis carolinensis*) and found a significant difference in leg length, body mass, clinging ability and habitat structure and use. Gillis (1991) performed a similar study on red-chinned lizards (*Sceloporus undulatus erythrocheilus*) in habitats approximately five km apart. He focused solely on variation in body temperatures, and found that mean body temperature across habitats, time, and age class was conserved, although females maintained a slightly higher mean body temperature than males. He also found that lizards thermoregulated better in the more open habitat.

In the Arkansas River Valley, open rocky habitats are often located close to forested habitats. These habitats are often isolated from each other by wide areas of open habitat such as grass or water. Consequently, lizard populations on these habitats would be somewhat isolated from the other habitat. Because rocky and forested habitats appeared to be thermally different, I suspected that lizard populations would exhibit differences in morphology and other life history traits due to the different temperature regimes in the two habitats. I initiated an investigation to determine if forested and rocky habitats were thermally different and if lizards in those habitats exhibited morphological

differences. Mean environmental temperatures for open and forest habitats in close proximity often vary substantially and open habitats (generally rock outcrops) are generally warmer throughout the activity season than forested habitats (Huey et al. 1989; Diaz 1997; Blouin-Demers and Weatherhead 2002; Row and Blouin-Demers 2006). Consequently, I expected that the lizards in the two habitats would either maintain different body temperatures or would differ in rates of behavioral thermoregulation, since the difference in habitat temperature would affect thermoregulation. Additionally, given differences in the thermal environment, lizard populations should exhibit different daily and seasonal activity patterns and thermoregulatory and non-thermoregulatory behavior (ex: Sinervo 1990). I also expected lizard morphology to differ between the two habitats (ex. Angilletta et al. 2004).

Sceloporus’ attempt to thermoregulate will affect microhabitat use, and habitat structure will in turn affect how well an individual is able to thermoregulate (Huey and Slatkin 1976; Moermond 1979; Adolph 1990). Because a major method of thermoregulation involves shuttling among thermally different microhabitats, maintaining body temperature depends on the distribution of various microhabitats in the environment (Dewitt 1967). Adolph (1990) found that two species of *Sceloporus* used microhabitats where the desired body temperature was most easily attained; in his study sites, all substrate types reached suitable temperatures at some point during the day but differed in abundance, distribution and accessibility. Microhabitats of suitable temperature that were safer and easier to reach involved less risk for the lizard and were used more frequently. The dissimilar structural features of forested and rocky habitats probably create a difference in both distribution and ease of access of different thermal microhabitats. This

difference should lead to differences in both activity patterns and behavioral thermoregulation, which will in turn affect physiological rates and morphology.

METHODS

Study Organism

Sceloporus consobrinus is a small (4-6 cm snout-to-vent length (SVL)) diurnal lizard found in an area ranging from the Mississippi River to eastern New Mexico and Colorado (Leache and Reeder 2002). It utilizes a wide variety of habitats, including forests, open areas and mixed habitat (Conant and Collins 1998).

Study Area

I captured lizards at eight rocky sites and seven forested sites within the Arkansas River Valley. All study sites were located ≤ 6 km of Russellville, AR (N 35.259147, W 93.093266). Russellville is in a temperate river valley between the Ozark and Ouachita mountain ranges. The area has, on average, 200 sunny days per year and averages 48.89 inches of rain a year, peaking in spring and fall. Temperatures tend to be lowest between December and February and highest in July and August (National Centers for Environmental Information 2015).

Lizards were captured at fifteen sites; eight sites were categorized as warmer habitat (“rocky”) and seven as cooler habitat (“forested”). Rocky habitats were composed of mixed gravel, cobble and boulders and supported very little vegetation. Woody debris was sometimes found in rocky habitats that bordered water. Rocky habitat was relatively open and flat so there was little variation in lighting; the top substrate was in direct sunlight most of the day and reached temperatures $\geq 50^{\circ}$ C in the summer. The majority of shade available was under rocks. All rocky sites are anthropogenic features created within the last 50 years and isolated from forested habitats by roads, water, and/or large open patches of grass.

Forested habitats were primarily mixed deciduous forests that supported an understory of small trees, bushes and vines. There were also small scattered patches of semi-open ground as well as a large amount of leaf litter and fallen woody debris. The forest overstory influenced the range of light intensities and microhabitats available to lizards. Further, the forest exhibited a greater primary production than was present in rocky sites. Sites were accessed via a paved or dirt trail which also provided potential basking habitat.

Habitat Temperature Profiles

Temperature profiles of each habitat were collected to categorize the substrate temperatures available to lizards and to determine if habitats were thermally different. Temperatures were collected via Thermochron iButtons (Maxim Integrated Products, California), stainless steel 17.35 mm diameter by 5.89 mm height temperature gauge/recorders. The associated computer program 1-Wire ® Drivers (Maxim Integrated Products, California) was used to program and retrieve stored information from iButtons, which are accurate to $\pm 0.5^{\circ}\text{C}$ between -40°C and 85°C . These iButtons were placed in the field for a period of one week in each month April-September and set to record temperature at 30 minute intervals. In rocky sites, iButtons were situated on open rock faces (basking and daily activity) and underneath rocks (refuge and cooling). In forested sites, iButtons were placed in common lizard microhabitats: on randomly selected sides of trees 1.5 meters above the substrate, on fallen woody debris, and in shaded areas underneath vegetation. To allow for weekly comparisons between habitats, iButtons were located in randomly paired sets of one forested and one rocky site. Overall temperatures and daily maximums and minimums for one week were compiled from the various

microhabitat types and averaged, and these averages were compared via a paired Student's t-test (Williams and Morritt 1995; Crist and Ahern 1999; Suggitt et al. 2011).

Capture and Morphology

Between March and early July, I used visual area-based searches to locate lizards in both habitat types. I captured individuals by hand noosing, and used a 2-3 m bamboo pole and a small noose made from dental floss. For each lizard captured, I recorded date, time of capture, and sex, and measured SVL and tail length of each individual by using a dial caliper (Swiss Tech SPi, accurate to ± 0.04 mm, 0-150 mm capacity). If the tail was broken, I measured both tail length to the break and length of any regrowth. Each lizard was placed inside a pre-weighed plastic bag and weighed by using a spring scale (Pesola Liteline, 20 g capacity). A spot of acrylic paint was placed on each lizard on the dorsal aspect of the neck, which has not been shown to affect mortality (Jones and Ferguson 1980; Simon and Bissinger 1983; Murray and Fuller 2000). This marking prevented same-day recapture and allowed for visual recapture of individuals until the lizard shed.

For each morphological variable, I performed a t-test to determine if there was a significant difference between years for each habitat. Data from 2013 and 2014 were combined for morphological and variables that did not vary significantly between years. Given that some studies have found differences in growth rates and morphology between subadults and adults (Ferguson and Talent 1993; Cox et al. 2005), I also sorted lizards into three size classes based on estimates of size at various ages in *S. undulatus* (Ferguson and Brockman 1980; Adolph and Porter 1996; Angilletta et al. 2004): subadults (SVL < 48 mm) are pre-reproductive, adult I (SVL between 48 - 59.99 mm) includes lizards ≥ 1

year old and most likely sexually mature, but not fully grown, and adult II ($SVL \geq 60$ mm) are fully grown lizards, most likely ≥ 2 year old.

I compared SVL between the habitats, age classes, sexes and years by means of t-test or Mann-Whitney U-test, depending on normality of the data. Weight increased exponentially with SVL, so I log-transformed the data to analyze the relationship linearly. I used linear regression to test for covariation between SVL and both $\ln(\text{weight})$ and unbroken tail length. Since SVL was correlated with both lizard weight and unbroken tail length, I used ANCOVA to compare these two factors between habitat type, sex and year, with SVL as a covariate. Additionally, I estimated length of tail that was lost in lizards with autotomized tails. To do this, I performed a linear regression on unbroken tail length and SVL for each combination of sex and habitat. I then used the resulting equations to calculate an unbroken tail length for each individual. The difference between the individual's calculated unbroken tail length and the length of the tail segment that was not autotomized was utilized as the estimated length of the autotomized portion of tail sections between sexes and habitats.

I also performed proportion tests to compare capture frequencies and tail break frequencies between the age classes, sexes, years and habitats, and a log linear model to evaluate the association between tail-break frequency, sex and habitat.

Body Temperature and Thermoregulation

Before capturing each individual, I recorded body position, substrate type, and lighting at the location of first sighting to compare behavior and microhabitat use between forested and rocky habitat. Body position was categorized as: entire body resting on substrate (BROS), front legs extended, pelvis on substrate (FLEPOS), and all legs

extended, body not touching substrate (ALEBNTS). Newly emerged and basking lizards are generally found in BROS, as it maximizes solar radiation on the dorsum, while ALEBNTS is a body position taken for cooling or trying to reduce heat gain while active (Stevenson 1985). Basking but active lizards (foraging, etc.) tend to be seen in the FLEPOS position. Substrate type included leaf litter, dirt, concrete, gravel (<6.4 cm diameter), cobble (6.4-25.6 cm), boulder (>30 cm), fallen woody debris and in tree. These categories were the only substrates on which lizards were found in my sites. Thermal microhabitats were: filtered (lighting intensity between shade and full sun), shade (>50% of lizard shaded), dappled (50% lizard shaded), sun (< 50% lizard in full sun), and hazy (clouds covering sun; no direct sunlight present). Substrate and lighting are both measurements of microhabitat, and should affect temperature in that microhabitat. I used a chi-squared test to compare chosen lighting, substrate, and body position between the habitats, sexes, and years.

I inserted a quick-reading mercury thermometer (Schutheis) into each lizard's cloaca ≤ 30 seconds of capture to obtain body temperature (T_b). Dorsal (T_d) and ventral (T_v) surface body temperatures were also measured by means of a handheld infrared temperature gun (Raytek Minitemp MT6, $\pm 1.5^\circ \text{C}$) during this period of time. These measurements allowed me to analyze internal and external body temperature to determine whether body temperature is conserved between habitats, sexes, and years. To analyze this data, I used a t-test or Mann-Whitney U-test, depending on data distribution. I utilized a general linear model (GLM) to determine if active T_b differed between May, June, and July of each year, or if there were any interactions among the various temperature measurements.

The substrate temperature at each location where lizards were first sighted was measured via an infrared temperature gun at 4 orthogonal points 1 m from the location of capture, as well as in the nearest full shade available to each individual. This gave me a sample of the temperatures immediately available to each lizard for potential thermoregulation. I then compared this sample to substrate temperature of the lizard's location to determine if lizards selected for certain substrate temperatures. A shaded mercury thermometer was used to measure air temperature at time of capture. I ran a linear regression, with air temperature on the x-axis, to determine if air temperature and substrate temperatures had an effect on T_b .

Population Activity

Because the two habitat types had different temperature regimes, I expected to find differences in the number of lizards active throughout the day as well as the times lizards were active between the two habitat types. To obtain an estimate of population activity I marked 400-meter transects across the length of each of six different sites (three rocky and three forested). Each transect was walked hourly by two people for at least one full day each month from April to July. Equal catch per unit effort and similar conditions between transects allowed for direct comparison of population activity in rocky and forested habitats. Sites were paired so at least one rocky and one forested site were always walked on the same day. Because of time limitations, pairs were determined by proximity instead of randomly pairing sites. Where there were \geq two sites close by, a coin was flipped to determine which site would be used for the duration of the field season.

During each run of a transect on a site, I recorded time, substrate and air temperature, and number of lizards seen. This allowed me to compare not only lizard

activity throughout the day but also lizard activity as a correlate to air and substrate temperature. To maintain comparability of activity levels among and between sites, transects were only walked on sunny days (<25% cloud cover). I also walked transects to record lizard activity during the non-summer months (August-March) once a month if there was at least one sunny day with few clouds.

I estimated total population size for each site by determining the number of lizards captured at that site throughout the field season and adding the number of known uncaptured lizards from general observation during fieldwork. For each transect hour, I calculated the proportion of the estimated population of the site that was active. I then graphed the proportion of lizards against time and substrate temperature to determine if these factors affected population activity in the two habitats.

Lizard Behavior

To compare lizard behavior between the two habitat types, I filmed (Fujifilm FinePix S4500, Nikon Coolpix P510, Nikon Coolpix P520) undisturbed lizards opportunistically throughout the month of June in both 2013 and 2014. I attempted to record each lizard for ≥ 10 minutes from a distance of 5-10 m. This length of time was chosen to allow for filming of multiple individuals within the constraints of the sampling day, while still maintaining a period of time that encompassed at least some variety of lizard activity. The distance was chosen to maintain reasonable video quality while minimizing disturbance to the lizard. If a lizard was obviously disturbed by human presence (i.e. displaying directly toward the filmer, running from a passerby, etc.), filming was stopped.

After filming, each video was transcribed and the data tabulated for analysis. The number of times each behavior occurred per minute a lizard was visible was calculated for each video sequence. Head bobs (a display that involves only the head bobbing up and down), pushups (a display that involves entire front half moving up and down by bending the legs), changes in body position (BROS, FLEPOS, ALEBNTS), reorientations (change in orientation without changing location), movements toward prey, movements toward other lizards, movements between and within substrates, movements between and within lighting conditions, head movements or tilts, attacks on prey, and predation events upon the lizard were all tabulated when observed in video segments. A movement was defined as a lizard traveling at least a full body length and stopping, with no continued movement for at least three seconds. This definition was to distinguish purposeful movement to a specific location from a pause in traveling. I also calculated the amount of time lizards spent in different body positions and time performing different behaviors (e.g. traveling and display). These data were reported as a percent of the total time the lizard was visible in the video segment. Distance travelled per minute was estimated for each lizard, assuming 2 m/s as average adult running speed (Van Burkum et al. 1989; Sinervo et al. 1991; McMillan et al 2011). Data were analyzed by means of t-tests and Mann-Whitney U-tests (depending on distribution) to compare rates of behaviors between the habitat, sexes and years.

RESULTS

Temperature

Habitat temperature.— Rocky and forested habitats differed significantly in the overall average daily temperature and daily maximum throughout the summer season (April-July; Tables 1, 2). In April, the rocky habitat averaged 3 degrees warmer overall (Table 1; 15.6 ± 0.48 °C versus 12.5 ± 0.36 °C), but the daily maximum in the rocky habitat was 7 °C higher on average than in the forested site (Table 2; 24.8 ± 4.29 °C versus 18.0 ± 2.61 °C). By August, the rocky habitat averaged 6 degrees warmer overall (Table 1; 33.3 ± 3.21 °C versus 27.3 ± 0.478 °C), and daily maximums in rocky habitats averaged 16.6 degrees warmer than those in forested habitats (Table 2; 53.0 ± 0.37 °C in rocky versus 36.4 ± 0.53 ° in forest; $t_{15} = -28.7$, $P < 0.001$). The rocky habitat heated much more rapidly than the forested habitat (Figure 1; approx. 3 °C/hour of warming in the rocky habitat versus 1.7 °C/hour in the forested habitat). Fall months displayed a similar pattern (Table 1, 2). In October, the daily maximum in the rocky habitat averaged 7.6 °C warmer while in November, the rocky habitat daily maximum averaged 6.7 °C warmer (Table 2). The daily minimum temperatures in the rocky habitat averaged 3.5 and 3.8 °C warmer in June and July, respectively, but those differences were not statistically significant (Table 2). Average environmental temperature when lizards were active (measured by sampling a random microhabitat in each of the four cardinal directions a meter from each lizard's location) was significantly different between years (31.4 ± 0.48 °C in 2013 versus 29.7 ± 0.45 °C in 2014; $t_{220} = 2.68$, $P < 0.01$).

Thermoregulation.— Body temperatures of lizards were very similar between the two habitats (median = 33.5 °C in forest and 33.8 °C in rocky, $Z = -0.392$, $P = 0.685$) and

between years (median = 33.8 °C in 2013 and 33.5 °C in 2014; $Z = -0.491$, $P = 0.616$).

However, in both habitats, lizards had slightly higher body temperatures in June than in April and May (34.1 ± 0.33 °C, 33.4 ± 0.29 °C, and 33.1 ± 0.14 °C, respectively; $F_{2,256} = 3.33$, $P = 0.037$). There was no difference in body temperature between sexes (median=33.7 °C in females versus 33.6 °C in males; $Z = 0.365$, $P = 0.705$).

Body temperature was not related to behavior at time of capture (Table 3; $F_{6,250} = 0.893$, $P = 0.513$). Body temperature was related to light intensity (6 categories) at location of initial capture ($F_{5,127} = 4.89$, $P < 0.001$ for 2013 and $F_{5,118} = 4.31$, $P < 0.001$ for 2014), with lizards in hazy/cloudy lighting being much colder (31.8 °C in 2013 and 29.7 °C in 2014) than lizards in full sun (34.0 °C in 2013 and 33.1 °C in 2014).

Body temperature was not affected by substrate type in 2013 ($F_{6,126} = 1.73$, $P = 0.121$), but substrate did have an effect in 2014 (Table 4; $F_{6,118} = 4.14$, $P < 0.001$); lizards had much a higher average body temperature on fallen woody debris, concrete, and boulders (mean temperatures =33.9 °C, 35.5 °C, and 33.5 °C, respectively) than on trees (32.2 °C).

Ventral temperature of the lizard was correlated with body temperature in both 2013 and 2014 (Figure 2; $r^2 = 0.570$, $t = 11.4$, $P < 0.001$). Dorsal temperature (Figure 3; $r^2 = 0.674$, $t = 14.0$, $P < 0.001$) was also correlated to body temperature. Dorsal and ventral temperatures were significantly cooler in 2014 (dorsal: median = 34.0 °C in 2013 and 33.1 °C in 2014, $Z = 3.23$, $P < 0.001$; ventral: median = 33.4 °C in 2013 and 32.8 °C in 2014, $Z = 3.23$, $P < 0.001$). Year and habitat both had a slight but significant effect on the relationship between body temperature and dorsal (year: $F_{1,219} = 7.96$, $P < 0.01$; habitat: $F_{1,219} = 10.5$, $P < 0.001$) and ventral temperature (year: $F_{1,219} = 9.17$, $P < 0.01$;

habitat: $F_{1,219} = 12.1$, $P < 0.001$). Mean body temperature was approximately 1 °C cooler in the forest habitat for both years.

Although substrate temperature was only slightly correlated with body temperature ($r^2 = 0.204$, $F_{1,115} = 27.8$, $P < 0.01$), substrate temperatures influenced activity periods in lizards; lizards were active when substrate temperatures were between 20 °C and 40 °C (Figure 4). Air temperature exhibited a similar relationship with lizard activity (Figure 5; $r^2 = 0.117$, $F_{1,115} = 17.3$, $P < 0.01$).

Morphology

Lizards in the two habitats were similar in snout-vent length (SVL) (55.1 ± 0.72 mm in forest versus 54.5 ± 0.51 mm in rocky; $t_{262} = 0.612$, $P = 0.536$). There was no difference in SVL between the sexes (55.2 ± 0.70 mm in females versus 54.0 ± 0.55 mm in males; $t_{255} = 1.37$, $P = 0.166$) or between years (55.2 ± 0.604 mm in 2013 versus 54.3 ± 0.620 mm in 2014; $t_{262} = 1.11$, $P = 0.265$). However, adults (SVL > 50) did show a difference in SVL for habitat (forest median = 57.9 versus rocky median = 56.1; $Z = 3.59$, $P < 0.001$); there was no difference between years.

In both years, I found a higher proportion of lizards in the medium size class (SVL = 50–59.9) in the rocky habitat than in the forested habitat (Figure 6a, 6b; 2013: 40.0% versus 58.0%, $P = 0.037$; 2014: 63.0% versus 38.0%, $P < 0.01$). In 2013, although similar proportions of sub-adult (SVL < 50 mm) lizards were observed in both habitat types (19.5% in rocky, 25.4% in forest), subadult lizards from the rocky habitat tended to be larger ($t_{29} = -2.84$, $P < 0.01$). In 2014, I did not see a difference in distribution between the habitats in the sub-adult age class, but the forested habitat had a much higher proportion of sub-adult lizards than were captured in rocky habitats (Figure 6b; 35.0%

versus 19.0%, $P = 0.045$). In the Adult II age class (SVL > 59.9 mm), I saw similar numbers of males and females (Figure 7a, 7b; 20.0% versus 34.0%, $P = 0.660$), but females were spread to the larger side of the size class (Kolmogorov–Smirnov test, $t = -2.42$, $P = 0.020$). All other proportions were similar, and there was no difference in sexes between years (Table 5).

Other morphological features were associated with SVL. Lizard weight covaried with SVL ($R^2 = 0.812$, $t = 24.1$, $P < 0.001$ in 2013; 6; $R^2 = 0.887$, $t = 25.8$, $P < 0.001$ in 2014). Log-transformed weight did not differ between rocky and forested habitats (6.34 ± 0.09 g versus 6.04 ± 0.09 g; $F_{1,256} = 0.213$, $P = 0.651$). Lizards averaged heavier in 2013 (6.48 ± 0.09 g versus 5.87 ± 0.08 g; $F_{1,258} = 25.8$, $P < 0.001$). Ln(weight) was significantly different between the sexes, with females averaging larger than males (6.42 ± 0.09 g for females and 5.88 ± 0.08 g for males, $F_{1,246} = 4.96$, $P = 0.027$). There were no interactions between habitat, year, or sex for lizard mass.

Unbroken tail length ($R^2 = 0.468$, $t = 7.57$, $P < 0.001$ for 2013. $R^2 = 0.711$, $t = 14.1$, $P < 0.001$ for 2014) covaried with SVL in both habitats. There was a significant difference between the sexes, with males exhibiting longer tails as SVL increased (Figure 8; 81.2 ± 0.73 mm versus 73.6 ± 0.66 mm; $F_{1,146} = 54.7$, $P < 0.001$). Unbroken tail length was slightly longer in 2013 than in 2014 (78.5 ± 0.75 mm versus 76.4 ± 0.65 mm; $F_{1,146} = 4.43$, $P = 0.037$), but was not significantly different between the forested and rocky habitats (76.6 ± 0.720 mm in forest versus 78.3 ± 0.690 mm in rocky; $F_{1,146} = 3.03$, $P = 0.079$).

Tail-break frequency was almost identical in the two habitats in both years (in 2013: 27.4% in forest versus 28.2% in rocky; $\chi^2_1 = 0.01$, $P = 0.913$; in 2014: 33.3% in

each habitat, $\chi^2_1 = 0.00$, $P = 1$). However, males were found with broken tails significantly more often than females (39.0% in males versus 20.3% in females; $\chi^2_1 = 10.7$, $P < 0.001$). That difference was consistent between habitats; I did not find a significant difference in tail-break frequency between the two habitats in males or females (loglinear model $Z_1 = 1.25$, $P = 0.263$). Estimated length of the break was not significantly different between sexes ($t_{74} = -0.479$, $P = 0.633$), years ($Z_{76} = -1.67$, $P = 0.095$) or habitats ($t_{74} = 0.903$, $P = 0.369$).

Microhabitat

Microhabitat Use.—In 2013 and 2014, I found a significant difference between habitat types in light category in which lizards were first sighted (2013: $\chi^2_4 = 69.5$, $P < 0.001$; 2014: $\chi^2_4 = 45.6$, $P < 0.001$). In both years, most of this difference stemmed from higher percentages of lizards first seen in filtered lighting in the forested habitat (2013: χ^2 contribution = 21.7 of 69.5; 2014: χ^2 contribution = 13.3 of 45.6) and sun in the rocky habitat (2013: χ^2 contribution = 5.04 of 69.5; 2014: χ^2 contribution = 7.76 of 45.6). The sexes used substrate (2013: $\chi^2_6 = 9.74$, $P = 0.136$; 2014: $\chi^2_6 = 4.70$, $P = 0.583$) and light categories similarly (2013: $\chi^2_4 = 11.5$, $P = 0.075$; 2014: $\chi^2_4 = 8.48$, $P = 0.076$) in both years.

Microhabitat Temperature.— In 2013, temperature of substrates used by lizards in forest and rocky habitats were almost identical (Figure 9a; 31.5 ± 0.629 °C in forest habitat and 31.0 ± 0.578 °C in rocky; $Z_{127} = 0.733$, $P = 0.463$), and there was no difference between selected substrate temperature and average surrounding temperatures (31.6 ± 0.45 °C versus 31.4 ± 0.51 °C; $t_{93} = 0.653$, $P = 0.516$). However, in 2014, substrate temperature at the location of capture showed a small but significant habitat

related difference, with forest lizards found on slightly warmer substrates when compared to lizards in the rocky habitat (Figure 9b; 31.3 ± 0.671 °C versus 29.3 ± 0.570 °C; $t_{116} = 2.34$, $P = 0.021$). Chosen substrate temperature for all lizards in 2014 was also slightly warmer than surrounding substrate temperatures (30.3 ± 0.451 °C versus 29.5 ± 0.447 °C; $t_{118} = 2.25$, $P = 0.026$). Males and females did not differ in their substrate temperature either year (2013: 31.3 ± 0.59 °C for females versus 30.9 ± 0.65 °C for males; $t_{120} = 0.432$, $P = 0.667$; 2014: median of females 29.6 °C, median of males 30.4 °C; $Z_{118} = -0.922$, $P = 0.357$).

Population Daily Activity

Summer.— In summer, I saw a distinct activity pattern in both habitats. In rocky habitats, the proportion of active lizards increased very quickly from 0 early in the morning until the substrate temperature reached roughly 35 °C. As the substrate temperature increased beyond 35 °C, the proportion of lizards observed decreased until few or no lizards were visible when substrate temperatures reached more than 45 °C (Figure 10). Activity usually peaked early to mid-morning (800-1000 daylight savings time), and then tapered off throughout the day as the temperature increased (Figures 11, 12, 13).

In forested habitats, fewer lizards were sighted in the morning (Figure 13). Activity increased as temperature increased until the air temperature reached about 25 °C; after this point the number of active lizards remained roughly constant, until the sun began to set. However, there was a slight increase in numbers of lizards during midday.

Non-summer— Between December and February, I only observed lizards on 9 days and all active lizards were located in the rocky habitat. Lizards were found only

when surface substrate temperatures were above 15 °C and air temperatures were above 10 °C. Lizards were only seen in areas of partial or full sunlight; once any portion of a habitat became shaded, lizards were no longer seen in that area. More lizards were active in rocky habitats, and for longer periods, since the substrate temperatures were warmer overall (Figure 14). In winter months, the majority of forested sites were shaded almost the entire day. Rocky sites were shaded by late afternoon, and lizards were active for less than three hours in the midafternoon.

Lizard Behavior

In both years, lizards in the forested habitat were most commonly first sighted either running (2013: 40.3%; 2014: 38.1%) or in the “body resting on substrate” (BROS) basking position (2013: 32.3%; 2014: 44.4%). Lizards in the rocky habitat were most often first sighted while in the BROS position (2013: 44.9%; 2014: 57.1%) or the “front legs extended pelvis on substrate” (FLEPOS) position (2013: 30.8%; 2014: 23.8%). There was very little difference in behavior at first sighting between the sexes in either year (2013: $\chi^2 = 3.13$, $P = 0.873$; 2014: $\chi^2 = 0.233$, $P = 0.994$).

Video Data.— Lizards in the forested habitat moved between light microhabitats more often than did lizards in the rocky habitat (0.102 ± 0.03 times per minute of video in forest versus 0.0107 ± 0.01 in rocky; $t_{98} = 3.43$, $P < 0.001$), but lizards in rocky habitats moved between substrates more often (median = 0.588 movements between substrates per minute in rocky versus median = 0.209 in forest; $Z_{98} = -2.077$, $P = 0.044$). However, habitat did not influence the frequency of other observed activities or the percent of time spent running or in the various body positions (Table 6, Table 7).

Male lizards had a slightly higher rate of movement between substrate types (0.60 ± 0.16 movements per minute in males versus 0.26 ± 0.13 in females; $t_{96} = -2.41$, $P = 0.016$) and lower rates of movement towards prey (median = 0.00 in both males and females; $Z_{98} = 2.04$, $P = 0.041$). Males also spent more time running than females (median percent running = 9.43×10^{-5} in males versus median = 0.00 in females; $Z_{98} = -2.94$, $P < 0.001$). Males performed more pushup sets (median = 0.58 in males versus 0.00 in females; $Z_{98} = -4.18$, $P < 0.001$) and total pushups per minute (median = 5.00 in males versus 0.00 in females; $Z_{98} = -4.32$, $P < 0.001$), but there was no difference in display frequency between the two habitats when comparing only males or only females. The sexes exhibited no difference in movement frequency between light microhabitats, within substrate types, movements to other lizards, or time spent in each body position.

DISCUSSION

Temperature

Temperature is extremely important to ectotherms, and generally habitats that differ in temperature support populations of ectotherms that vary in activity, morphology, and other life history factors (Bennett 1980; Marsh and Bennett 1986; Adolph 1990; Van Damme et al. 1992; Angilletta 2001; Angilletta et al. 2002; Pinch and Claussen 2003; Sears 2005). I found that rocky habitats averaged warmer throughout the year; this is expected because of increased radiative heating compared to the forested habitat, which is shaded by canopy cover. Long periods of unfiltered sun are the basis for the increased temperature difference between rocky and forested habitats. I also found that temperatures differed between years; March - June 2014 was cool and cloudy compared to the same period in 2013, although 2014 had less overall precipitation.

Substrate and air temperatures at which lizards are found is important when looking at thermal ecology of an ectotherm. Although rocky and forested sites differed in temperature, substrate and air temperatures when lizards were active did not differ between sites, this means lizards are selectively active with respect to environmental temperatures. Although individuals are active during the same thermal conditions, these conditions are found in differing amounts and at dissimilar times in the two habitat types.

Morphology

Surprisingly, I did not find any differences in snout-to-vent length (SVL) or weight between the two habitats. Given the thermal difference between rocky and forested habitats, I expected populations to differ in snout-to-vent length (SVL), weight, and tail length as found in many other investigations on reptiles (Tinkle and Ballinger

1972; Jameson and Allison 1976; Grant 1990; Niewiarowski and Roosenburg 1993; Beaupre 1995; Adolph and Porter 1996; Tinkle et al. 1993; Shine 2004; Sears 2005; Angilletta et al. 2004). The *Sceloporus undulatus* species complex tends to be larger in cooler environments (Angilletta et al. 2004; Sears and Angilletta 2004), while longer tail length tends to be associated with hatchlings incubated at higher temperatures (Andrews et al. 2000; Parker and Andrews 2006). I did find a difference in tail length which may have been due to warmer nest temperatures in the rocky habitat (Andrews et al. 2000; Parker and Andrews 2006).

One of the reasons I may have found no difference in SVL between habitats, especially in 2013, is because the study area had been suffering a drought the past three years. Many lizards exhibit lower growth rates and body weights in dry years when compared to wet years, probably because precipitation is linked to arthropod abundance (*Urosaurus ornatus*, Ballinger 1977; *S. merriami*, Dunham 1981; *Tiliqua rugosa*, Kerr and Bull 2006). The majority of a lizard's growth is between hatching and first reproduction, which is a year in *S. consobrinus* in Arkansas. Since *S. consobrinus* lives up to 3-4 years, the majority of adults I captured would have had at least their first year of growth under drought conditions, which may have reduced energy available for survival, growth, and development (Winne et al. 2010). The higher amount of rainfall and warmer weather in 2013 may be why populations exhibited significantly higher weight and unbroken tail length than in 2014. Although adult lizards increase SVL much slower than subadults, excess energy may be stored as increased mass to increase resources for reproduction and winter hibernation.

Sceloporus undulatus also has female-larger sexual size dimorphism which may result from environmental and behavioral variation between the sexes (Ferguson and Talent 1993; Haenel and John-Alder 2002; Cox et al. 2005). Although I did find sex-related differences in weight and tail length, I found no difference between males and females in SVL. The lack of a difference in sexual dimorphism may be due to reduced prey during drought conditions, or these populations may not exhibit significant dimorphism. The overall lower weight in males is most likely caused by their higher activity levels (Huey and Slatkin 1976; Wilson 1991).

Thermoregulation

Another explanation for why lizards in rocky and forested habitats were similar in SVL is that they maintained similar body temperatures. Given similar body temperatures, they would exhibit similar physiological metabolic efficiency. *Sceloporus* species are well known for their conservative active body temperatures (T_b) across the range of the genus (reviewed in Adolph 1990). As expected, T_b data matched those seen in other studies; although my data are on the lower end of the observed range for *Sceloporus*, they fall within the range found in other studies on *S. undulatus* (33-35 °C, Gillis 1991; 32-33 °C, Cox et al. 2005). This similarity in body temperature of lizards in the two habitats may be partly responsible for the lack of morphological differences. Similar body temperatures would lead to similarities in growth rate and energy assimilation, and therefore similar SVL, weight, and tail length.

Differences in population activity between habitats should cause differences in body size; warmer environments could provide longer periods of activity, given that suitable habitat is available for thermoregulation (Sears and Angilletta 2004). Since

lizards actively thermoregulate to maintain body temperature, differing available environmental temperatures should shift periods of lizard activity daily and seasonally (Sears and Angilletta 2004). Population activity is usually limited by habitat temperature, and lizards are often only found active when air and substrate temperatures allow for lizards to thermoregulate at optimal body temperature (Grant and Dunham 1988; Adolph 1990; Grant 1990; Asbury and Adolph 2007). I did find the difference in activity periods I expected, with lizard activity related directly to air and substrate temperature; the highest lizard activity was when air and substrate were near optimal T_b , and lizard activity decreased as the temperature moved further from this point and maintaining optimal T_b was more difficult. Lizards in the rocky habitat were active earlier in the morning and later in the evening, and in fall and winter were active more often than lizards in the forested habitat. This should mean that lizards in the rocky habitat have more time at optimal body temperature, and therefore more time to gain energy for growth (Du et al. 2012). This increase in activity should cause some morphological differences, most likely allowing them to grow faster and mature earlier, leading to a smaller overall size (Sears and Angilletta 2004). However, the longer period of seasonal activity may be compensating for the reduced daily activity during midday, causing the overall activity period to be equal between the habitats, and therefore lead to equal body size.

Lizards alter microhabitat use and basking frequency to compensate for differences in environmental temperature (McGinnis 1970; Adolph 1990; Asbury and Adolph 2007; Kearney et al. 2009; Guizado-Rodriguez et al. 2011). Consequently, I expected to find differences in behavioral thermoregulation between rocky and forested

habitats. Surprisingly, I didn't find any differences in behaviors that would change the amount of heat absorbed by a lizard, such as percentage of time in various body positions, which relates to basking frequency, or specific substrate use. Since lizards in both habitats are selectively active within the same range of air and substrate temperatures, if these behaviors are related to environmental temperature, the similar temperatures would lead to similar rates of behavior and therefore similar energy expenditures. Some lizards were captured when environmental temperatures were within the optimal T_b range. In circumstances such as this, there is little cost to thermoconformity and the importance of active thermoregulation decreases (Huey and Slatkin 1976; Blouin-Demers and Nadeau 2005), which may reduce the connection between behavior and body temperature.

A higher volume and diversity of vegetation should support a larger arthropod abundance (Shure and Phillips 1991; Siemann et al. 1998; Thomas and Marshall 1999; Silva et al. 2010); consequently, one would expect the forested habitat to provide more food. Increased food availability should significantly increase growth of *Sceloporus* lizards, including increased SVL and weight (Waldschmidt et al. 1986). Surprisingly, as noted above, I did not find substantial differences in body size between lizards in the two habitats. However, Waldschmidt et al. (1986) pointed out that both food passage time and the rate of food consumption are directly related to temperature in lizards; as temperature increases, food consumption increases and food passage time decreases. I did not find a difference in rate of predation attempts by lizards, which would imply that, even if food resources are higher in one habitat, lizards are utilizing them equally. In cooler forested

habitats, the benefits of increased food availability may be outweighed by the longer periods of inactivity in the morning and afternoon.

The warmer overall temperature in the rocky habitat would imply shorter food passage times and increased rates of feeding (Bennett and Dawson 1976; Waldschmidt et al. 1986); even if lizards are not active on the surface during the hottest part of the day, they may still be maintaining optimal body temperatures in cooler microhabitats. While temperatures under rocks were lower than optimal body temperature in summer, they still reached temperatures at which lizards could be active (high 20s-low 30s). Since lizards in the rocky habitat are active earlier in the day than lizards in the forest habitat, rocky lizards are at optimal body temperature for a larger portion of the day and therefore may be utilizing food resources more efficiently. This would allow them to match the potentially higher growth rates in the forested habitat, and would cause them to have similar SVL and weight.

The difference I found in use of thermal microhabitats and substrates between the two habitats supports the idea that lizards in the two habitats may be utilizing food resources differently. Lizards in forested habitat moved between thermal microhabitats more often but often remained on one substrate, while lizards in the rocky habitat moved from location to location while remaining in the same thermal microhabitat. In the forested habitat, the majority of movements made by lizards were to specific thermal microhabitats and were most likely for thermoregulation purposes. Some of this difference is due to the difference in habitat structure; forest lizards have many more thermal microhabitats available, and can thermoregulate within a smaller area; for example, a single tree branch with some overhanging vegetation. However, because the

rocky habitat is much warmer, lizards may be able to maintain optimal body temperature more easily, and some of the movement is most likely non-thermoregulatory.

Additionally, if lizards in the rocky habitat are covering a larger spatial area per unit of time, they are more likely to come across prey than the lizards in the forested habitat.

Even if the rocky habitat has a lower overall arthropod abundance, the higher rate of prey encounters may cause overall prey consumed to be similar between the two habitats, although the higher rate of movement per prey encounter would decrease the net gain in energy per prey item.

Predation

Differences in predation between habitats could be influencing average body size and age class distribution within populations of lizards. Habitat and community structure among and between populations may lead to variation in both predator type and predation intensity, and therefore a difference in predation on age class, which would shift the average SVL, and tail-break frequencies. Because *Sceloporus* as a genus is adapted for easy and frequent tail loss as a survival mechanism, I decided to use tail loss as an index of predation (reviewed in Ballinger and Tinkle 1979).

Some data suggest a tendency for species that utilize exposed microhabitats to have a higher rate of tail loss (reviewed in Bateman and Fleming 2009). In this case, I might expect the forest habitat to have lower proportion of tail loss. However, the rocky habitat may provide better refuge from predation; the structure of the habitat is such that a lizard is never far from access to many solid refuges under rocks. In forest habitat, although there is more vertical structure and microhabitat variation, the cover available (leaf litter, ground cover, trees) may provide less effective refugia; this means that,

although the forest lizards may be less exposed to predators, they are more susceptible to predators that do see them. Lizards also may behave differently when exposed to predators; I noticed differences in behavior when lizards in the two habitats were approached by humans. Lizards in the forested habitat often ran into cover if in a relatively exposed location or would freeze if already concealed. If pursued, the lizard would travel deeper into the underbrush or ascend a tree so as to be out of reach. In the rocky habitat, lizards were much more exposed, but would watch the human until it was very close and then either move further away while staying on the surface, or retreat under a nearby boulder. So again, I expected differences in frequency of predation on lizards in the two habitats based on observed anti-predation behavior.

Finally, abundance and type of predators that feed on lizards most likely differed between the two habitats because of the structural differences and the presence of shoreline in most rocky habitats. Snakes were common in both habitats, although species differed. Consequently, I expected to find a difference in predation levels on lizards in the two habitats, and potentially an effect on body size. However, I found no difference between the two habitats in proportion of lizards with autotomized tails. My results match those of Smith (1996), who found that tail loss in *Sceloporus virgatus* was similar between cooler and warmer habitats. This may reflect similar predators in both habitats, or, more likely, similar proportions of inefficient predators. Medel et al. (1988) observed that tail autotomy reflects attempts at predation by inefficient predators as opposed to overall predation levels; he found that predatory birds were almost always effective predators, while other predators, such as snakes, were more inefficient.

The majority of research reports no sexual dimorphism in tail loss (reviewed in Bateman and Fleming 2009), including in a number of *Sceloporus* species (Vinegar 1975; Ballinger 1979). However, I did find a difference in tail autotomy between the sexes; males had a much higher instance of tail autotomy in both 2013 and 2014. This could stem from a higher rate of unsuccessful predation attempts on males than on females. Medel et al. (1988) found that in three species of lizards, lizards with longer tails escaped more often from some predators. Average male tail length was 5 mm longer than females of the same size; while not a large amount, this still could make the difference in survival and tail loss between otherwise equal predation attempts. Similarly, males generally have higher levels of activity, which makes them more visible to predators and may increase the chances of a predation attempt (Huey and Slatkin 1976; Wilson 1991). I found that males move further and more frequently than females, as well as performing more displays, which may be related to movement rates as well as intraspecific interaction (Martins 1993). This higher level of activity supports the increased level of attempted predation suggested by the higher proportion of tail autotomy in males. Male competition may also be causing more tail autotomy than expected; if this is the case, it may explain the similarity in tail loss between the habitat types as well as the lower rate of tail autotomy in females.

Bateman and Fleming (2009) posit that one sex may be more adept at escaping through tail autotomy than the other. If females are less adept at escaping predation, the removal of females from the population may be shifting the size distribution of the population, and contributing to the lack of morphological differences between the sexes and the habitats. Similarly, if relatively more females are unsuccessful in escaping

predation, the majority of observed females would be those who have not been exposed to serious predation attempts and therefore would not have autotomized tails. This may balance the lower overall risk of predation on females from lower activity levels, and could explain why some researchers report no difference in tail loss between the sexes.

While I attempted to catch all lizards in a site, capture may have been skewed towards lizards that spent more time active or in exposed microhabitats, or had a reduced ability to escape. These lizards would also be the ones most likely exposed to predation, intraspecific competition, or other methods of tail loss. This may also explain the slightly higher tail loss frequency in 2014 compared to 2013. Since 2014 was cooler, more “bold” lizards (i.e. ones with more risk-prone behaviors) may have been active more often and therefore were more likely to be captured (Lopez et al. 2005; Carter et al. 2012). The cooler weather may also have made lizards more susceptible to predation, as they would have to thermoregulate longer and more often and would also have lower body temperatures for a higher proportion of the day, leading to a reduced ability to escape from predators.

Although the habitats in my study differ in overall temperature, patterns of available temperatures, and physical structure, the populations in these habitats do not exhibit the expected morphological and behavioral differences seen in the majority of populations in thermally different habitats (Bennett 1980; Marsh and Bennett 1986; Adolph 1990; Van Damme et al. 1992; Angilletta 2001; Angilletta et al. 2002; Pinch and Claussen 2003; Sears 2005). The populations in my study are most likely genetically similar even though there is limited movement between sites; any differences would stem from differences in environmental factors rather than genetics. Alternatively,

Niewiarowski and Roosenburg (1993) found that *S. undulatus* in New Jersey didn't exhibit phenotypic plasticity associated with different thermal environments. Perhaps the lizards in my populations are neither phenotypically plastic nor genetically isolated. Although there may be many reasons the populations in this study are not showing morphological differences, further research is needed to fully analyze the potential causes. This study draws attention to the erroneous assumption made by many: that morphological differences in habitats across latitudes or elevations are driven primarily by temperature. Instead, I suggest that more attention should be placed on the numerous other factors associated with changes in elevation and latitude that may be affecting population life history. On a broader scale, by comparing geographically close populations, we can better understand the nature of life history variations in general (Ballinger 1979). Knowledge of environmentally-based life history variations of ectotherms may be especially important to future research given the predicted increase in future temperatures. If we know how these environmental factors affect the life history of ectotherms, we have the potential to predict how populations and species will be affected in the future.

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TABLES

Table 1. Average substrate temperature (°C) \pm SE in both habitat types for one week each month April to November 2013.

Month	Rocky \pm SE	Forest \pm SE	Z	<i>P</i> value
Apr.	15.6 \pm 0.48	12.5 \pm 0.36	14.5	<0.001
May	23.8 \pm 0.63	18.2 \pm 0.24	18.1	<0.001
June	33.2 \pm 0.20	26.4 \pm 0.11	28.6	<0.001
July	32.8 \pm 0.18	27.7 \pm 0.12	26.7	<0.001
Aug.	33.3 \pm 3.21	27.3 \pm 0.48	16.6	<0.001
Sept.	31.9 \pm 0.70	25.9 \pm 0.27	11.9	<0.001
Oct.	13.7 \pm 0.17	11.9 \pm 0.11	21.7	<0.001
Nov.	12.9 \pm 0.34	11.7 \pm 0.31	7.1	<0.001

Table 2. Average daily minimum and maximum temperatures (°C) for both habitat types for one week each month

April - November 2013. Bolded p-values are significant.

Month	\bar{x} Daily Maximum				\bar{x} Daily Minimum			
	Rocky \pm SE	Forest \pm SE	t	P	Rocky \pm SE	Forest \pm SE	t	P
Apr.	24.8 \pm 4.3	18.0 \pm 2.6	8.75	<0.01	8.9 \pm 2.2	8.1 \pm 2.1	3.13	0.017
May	30.1 \pm 3.7	21.3 \pm 1.6	4.08	<0.01	15.5 \pm 2.1	15.7 \pm 2.1	0.21	0.490
June	42.6 \pm 1.4	31.6 \pm 0.6	7.28	<0.001	24.6 \pm 0.8	21.1 \pm 0.7	-16.03	<0.001
July	40.7 \pm 1.7	32.7 \pm 0.9	5.88	<0.001	26.7 \pm 0.9	22.9 \pm 0.7	-13.91	<0.001
Aug.	53.0 \pm 0.4	36.4 \pm 0.5	-28.71	<0.001	23.3 \pm 0.5	23.4 \pm 0.3	0.34	0.058
Sept.	53.0 \pm 0.5	35.3 \pm 0.6	-23.34	<0.001	20.3 \pm 1.5	20.6 \pm 0.9	1.02	0.122
Oct.	24.1 \pm 1.0	16.5 \pm 0.8	8.66	<0.001	8.0 \pm 1.2	7.8 \pm 1.1	0.55	0.591
Nov.	32.1 \pm 2.1	25.4 \pm 2.0	8.66	<0.01	3.9 \pm 1.9	3.5 \pm 1.8	0.92	0.387

Table 3. Average body temperature (T_b) for lizards engaged in 7 behaviors at time of capture. BROS (body resting on substrate), FLEPOS (front legs extended, pelvis on substrate), and ALEBNTS (all legs extended, body not touching substrate) are thermoregulatory positions.

Behavior	Count	$T_b \pm SE$
BROS	115	33.1 ± 0.18
Running	64	33.5 ± 0.24
FLEPOS	56	33.5 ± 0.26
Displaying	14	33.2 ± 0.52
ALEBNTS	4	33.3 ± 0.98
Eating	2	33.8 ± 1.38
Mating	2	31.0 ± 1.38

Table 4. Average body temperature (T_b) in degrees Celsius and sample size (n) for lizards captured on 7 substrates in 2013 and 2014.

Substrate	2013 n	2013 $T_b \pm SE$	2014 n	2014 $T_b \pm SE$
Boulder	50	33.3 ± 0.27	60	33.5 ± 0.23
Fallen Woody Debris	22	33.9 ± 0.41	23	33.9 ± 0.37
Tree	24	32.1 ± 0.39	17	32.2 ± 0.44
Leaf Litter	14	32.9 ± 0.52	19	33.0 ± 0.41
Cobble/gravel	14	32.5 ± 0.51	2	32.1 ± 1.28
Concrete	7	33.8 ± 0.72	2	35.5 ± 1.28
Dirt	2	36.1 ± 1.36	2	29.1 ± 1.28

Table 5. Proportion of lizards captured in each age class for habitat, sex, and year.

Year	Age class	Forest	Rocky	Male	Female
2013	Subadult (SVL<50)	25.4	19.5	24.6	19.4
	Adult I (50<SVL<59.99)	40.0	58.4	55.4	46.3
	Adult II (SVL≥60)	34.5	22.1	20.0	34.3
2014	Subadult (SVL<50)	34.9	19.1	25.7	29.1
	Adult I (50<SVL<59.99)	38.1	63.5	54.3	47.3
	Adult II (SVL≥60)	26.9	15.9	20.0	23.6

Table 6. Comparison of rates of common lizard activities in number of times activity was performed per minute for rocky and forested habitats (n=98). BROS (body resting on substrate), FLEPOS (front legs extended, pelvis on substrate), and ALEBNTS (all legs extended, body not touching substrate) are thermoregulatory positions.

Activity	Forest	Rocky	<i>t</i>	<i>P</i>
Movement between light categories	0.102 ± 0.03	0.011 ± 0.01	3.43	<0.001
Movements to prey	0.028 ± 0.02	0.009 ± 0.00	0.85	0.39
Pushups	2.840 ± 0.87	2.691 ± 0.67	0.15	0.88
Pushups per set (n=42)	5.143 ± 0.58	6.783 ± 0.61	-1.93	0.06
Consuming prey	0.047 ± 0.02	0.018 ± 0.01	1.14	0.26
Substrate licks (chemosensory)	0.088 ± 0.05	0.067 ± 0.04	0.34	0.73
% of time running	0.002 ± 0.00	0.002 ± 0.00	0.22	0.82
% of time in BROS	45.808 ± 0.06	44.500 ± 0.07	0.14	0.89
% of time in FLEPOS	23.421 ± 0.05	31.893 ± 0.07	-0.92	0.36
% of time in ALEBNTS	0.029 ± 0.02	0.035 ± 0.02	-0.21	0.83

Table 7. Comparison of rates of common lizard activities in number of times activity was performed per minute for rocky and forested habitats (n=98). BROS (body resting on substrate), FLEPOS (front legs extended, pelvis on substrate), and ALEBNTS (all legs extended, body not touching substrate) are thermoregulatory positions.

Activity	Forest (median)	Rocky (median)	<i>Z</i>	<i>P</i>
Movement to new substrate	0.209	0.588	-2.08	0.044
Movement within current substrate	0.331	0.094	1.65	0.097
Movements to other lizards	0.000	0.00	1.22	0.221
Headbobs	0.000	0.00	1.25	0.208

FIGURES

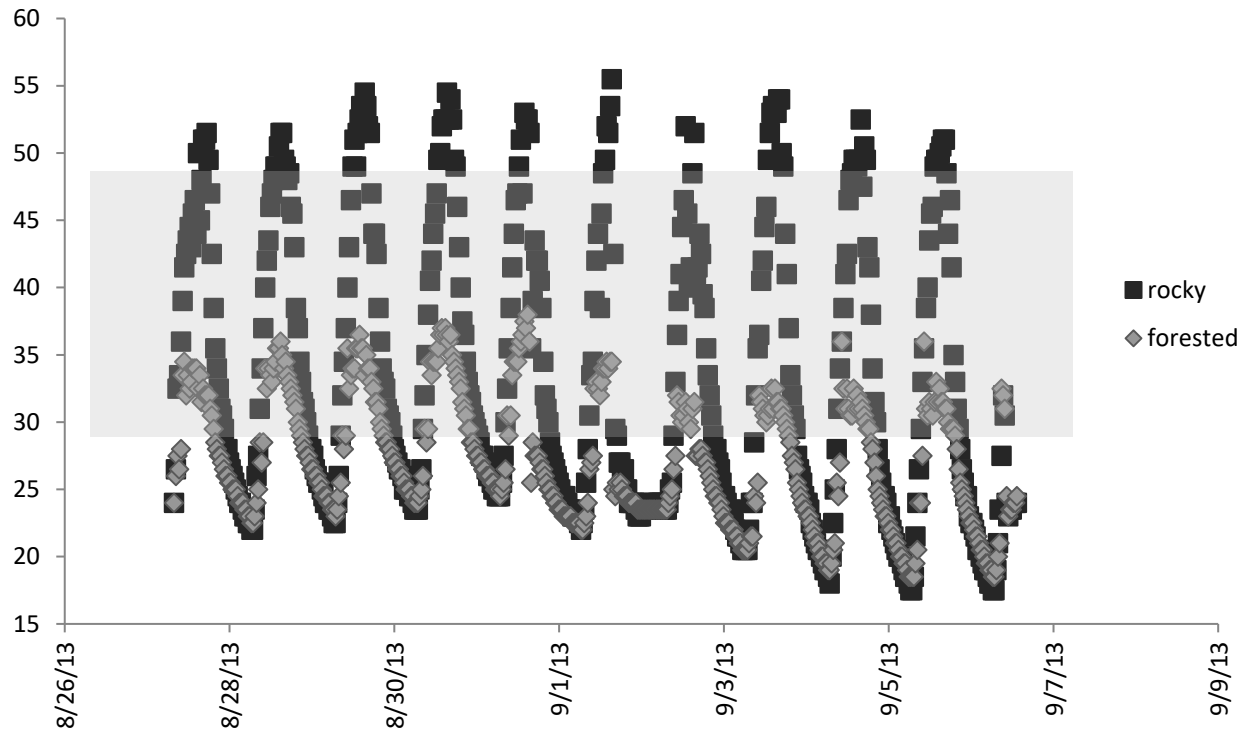


Figure 1. Pattern of daily temperatures ($^{\circ}\text{C}$) in the rocky and forested habitat for August 26, 2016 to September 7, 2016. The shaded area is the range of temperatures in which lizards are found active. This data is from one logger representative of the pattern seen in all summer data in each habitat.

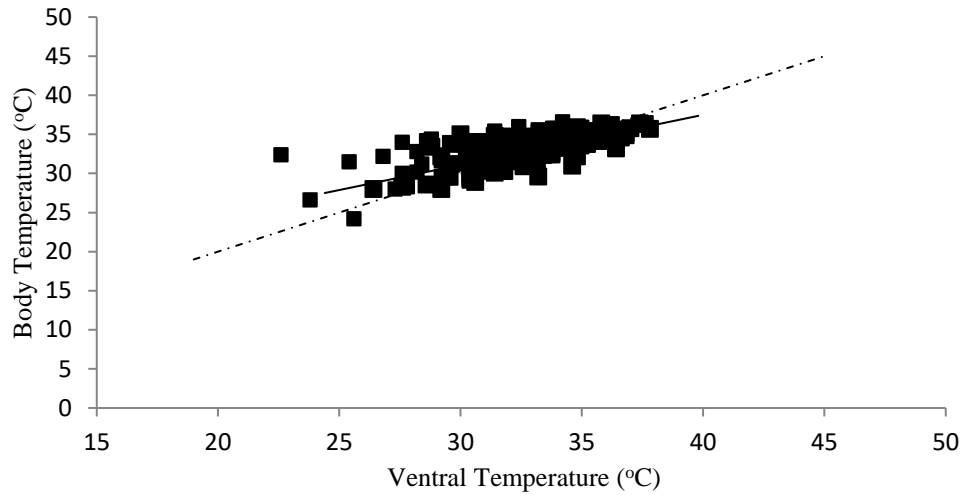


Figure 2. Core body temperature compared to ventral temperature for lizards in 2013 and 2014. Dotted line is the slope where body and ventral temperature are equal. Solid line is the trendline of the data; $R^2 = 0.570$, $P < 0.001$.

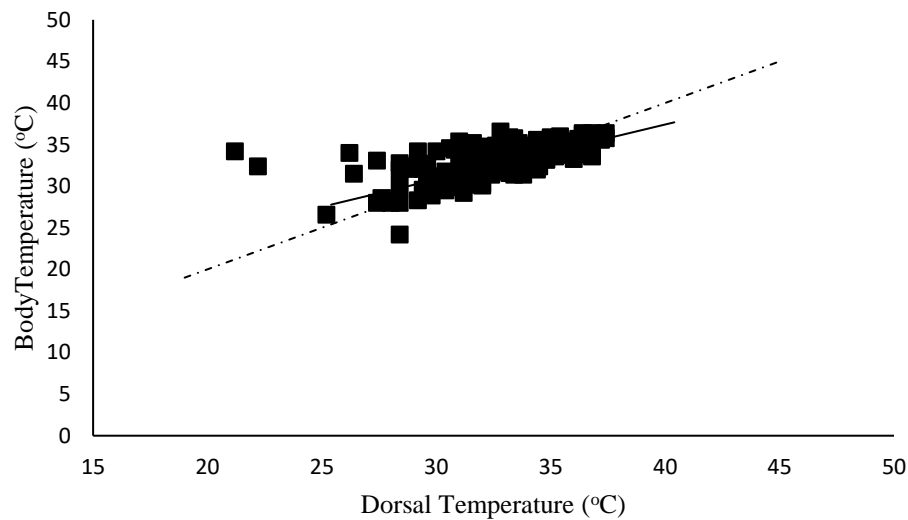


Figure 3. Core body temperature compared to dorsal temperature for lizards in 2013 and 2014. Dotted line is the slope where body and ventral temperature are equal. Solid line is the trendline of the data; $R^2 = 0.668$, $P < 0.001$.

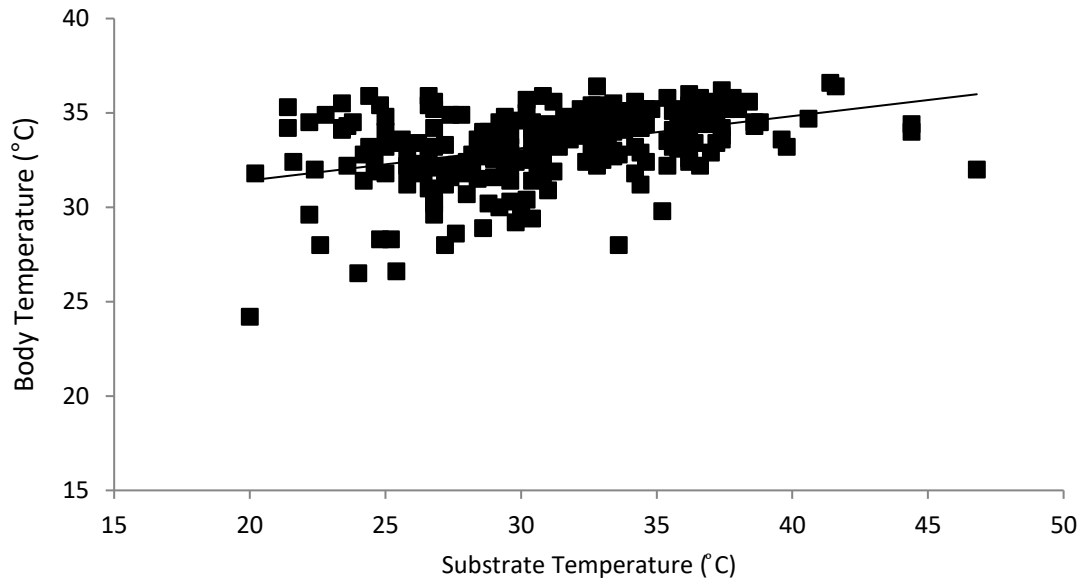


Figure 4. Substrate temperature at initial capture location plotted against core body temperature at capture for the 2013 and 2014 field seasons. $R^2 = 0.204$.

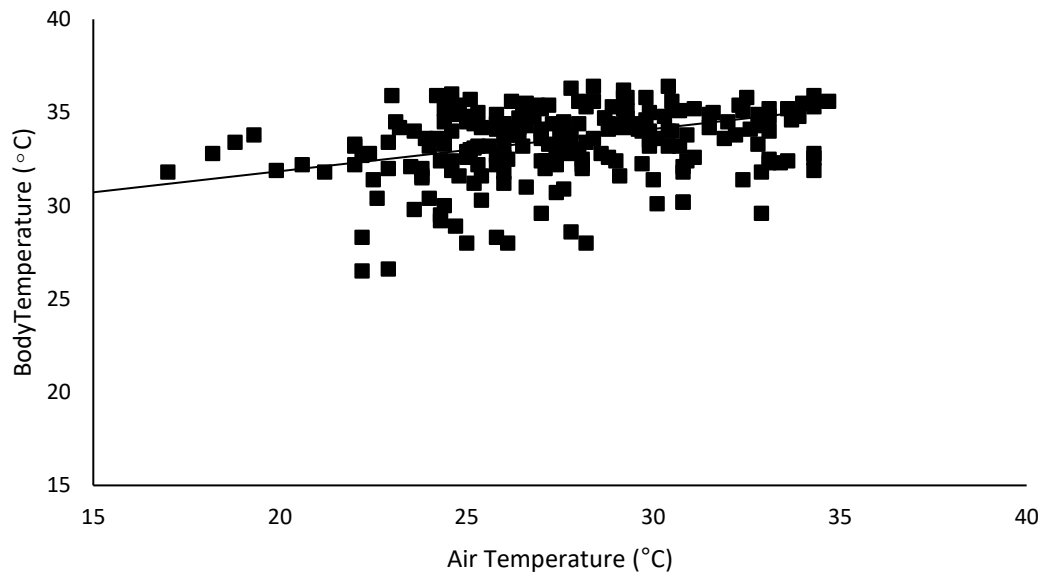
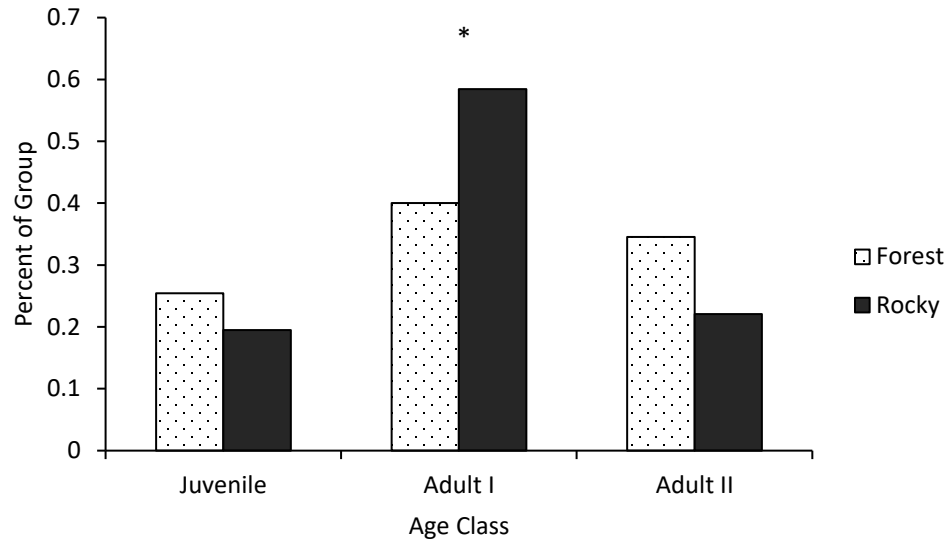
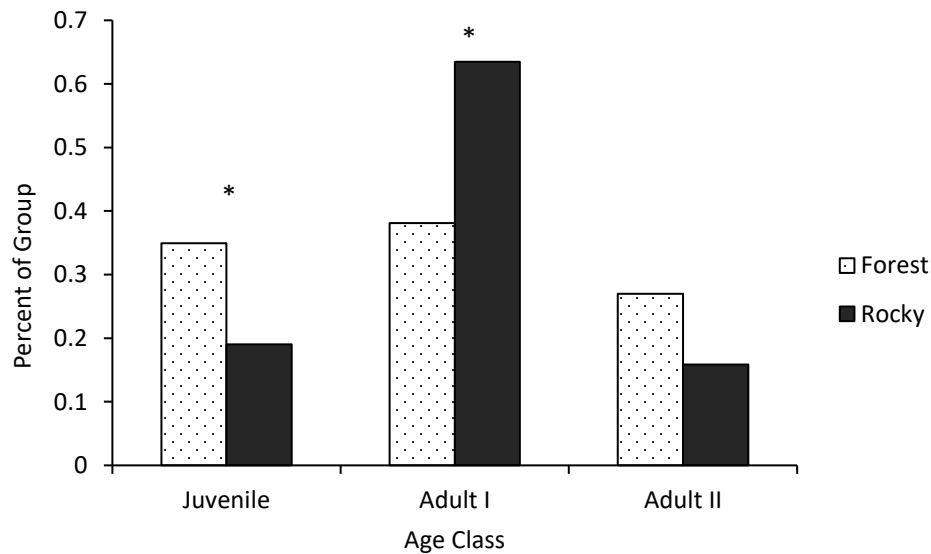


Figure 5. Air temperature at initial capture location plotted against core body temperature at time of capture for the combined 2013 and 2014 field seasons. $R^2 = 0.117$.



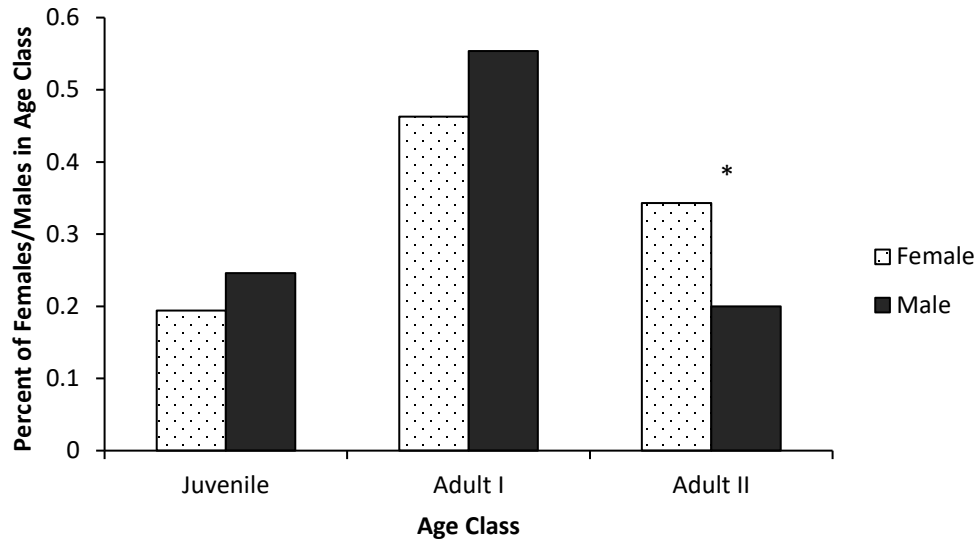
a



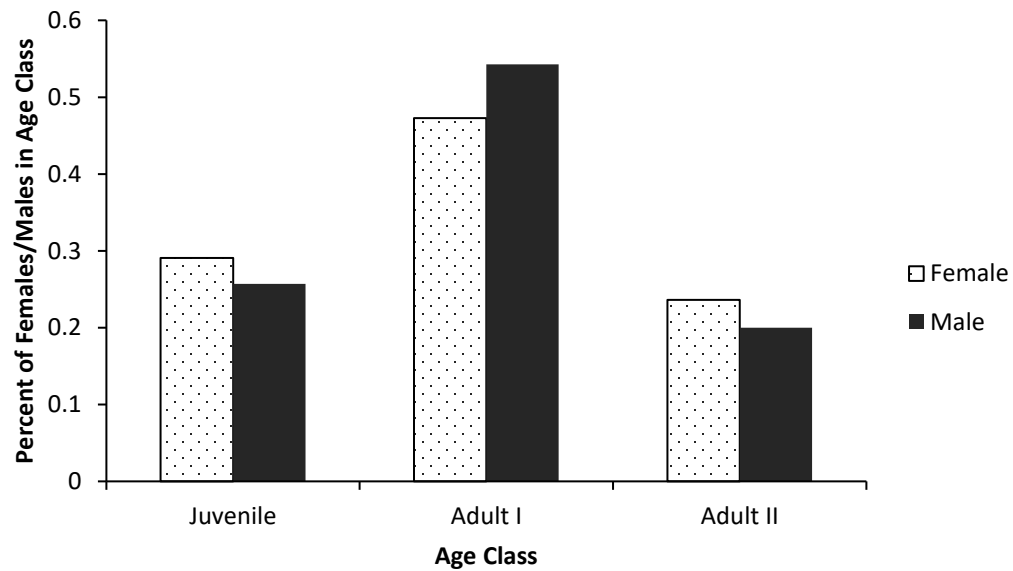
b

Figure 6a and b. Percent of lizards in each age class in rocky and forest habitats for 2013 (a) and 2014 (b). * denotes significant difference between habitats for that age class.

Juvenile is individuals with SVL >50 mm, Adult I consists of individuals with SVL 50-59.99 mm, and Adult II consists of individuals with SVL \geq 60 mm.



a



b

Figure 7a and b. Percent of males and females in each age class for 2013 (a) and 2014 (b). * denotes significant difference between the sexes for that age class. Juvenile is individuals with SVL >50 mm, Adult I is individuals with SVL 50-59.99 mm, and Adult II is individuals with SVL \geq 60 mm.

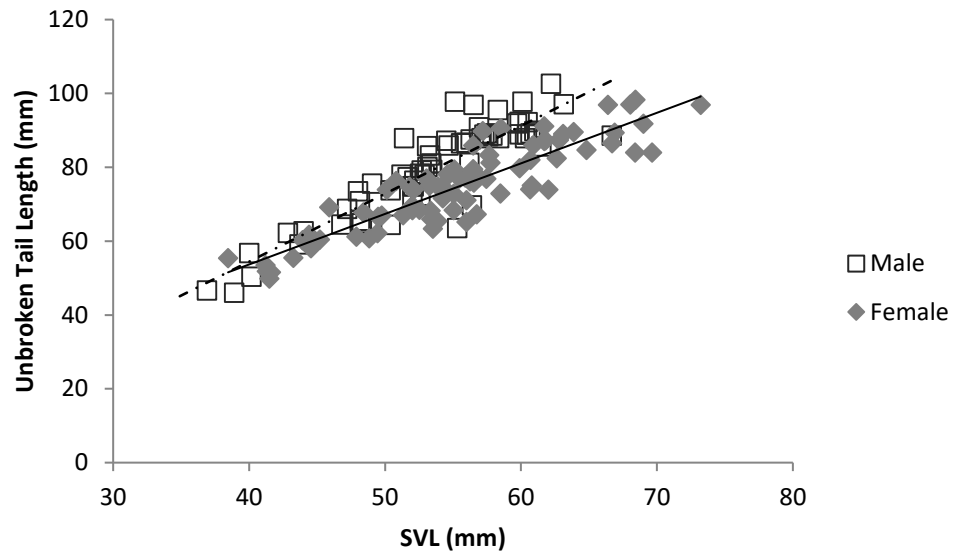
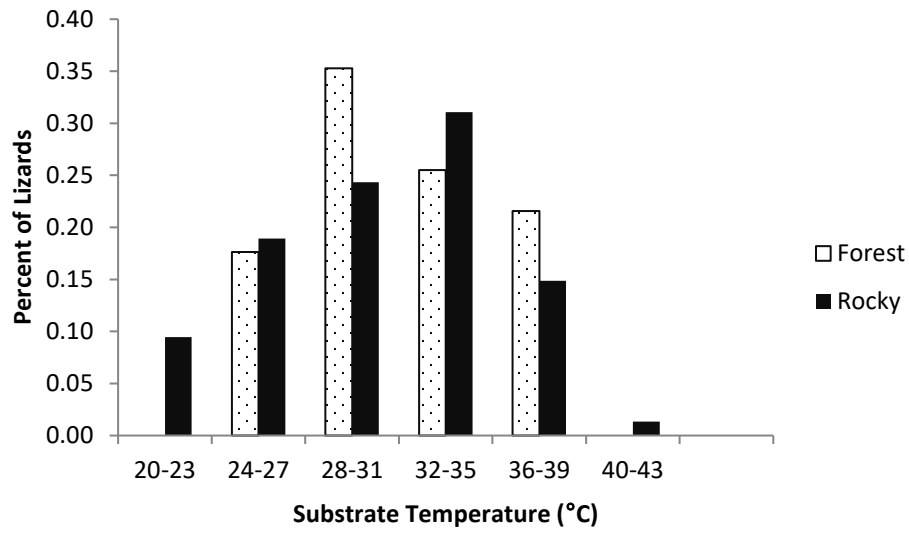
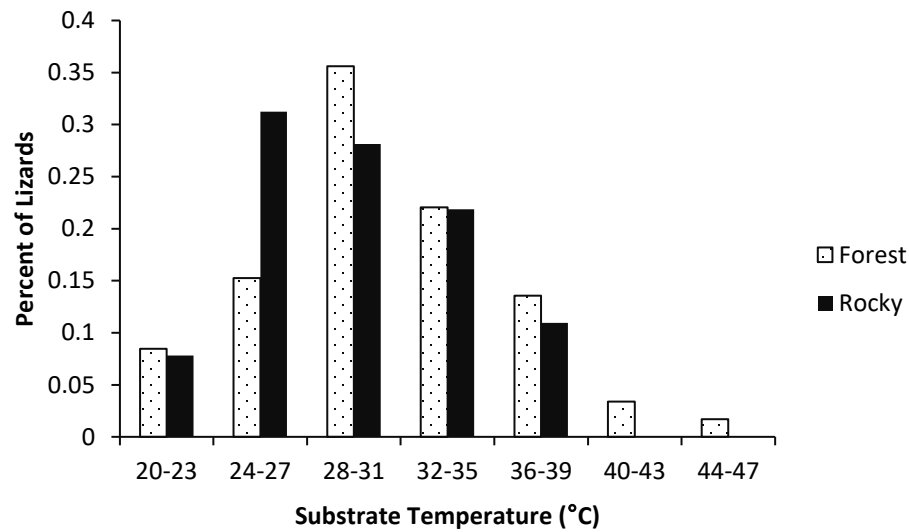


Figure 8. Unbroken tail length versus snout-to-vent length (SVL) for male ($R^2 = 0.7925$) and female ($R^2 = 0.801$) lizards.



a



b

Figure 9a and b. Substrate temperature at location of capture for lizards captured in each habitat in 2013 (a) and 2014 (b). Data include only the first capture site for any lizards that were captured more than once. Y-axis is percent of lizards caught in that habitat.

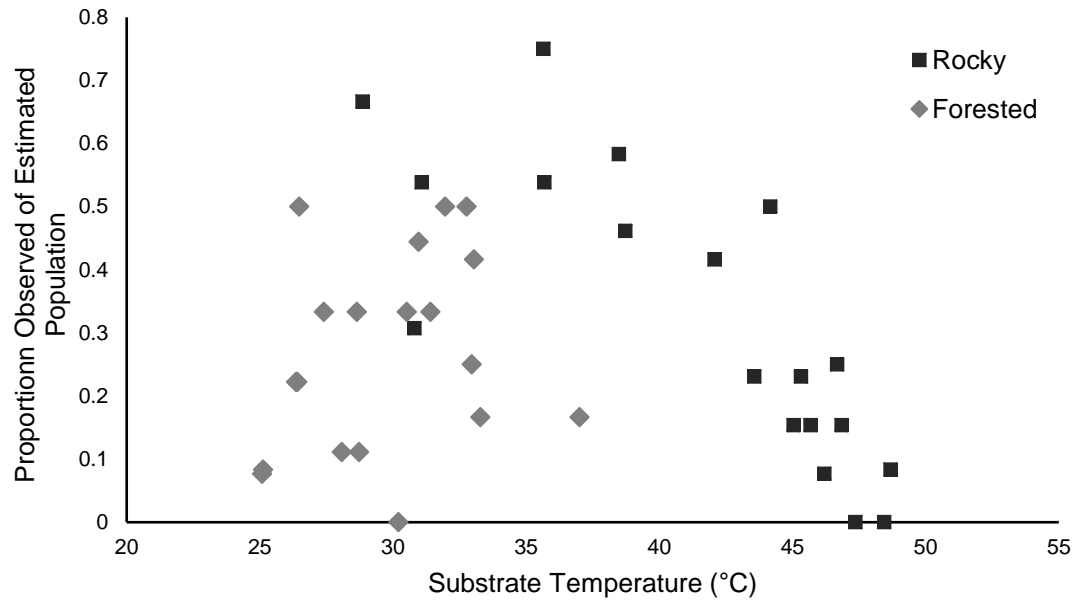


Figure 10. Proportion of lizards observed of the total estimated population at each site compared to average substrate temperature for that transect during the summer season (April-June). Each point represents the proportion of the estimated population that was active at a site over the course of an hour for three forest and three rocky sites.

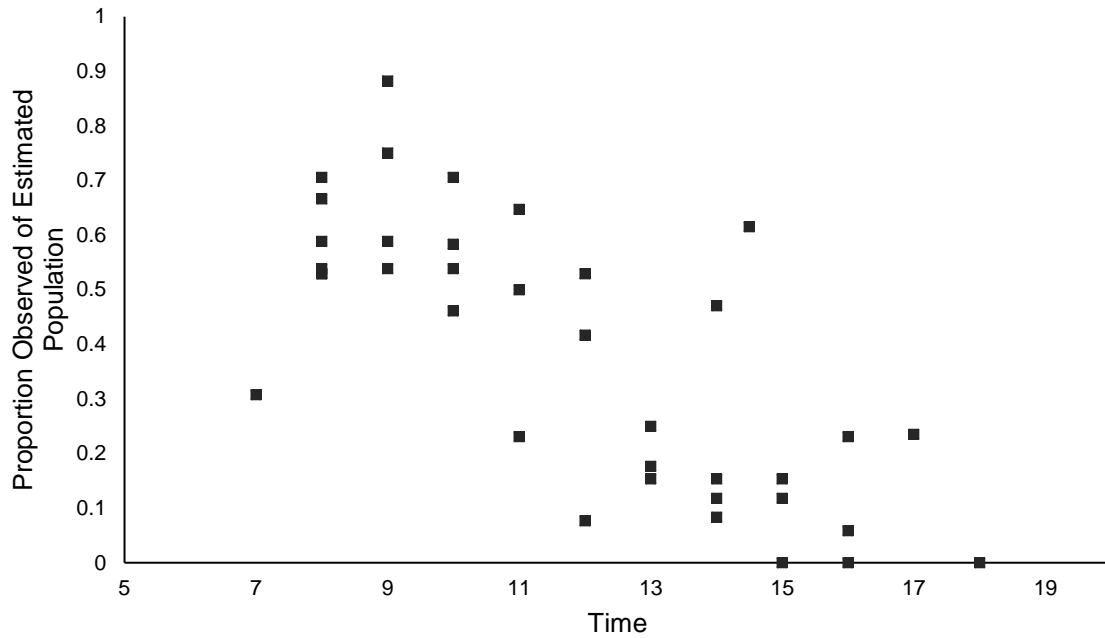


Figure 11. Proportion of estimated site population observed active per hour of the day (daylight savings time) during the summer activity season (April-June) in the rocky habitat. Each point represents the proportion of the estimated population that was active at a site over the course of each hour for three sites.

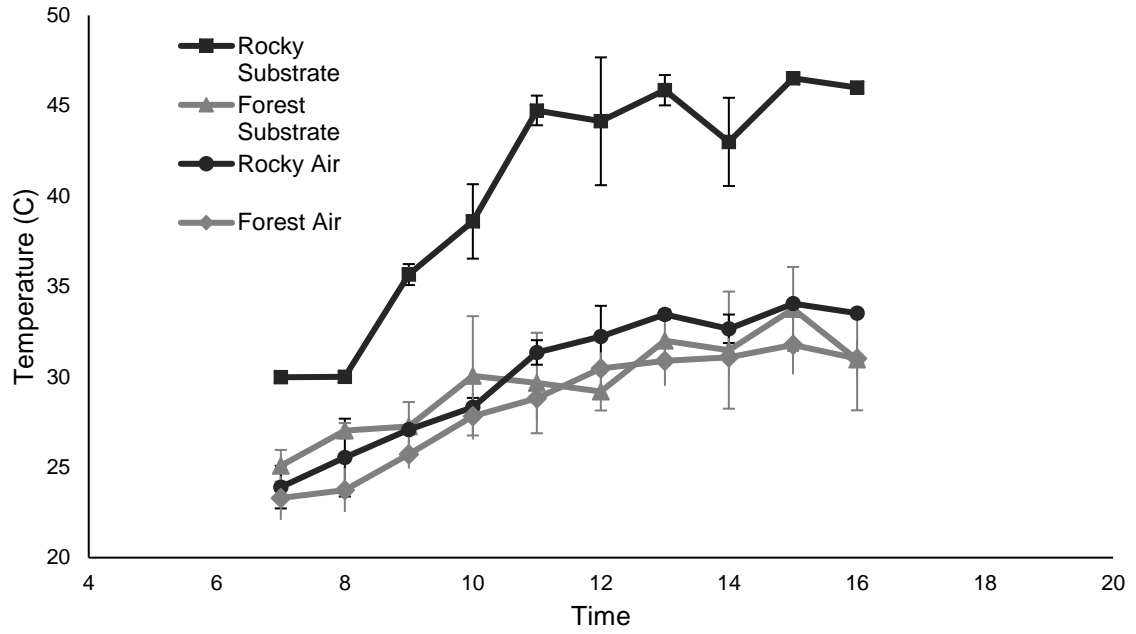


Figure 12. Air and substrate temperatures for the forest and rocky habitats over a 9-hour period in June. Data is averaged from 3 forest and 3 rocky sites, with 6 ibuttons per site.

Error bars are standard error.

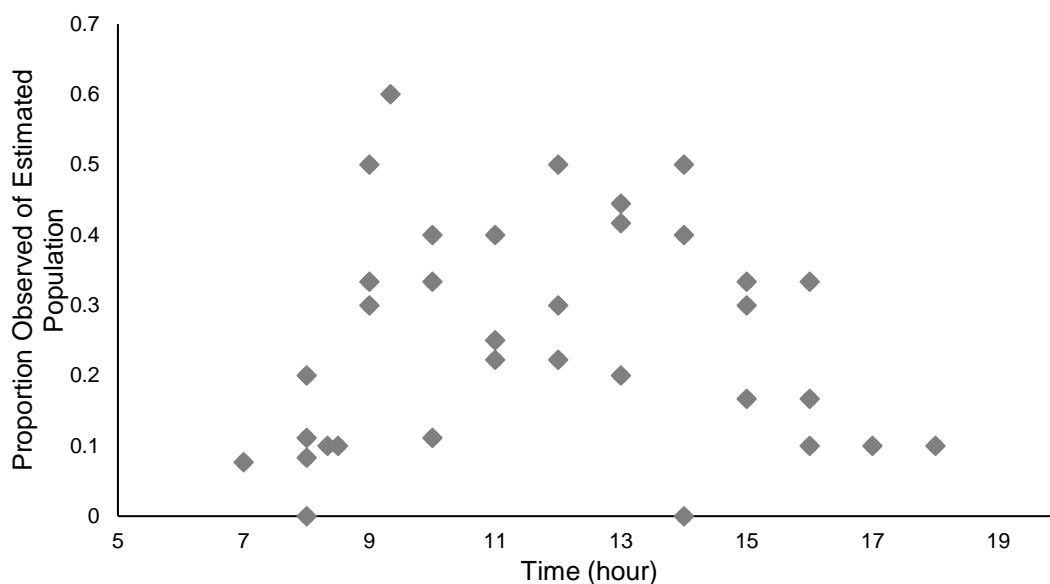


Figure 13. Proportion of estimated site population observed active per hour of the day (daylight savings time) during the summer activity season (April-June) in the forest habitat. Each point represents the proportion of the estimated population that was active at a site over the course of each hour for three sites.

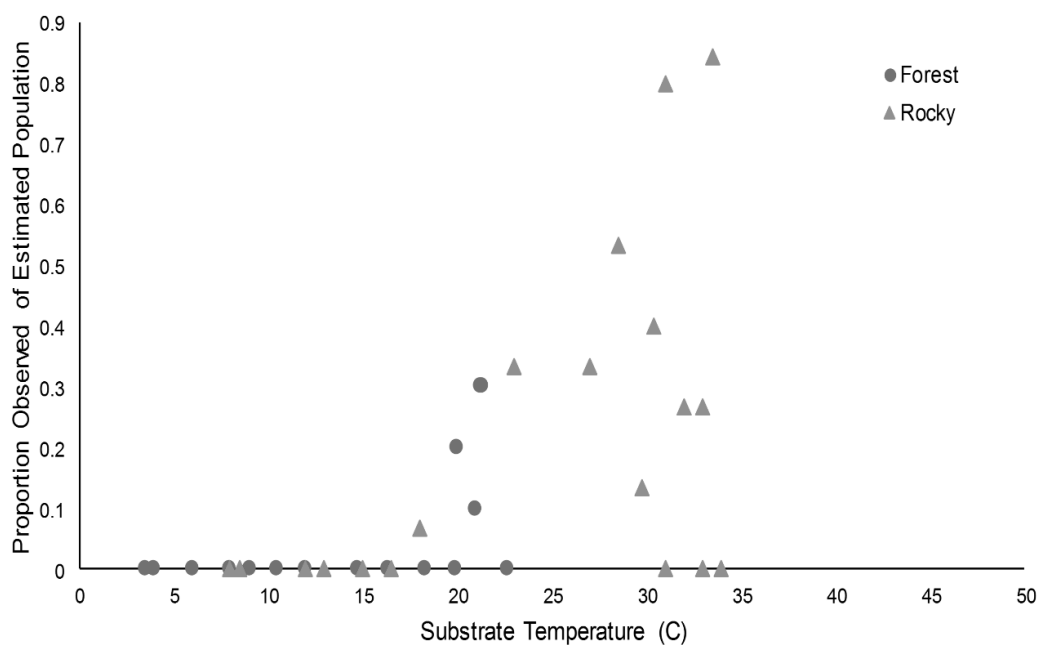


Figure 14. Proportion of lizards observed of the total estimated population at each site compared to substrate temperature during fall and winter (October-February).

