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Physiological Performance in Ecologically Distinct
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woodi*

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THE EFFECTS OF THERMAL OPPORTUNITY AND HABITAT ON PHYSIOLOGICAL
PERFORMANCE IN ECOLOGICALLY DISTINCT POPULATIONS OF THE FLORIDA
SCRUB LIZARD (*SCELOPORUS WOODI*)

by

LAUREN K. NEEL

(Under the direction of Lance D. McBrayer)

ABSTRACT

An ectotherm's ability to thermoregulate affects many physiological traits. Therefore, thermal factors are paramount when considering behavior, activity time, body temperatures, energy budget, and performance capabilities. The Florida scrub lizard (*Sceloporus woodi*) is a ground-dwelling lizard that occupies longleaf pine and sand pine scrub habitats in the Ocala National Forest. Here, this species' habitat is maintained by either clear-cut logging in scrub stands, or prescribed burning in long leaf pine stands. These habitat types differ in their dominant vegetation, canopy cover, and availability of vertical perches and thus are ecologically different. I used biophysical models to measure the available environmental temperatures in longleaf pine and sand pine scrub populations. Thermal opportunity is used to describe the availability of preferred temperatures within specific habitats so as to understand the thermal constraints that may influence available activity times as well as the energy and resources spent on thermoregulation in a given environment. Longleaf pine populations had higher thermal opportunity which allowed populations to thermoregulate more effectively overall. However, when thermal quality of habitat was poor, all populations increased thermoregulatory effort despite the higher costs of thermoregulating. Furthermore, the difference in available temperature distribution in each

environment was examined in the context of the thermal sensitivity of locomotor performance. Thermal performance curves were generated to compare traits associated with physiological performance. Higher operative temperatures in sand pine scrub habitats were correlated with higher critical thermal limits and thermal optima in these populations. Despite the range of preferred temperatures being the same, the data suggest that the thermal physiology of this species is evolutionarily labile. Thus, variation in thermal opportunity between longleaf pine and sand pine scrub stands is likely driving the observed divergence in thermal physiology among these populations.

INDEX WORDS: Thermoregulation, Operative temperature, Thermal performance curve

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by

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Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

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CHAPTER 1

THE EFFECTS OF THERMAL OPPORTUNITY AND HABITAT ON
THERMOREGULATORY EFFECTIVENESS IN THE FLORIDA SCRUB LIZARD,
SCELOPORUS WOODI

ABSTRACT

An organism's ability to thermoregulate affects many physiological traits in ectotherms, and is therefore paramount when considering activity time, body temperatures, energy budget, and performance capabilities. I examined populations of the Florida scrub lizard *Sceloporus woodi* that live in two contrasting habitats that are maintained by different management practices. In the Ocala National Forest much of the Florida scrub lizard's habitat is maintained by clear-cut logging and prescribed burning in place of the historical fire cycle. I estimated thermal quality of a habitat via an index of how closely the available operative temperatures in a habitat aligns with an animal's preferred range of temperatures determined in a thermal gradient. Available operative temperatures were measured using biophysical models placed throughout ecologically relevant sites. Available operative temperatures were higher in sand pine scrub habitats. However, field active body temperatures were the same among all populations, indicating possible differences in thermoregulatory behaviors. Lizards in longleaf pine populations had greater thermoregulatory effectiveness due to the relatively low costs associated with thermoregulation in this environment. However, contrary to a classic cost-benefit model of ectotherm thermoregulation, all lizards increased thermoregulatory effort when thermal quality of habitat was poor. Furthermore, lizards increased thermoregulatory effort significantly more when unfavorably hot environmental temperatures were experienced, compared to when unfavorably cold temperatures were experienced. My results show that when environmental temperatures are cooler, reptiles can afford

imprecision, however at high temperatures reptiles must increase thermoregulatory effort and precisely regulate body temperature.

INTRODUCTION

Globally, habitats are being altered by humans at an alarming rate. Anthropogenic climate change and resource extraction from natural systems is increasing with the expanding human population size. In addition, the intensification of human land use and management is altering habitats thereby impacting biodiversity, population sizes, genetic and ecosystem diversity (Flather et al., 1998; Foley et al., 2005; Haddad et al., 2015; Newbold et al., 2015). Many landscapes persist via management so as to preserve some natural flora and fauna, but also subject them to the desired outcome(s) of the management practices used (Tylianakis et al., 2007; Fuller et al., 2015). By its very nature, land management alters habitat structure (e.g., vegetation distribution, tree and shrub diversity, canopy cover, and ground cover) to influence biotic and abiotic environmental conditions (Gross et al., 2007). For example land management has been shown to influence predation risk (Lima and Dill, 1990; Whittingham and Evans, 2004), species abundance (Bateman et al., 2015), and the thermal environment (Chen et al., 1999; Zhou et al., 2011). Furthermore, biotic and abiotic factors may interact to influence microhabitat selection and/or thermoregulatory behavior due to alterations in the available thermal environments (Martin, 2001).

In any microhabitat, a suite of environmental factors (e.g., light, wind speed, moisture, and temperature) interact to generate variation in the thermal environment (Chen et al., 1999; Pringle et al., 2003). In ectotherms, thermoregulation is important as many fitness related behaviors are optimized in a narrow, preferred range of body and/or environmental temperatures (Gilchrist, 1995). Due to diel shifts in the angle of solar radiation, many ectotherms move among ephemeral patches to maintain a preferred body temperature. The energy needed for such activities is the inherent cost of thermoregulation (Huey and Slatkin, 1976).

However, variation in thermal environments can also be altered by anthropogenic climate change, land management, and habitat fragmentation (Deutch et al., 2008; Tuff et al., 2016). Ambient temperature directly impacts the quality of the thermal environment, but habitat structure does as well via alteration of solar radiation (sun/shade) and wind. Thus, defining the thermal quality of a habitat depends upon the variation within its constituent microclimates. In habitats of poor thermal quality, where preferred microclimates may be unavailable, the alteration of thermoregulatory behavior may be observed (e.g., shift of activity time) (Diaz, 1997).

Ectotherms often exhibit narrow ranges of thermal preference in variable environments (Gilchrist, 1995). When environmental temperatures are below an organism's preferred temperature range, the cost of thermoconformity rises. These costs include decreased physiological performance (Cowles and Bogert, 1944; Huey and Stevenson, 1979; Bauwens et al., 1995) which may affect an organism's ability to forage (Van Damme et al., 1991), evade predation (Martin and Lopez, 2000), and acquire mates (Zani et al., 2005). However, when environmental temperatures are above an organism's preferred temperature range, costs of thermoconforming might also rise if temperatures approach an organism's critical thermal limits (Kearney et al., 2009; Sinervo et al., 2010). Under this scenario, any benefit of thermoconformity may be lower than expected (Vickers et al., 2011). In light of future climate models, a scenario where environmental temperatures are above an organism's preferred temperature range is also possible. Here, the disadvantages of thermoconforming outweigh the costs of thermoregulating as operative temperatures approach an organism's critical thermal limits (Blouin-Demers and Nadeau, 2005; Vickers et al., 2011)

Hence, habitat thermal quality influences thermoregulatory behavior, i.e., the amount of time and energy required to maintain a field active body temperature (T_b) within the preferred range (Huey and Slatkin, 1976; Hertz, 1993; Diaz, 1997; Diaz and Cabezas-Diaz, 2004). The

influence of habitat thermal quality on the extent of thermoregulation may be quantified via a set of metrics defined by Hertz et al., (1993). The thermal quality of the habitat (d_e) is defined as the deviations of operative temperatures (T_e) from the preferred temperature range (T_{set}). Thermal quality (d_e) is typically regarded as high for values less than 3 and low for values greater than 5 (Hertz, 1993; Diaz, 1997; Vickers et al., 2011). Accuracy in thermoregulation (d_b) is defined as the deviation of field active body temperatures (T_b) from the preferred temperature (T_{set}). The costs of thermoregulation are expected to be lower when thermal quality is highest (i.e., < 3). Thus, thermoregulation is expected to be more accurate (i.e., low d_b) when thermal quality is high. Thermal quality and thermoregulatory accuracy function in concert as a measure of efficiency. Thermoregulatory effectiveness (E) refers to the improvement in accuracy of thermoregulation with respect to habitat thermal quality (determined from operative temperatures) (Hertz, 1993; Diaz, 1997; Table 1.1). By calculating E , the relative intensity of thermoregulation can be inferred. Random use of thermal microclimates (thermoconformity) results in $E = 0$, while perfect regulation of body temperature results in $E = 1$ (Hertz, 1993).

Furthermore, thermoregulatory effort can be quantified by regression of d_b on d_e (Blouin-Demers and Nadeau, 2005; Vickers et al., 2011). A slope of 1 indicates perfect thermoconformity. Thus, accuracy in thermoregulation is predicted to increase as thermal quality of habitat decreases (i.e., d_e increases; $M > 1$; Huey and Slatkin, 1976). Conversely, slopes < 1 indicate accuracy in thermoregulation increases as thermal quality of habitat gets poorer. In turn, the relationship between d_b and d_e can be translated to describe thermal opportunity.

Thermal opportunity describes the availability of preferred temperatures within specific habitats to understand the thermal constraints that influence activity levels, as well as the costs of thermoregulation (Sinervo and Adolph, 1994). Given that habitat quality and structure are

influenced by land management and human alteration (McIntyre and Hobbs, 1999), managed habitats also effect the thermal opportunity for organisms within them.

Here, I examine the relationship between habitat quality and the extent of thermoregulation in a small lizard (*Sceloporus woodi*). This species inhabits managed, xeric uplands of both longleaf pine and sand pine scrub habitats (Campbell and Christman, 1982; Greenberg et al., 1994). Longleaf pine habitats are managed by frequent prescribed burns, while sand pine scrub habitat is managed for *S. woodi* by clearcut logging (Campbell and Christman, 1982; Greenberg et al., 1994; Tiebout and Anderson, 2001). These management practices generate variation in key characteristics of each habitat (e.g., ground cover vegetation and density, and canopy cover; Kaunert and McBrayer, 2015). And thus, are expected to yield different microclimates for *S. woodi*. Therefore, I addressed the following questions: 1) is the thermal quality of habitat (d_e) different between longleaf pine and sand pine scrub populations; 2) do lizards in longleaf pine and sand pine scrub habitats regulate body temperature with the same effectiveness? I predict that longleaf pine and sand pine scrub populations will differ in thermoregulatory opportunity and strategy. When habitat quality is poor, all populations will increase thermoregulatory effort despite any increased costs associated with thermoregulation. However, when thermal quality of habitat is intermediate, the extent of thermoregulation will be determined by the costs associated with regulating body temperature in each habitat. Finally, in habitats with greater thermal opportunity, I predict lizards will thermoregulate with greatest precision.

MATERIALS AND METHODS

Study System

The Florida Scrub Lizard (*Sceloporus woodi*) is a diurnal, ground-dwelling lizard that occupies longleaf pine and sand pine scrub habitat in central Florida. Scrub lizards are found in open, scrub habitats that historically were maintained with frequent wildfires (Anderson and Tiebout, 1993). In the Ocala National Forest (ONF) longleaf pines are managed via prescribed burns, whereas scrub habitats are managed by clear-cut logging (Anderson and Tiebout, 1993; Litt et al., 2001; Tiebout and Anderson, 1997). Longleaf pine and sand pine scrub habitats are ecologically distinct as they differ in their dominant vegetation, canopy cover, and perch availability (Pringle et al., 2003).

Sand pine scrub habitats are characterized by regenerating (0-7 years) sand pine (*Pinus clausa*) and a variety of understory oaks (*Quercus* spp.), crookedwood (*Lyonia ferruginea*), and palmetto (*Serenoa* spp.) shrubs (Greenberg et al., 1994). Longleaf pine habitats are dominated by longleaf pine (*Pinus palustris*), as well as scattered turkey oaks and wiregrass (*Aristida beyrichiana*) in the understory (Campbell and Christman, 1982; Hokit et al., 1999). Scrub lizards prefer open, shady sand substrates interspersed with leaf litter and scattered vegetation. Such microhabitats are commonly found in longleaf pine stands where prescribed fire is used to maintain the understory and groundcover (Campbell and Christman, 1982; Tiebout and Anderson, 2001). Conversely, mature sand pine scrub habitats are clear-cut and roller chopped (Greenberg et al., 1994; Tiebout and Anderson, 2001). In sand pine scrub habitats the management regime does not mimic the landscape-level scale of the historic fire cycle. As such, the resultant habitat becomes a dense network of young successional habitat interspersed with dense, overgrown forest not usable for the Florida scrub lizard (Kaunert and McBrayer, 2015). Scrub lizards disperse relatively short

distances (< 750m) around mature stands of scrub habitat (Tiebout and Anderson, 1997; Hokit et al., 1999). Fire reduction and logging of scrub habitat alters its physical structure (e.g., vegetation distribution, amount and type of ground or canopy cover, tree and scrub diversity), which likely alters the available microhabitats and microclimates (Williams and McBrayer, 2015). The habitat types occupied by *S. woodi* in the ONF are ecologically distinct, and thus present an ideal system to study how thermoregulatory strategies are altered in response to the changes in thermal opportunity.

Field Operative Temperatures

To quantify the thermal environment in longleaf and sand pine scrub habitats, we used cylindrical PVC models to measure available operative temperatures (T_e). The OTMs were made of cylindrical PVC equipped with Thermochron iButtons adhered on the end and inside of the model. The OTMs were sized to match adult male snout vent length (50-55 mm). The OTMs were painted grey to match the solar spectral absorptance of the Florida scrub lizard (Bakken and Gates, 1975; Bakken, 1992). The OTMs were calibrated against live animals prior to data collection to ensure their accuracy (Bakken and Gates, 1975; Dzialowski, 2005). The iButtons recorded temperature at 15 minute intervals. On each day of sampling, 16 OTMs recorded operative temperatures at one longleaf pine population, while 16 additional OTMs recorded temperatures at one sand pine scrub population in the ONF. Four models were placed in full sun, four models were placed in dappled sun, and four models were placed in full shade. The OTMs were also placed at random locations covering the greatest area possible within a site. Lizards were sampled in sites on the same day as OTMs logged temperatures. All models were placed on the ground and in locations 0-1.5 m up the base of a tree because lizards will perch on the bases of both turkey oak

and longleaf pine trees (Williams and McBrayer, 2011). This protocol was repeated at each longleaf pine and sand pine scrub site.

Field work was carried out June-July 2015 and July 2016. Immediately upon capture, field active body temperature (T_b) was measured using a Schultheis rapid reading cloacal thermometer. Only body temperature taken from animals caught within 60 seconds of sighting and 30 seconds of capture were used to ensure that excessive handling or locomotion did not alter body temperature (Hitchcock and McBrayer, 2006). Lizards were captured using a slip noose, and were temporarily stored in cloth bags in a cool environment while in the field, then transferred to the animal care facility at Georgia Southern University to measure preferred temperature ranges.

Preferred Temperature Ranges

A thermal gradient was used to quantify individual thermal preference (T_{set} , Bennett and Johnalder, 1984; Bauwens et al., 1995; Schuler et al., 2011). A six-laned, thermal gradient had temperatures ranging from 20°C to 50°C. Each lane was 15 cm wide by 2 m long and only one lizard was placed in each lane so they could move freely without disturbance. The substrate consisted of a thin (~1.5 cm) layer of sand. Heat tape and heat lamps were used to create a gradient of hot (50°C) to warm (35°C) to cool (20°C). Lizards were placed in the gradient for 1 hour to acclimate prior to the start of the trial. A thermocouple was taped to an individual's venter at the start of a trial to record temperature every minute for two hours.

To statistically determine the relationship between environmental temperature and traits associated with thermoregulatory behavior in longleaf pine and sand pine scrub habitats, a combination of ANOVA and nonparametric alternatives were used. When data met the required assumption of normality, ANOVA was used. When data did not meet the assumptions of

parametric tests, nonparametric Wilcoxon tests were used. The relationship between thermoregulatory strategy and habitat type was quantified using a linear regression. All statistical tests were performed using JMP Pro® v 12.0 (Cary, NC, USA) for all statistical analyses. I reported all means \pm 1 SE. I accepted significance of tests at $\alpha = 0.05$. All protocols were approved by the Georgia Southern University Institutional Animal Care and Use Committee (protocol I15011 and I15012), the State of Florida Fish and Wildlife Conservation Commission (permit #LSSC-15-00027), and the U.S. Forest Service (USFS permit #SEM540).

RESULTS

Thermal variation among sites

In 2016, the mean T_e was 2.9°C higher than the mean T_e in 2015 (2015: LLP $\bar{x} = 31.5 \pm 0.09^\circ\text{C}$; SPS $\bar{x} = 32.8 \pm 0.09^\circ\text{C}$; 2016: LLP $\bar{x} = 34.4 \pm 0.31^\circ\text{C}$; SPS $\bar{x} = 35.6 \pm 0.31^\circ\text{C}$). Combining 2015 and 2016 OTM data, showed that mean T_e in sand pine scrub habitats was 1.2°C higher than the mean T_e in longleaf pine habitats (Fig. 1.1), and the distributions of OTMs differed between longleaf pine and sand pine scrub habitats (Nonparametric Wilcoxon: $\chi^2_{1, 12.545} = 145.97$; $P < 0.0001$). All further results reflect combined 2015 and 2016 data. Field active lizard body temperatures were the same across the two habitat types (ANOVA; $F_{1, 92} = 0.08$; $P = 0.76$).

In longleaf pine sites, OTMs were warmer on the ground compared to temperatures on trees (Nonparametric Wilcoxon; $\chi^2_{1, 6205} = 7.6557$; $P=0.0057$; Fig. 1.2). Temperatures on the ground averaged 2.8°C warmer than the OTM temperatures on trees (ground $\bar{x} = 35.1 \pm 0.3^\circ\text{C}$; tree $\bar{x} = 32.2 \pm 0.4^\circ\text{C}$).

Selected temperatures and thermal quality of habitat

Thermal preference (T_{set}) did not differ between lizards from sand pine scrub and longleaf pine habitats (ANOVA; $F_{1, 66} = 0.002$; $P < 0.96$). The T_{set} range, or the central 80% of all body temperatures selected in the thermal gradient was 35.40 – 38.57°C and the median selected T_b was 37.25°C for all lizards across the two habitat types (Fig. 1.1).

Thermal quality of habitat (d_e) did not differ between longleaf pine and sand pine scrub habitats when tested across 800 to 1300 hours (Nonparametric Wilcoxon: $\chi^2_{1, 63} = 1.78$; $P < 0.18$). However these habitats have very different canopy cover, thus mornings (800 - 1000) were compared to midday (1100-1300) to reduce diel variation. Longleaf pine habitats had increased

thermal quality (evident by lower d_e values) in the middle of the day ($\bar{x} = 3.24$), compared to in the mornings ($\bar{x} = 6.79$) (Nonparametric Wilcoxon: $\chi^2_{1, 42} = 14.31$; $P = 0.0002$). Conversely, in sand pine scrub habitats, there was a higher thermal quality in the mornings ($\bar{x} = 4.85$), compared to in the midday ($\bar{x} = 11.53$) (Nonparametric Wilcoxon: $\chi^2_{1, 23} = 6.31$; $P = 0.01$; Table 1.2; Fig. 1.3).

Field observations confirmed that longleaf pine populations were more likely to be encountered in the midday (1100-1300) compared to in the mornings (800-1000) (Nonparametric Wilcoxon: $\chi^2_{1, 50} = 11.08$; $P = 0.0009$; Fig. 1.4). Conversely, in sand pine scrub habitats lizards were more likely to be encountered in mornings than in midday (Nonparametric Wilcoxon: $\chi^2_{1, 49} = 5.78$; $P = 0.01$).

Lizard body temperatures and extent of thermoregulation

The accuracy of body temperature (d_b) as a function of thermal quality of habitat (d_e) consistently had slopes < 1 , regardless of habitat type. This result is opposite of the predicted slope ($M > 1$). When environmental temperatures were unfavorably low ($T_e < T_{set}$), the slope was 0.34 ($R^2 = 0.30$; $F_{1, 44} = 16.73$; $P = 0.0002$; Fig. 1.5). In contrast when environmental temperatures were unfavorably high ($T_e > T_{set}$), the slope was - 0.48 ($R^2 = 0.37$; $F_{1, 17} = 9.33$; $P = 0.0076$; Fig. 1.5). Regardless of habitat type, thermoregulatory precision increases as thermal quality decreases (i.e., lower d_b as d_e increases). Although when unfavorably high temperatures (i.e., high d_b due to high T_e) were experienced, the degree of thermoregulatory precision was significantly greater relative to thermal quality of habitat (ANCOVA: $F_{1, 63} = 14.10$; $P = 0.0004$).

The accuracy of thermoregulation, i.e. the correspondence of field active T_b to T_{set} (d_b), was the same across all populations independent of habitat type (Nonparametric Wilcoxon: $\chi^2_{1, 68}$

= 0.61; P = 0.76). The index of thermoregulatory effectiveness (E) typically ranges from zero, where animals are thermoconforming, to 1, indicating more careful regulation of body temperature. Individuals in longleaf pine habitats were significantly more effective when thermoregulating (E: $\bar{x} = 0.61 \pm 0.04$) relative to individuals in sand pine scrub habitat (E: $\bar{x} = 0.4 \pm 0.05$; ANOVA: $F_{1, 59} = 4.03$; P=0.04; Table 1.3; Fig. 1.6). There were no diel shifts in thermoregulatory effectiveness in either longleaf pine or sand pine scrub populations (Nonparametric Wilcoxon: $\chi^2_{1, 55} = 0.07$; P = 0.78).

DISCUSSION

Regardless of habitat type, lizards increased thermoregulatory effort when thermal quality of habitat was poor due to unfavorably hot, not cold, temperatures (Fig. 1.5). Several studies have observed similar patterns in reptile thermoregulatory behavior, where thermoregulatory effort increases as thermal quality of habitat is poor (Blouin-Demers and Weatherhead, 2001; Blouin-Demers and Nadeau, 2005; Edwards and Blouin-Demers, 2007; Vickers et al., 2011). My results suggest that when environmental temperatures (T_e) are cooler, reptiles can afford imprecision, however at high temperatures reptiles must increase thermoregulatory effort and precisely regulate body temperature. Thus, in this system, lizards thermoregulate more effectively (i.e., are farther from thermoconformity) when the thermal quality of habitat is low due to warmer, not cooler, temperatures. My data suggests that the disadvantages of thermoconformity are higher than the costs of thermoregulation in habitats of low thermal quality. Tuataras (*Sphenodon punctatus*) increased accuracy of thermoregulation when experimentally subjected to habitats of poorer thermal quality (Besson and Cree, 2010). However, few studies have empirical evidence showing differences in thermoregulatory behavior when thermal quality is poor due to unfavorably hot, versus unfavorably cold, temperatures.

The thermal quality of the habitat (d_e) influences the amount of time and energy required to maintain body temperature within the preferred range (Huey and Slatkin, 1976; Hertz et al., 1993; Diaz, 1997). Lizards were more likely to be encountered when thermal quality was high (low d_e ; Fig. 1.4). Sand pine scrub habitats had greater habitat thermal quality in the mornings (800-1000), while, longleaf pine habitats had greater thermal quality midday (1100-1300) (Table 1.2; Fig. 1.2). Due to fundamental differences in habitat structure, longleaf pine and sand pine scrub habitats are starkly different in their composition and available microclimates (Chen et al.,

1999; Pringle et al., 2003). Longleaf pine stands consist of a moderately dense canopy with the forest floor consisting of sand and wiregrass patches (Myers, 1990). Therefore, much of the light reaching the substrate is filtered by the canopy. Whereas in sand pine scrub habitats, much of the substrate is dominated by open sand and woody debris which typically receive direct sunlight (Laessle, 1958; Greenberg et al., 1994). The variation in activity between longleaf pine and scrub populations is likely due to microclimatic variation and thus thermal quality. In turn, the availability of vertical perches is likely critical in that this microclimate is not as warm between 1100 and 1300. Postural adjustments on arboreal perches have a greater influence on operative temperature than similar adjustments on the ground (Bakken, 1989). Individuals in longleaf pine habitats may easily alternate posture, vertical height, and location (sun/shade) when using vertical perches, and thereby may buffer the temperatures experienced. Movement from sunny to shaded microhabitats on larger perches can change average operative temperature by up to 18°C (Bakken, 1989). Sand pine scrub populations are restricted to terrestrial perches thereby constraining their ability to effectively thermoregulate once temperatures rise (Fig. 1.6). Hence, we conclude that habitat structure (i.e., vertical perch sites) shapes the thermal opportunities available to *S. woodi* in these habitat types.

Thermal opportunity helps define the constraints that may influence daily activity levels, as well as the costs of thermoregulation in a given habitat (Sinervo and Adolph, 1994). The open, patchy microhabitats that lizards utilize in longleaf and sand pine scrub habitats are different thermally. The operative temperatures were 1.2 °C hotter in sand pine scrub habitats (Fig. 1.1). Logging of sand pine scrub in the Ocala National Forest dramatically alters the habitat structure by removing trees which otherwise would be utilized as perches. Likewise, the prescribed burns used in longleaf habitats result in this habitat type more closely resembling something like the

historical fire cycle (Tiebout and Anderson, 2001). The longleaf pine habitats have increased thermal opportunity as lizards have the option to retreat to cooler perches on trees when forest floor microclimate becomes too hot (Fig. 1.3). Whereas sand pine scrub lizards are restricted to terrestrial perches (Williams and McBrayer, 2015) which is likely influencing midday activity levels. Therefore, longleaf pine lizard activity time is less constrained by high midday temperatures due to the increased availability of thermal retreat sites on trees.

The greater thermal opportunity provided by longleaf pine habitats allows lizards there to thermoregulate more effectively (i.e., high E ; $E = 0.61 \pm 0.04$), compared to lizards occupying sand pine scrub habitats ($E = 0.45 \pm 0.05$). In many habitats, terrestrial microhabitats are warmer than arboreal perches during midday (Porter et al., 1973). The availability of vertical perches on longleaf pine trees likely allows lizards there to thermoregulate with greater effectiveness. The cost of behaviorally thermoregulating in longleaf pine habitats is low as there are abundant cooler arboreal perches that lizards can easily shuttle to/from when ground microclimates become unfavorably hot. However, due to the decreased thermal opportunity in sand pine scrub habitats, the costs of thermoregulation are higher as the habitat is more open, less patchy, and poses a greater risk of predation (Orton, unpublished data). In accordance with the cost benefit model of thermoregulation (Huey and Slatkin, 1976), longleaf pine populations are able to thermoregulate more effectively overall because of the lower costs of thermoregulation (Fig. 1.6). This trend has been observed in several other studies considering ectotherm thermoregulation (Withers and Campbell, 1985; Hertz, 1993; Herczeg et al., 2006; Cadena and Tattersall, 2009). The common lizard, *Zootoca vivipara*, was found to switch between thermoconforming and effective thermoregulation as preferred temperatures became readily available in a lab experiment (Herczeg et al., 2006). However, in contrast to the cost benefit model, our data also suggest that when

thermal quality of habitat gets exceptionally poor, the disadvantages of thermoconforming outweigh the costs of thermoregulation and lizards must increase thermoregulatory effort (Fig. 1.5). This trend has also been observed in several recent studies considering ectotherm thermoregulation (Blouin-Demers and Weatherhead, 2001; Blouin-Demers and Nadeau, 2005; Vickers et al., 2011).

The energetic tradeoffs associated with thermoregulation are influenced by many ecological factors (Huey, 1974). Habitat composition, available microclimates, and accessibility of perches are just some of the factors that interact to determine thermal opportunity. Land management practices shapes habitat composition (Bestelmeyer and Wiens, 1996; Rieman et al., 2001; Beschta et al., 2004; Woltz et al., 2012), which influences the available microclimates and thermal opportunity in a habitat. Behavioral aspects of thermoregulation, such as activity time, are determined by the thermal opportunities present in an environment. Such components shape the thermoregulatory strategies used by ectotherms. As climate change and human land management continue to shape habitat structure, future research should determine how such changes affect the thermal landscape and subsequently alter thermoregulatory strategies. Furthermore, when using the index of habitat thermal quality (d_e) to examine the thermal strategies, future studies should recognize that poor thermal quality (high d_e) due to low environmental temperatures (T_e) and poor thermal quality due to high environmental temperatures may not influence thermoregulatory behavior in the same manner.

Table 1.1. Indices of thermoregulation (Hertz et al., 1993).

Index	Definition
T_b	Field active body temperature
T_{set}	Preferred body temperature; measured as the central 80% of body temperatures measured in a thermal gradient
T_e	Operative environmental temperature; the equilibrium body temperature that non-thermoregulating lizards would experience
d_e	Thermal quality of habitat, measured as the mean absolute deviation of T_e from T_{set}
d_b	Accuracy of thermoregulation, measured as the mean absolute deviation of T_b from T_{set}
E	Effectiveness of thermoregulation (E), or the improvement in the accuracy of thermoregulation with respect to non-regulating operative models. Measured as:
	$E = 1 - (d_b/d_e)$

Table 1.2. Thermal quality of habitat (d_e , in °C: n, mean \pm SE) as estimated by operative thermal models in longleaf pine and sand pine scrub habitats.

Hour	Longleaf pine		Sand pine scrub	
	n	d_e	n	d_e
Early (800-1000)	17	7.16 ± 0.72	21	5.00 ± 0.75
Midday (1100-1300)	26	3.24 ± 0.41	3	11.53 ± 0.32
Daily (800-1300)	43	4.65 ± 0.47	24	5.68 ± 0.75

Table 1.3. Average thermal quality of habitat (d_e), accuracy of thermoregulation (d_b), and thermoregulatory effectiveness (E) calculated for lizards sampled in longleaf pine and sand pine scrub habitats. Mean \pm 1 S. E. shown

	Longleaf pine	Sand pine scrub
n	43	24
d_e	4.65 \pm 0.47	5.68 \pm 0.75
d_b	3.05 \pm 0.28	3.57 \pm 0.53
E	0.60 \pm 0.04	0.45 \pm 0.05

Figure 1.1. Frequency distribution of environmental temperatures (T_e) at longleaf pine habitats (top) and sand pine scrub habitats (bottom). Each observation represents the temperature logged by an OTM every 15 minutes from 800-1300. Shaded area represents the central 80% of all body temperatures selected in the thermal gradient (T_{set}). Vertical solid lines represent the lower (CT_{min}) and upper (CT_{max}) critical thermal limits. Vertical dashed lines represent the mean operative temperature in each habitat (LLP $\bar{x} = 31.8 \pm 0.09$; SPS $\bar{x} = 33.03 \pm 0.08$).

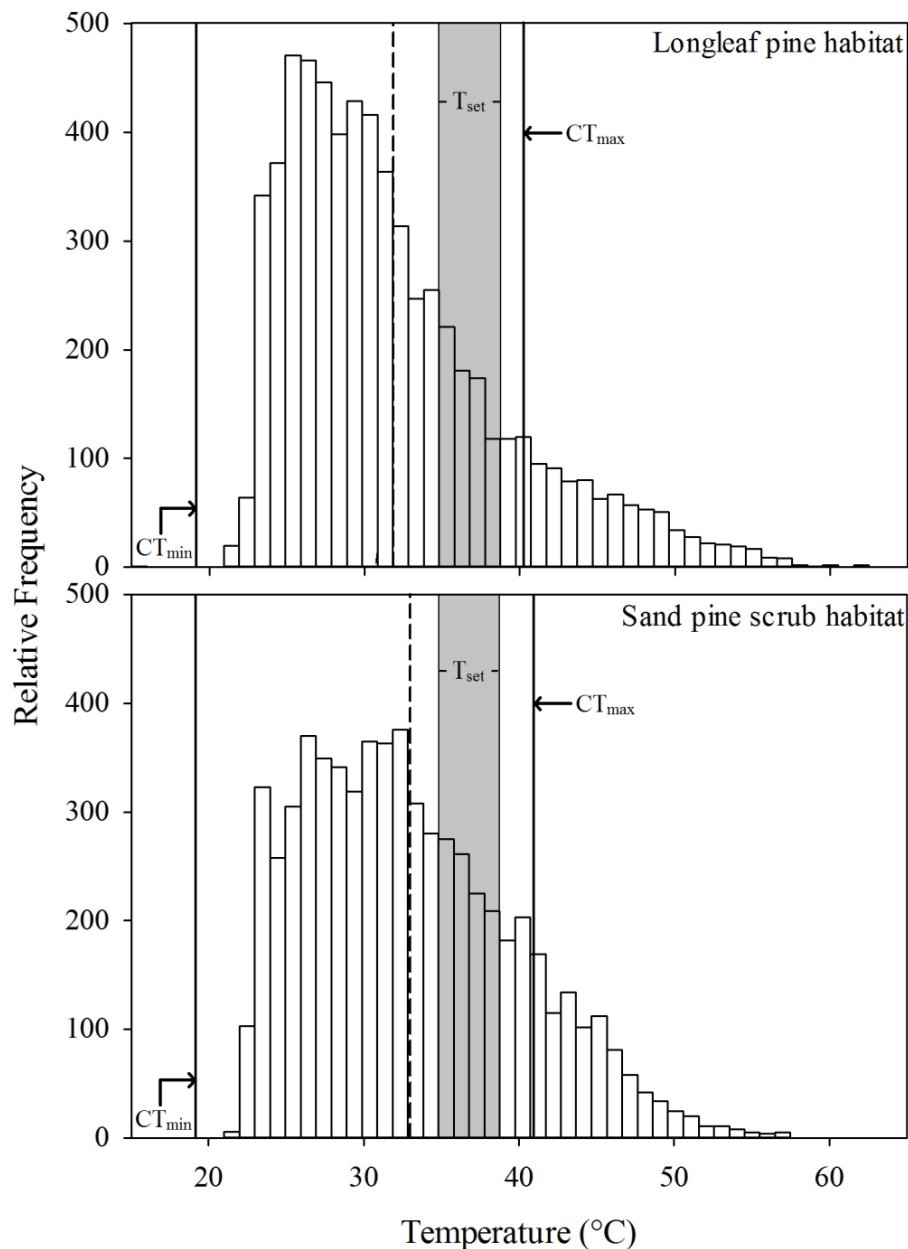


Figure 1.2. Average hourly operative temperature from models on the ground versus models adhered to vertical perching sites in longleaf pine habitats. Mean \pm 1 S. E. shown

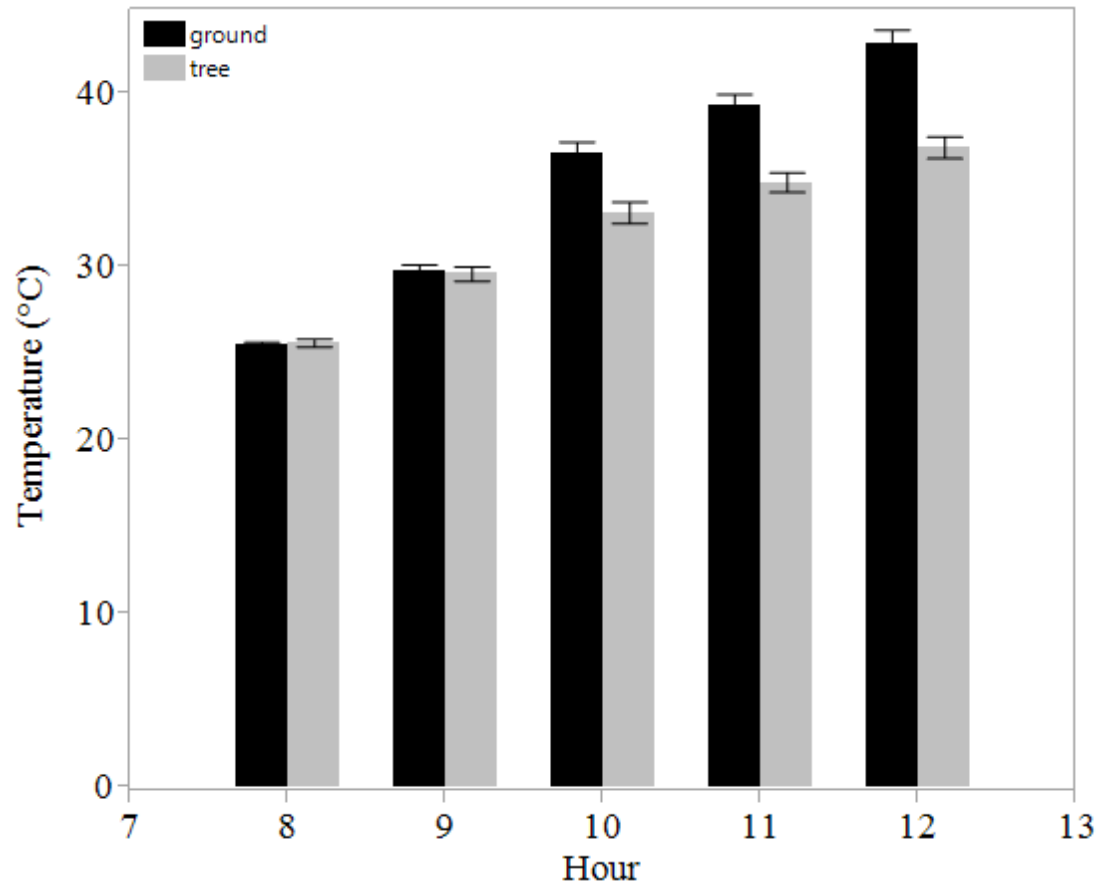


Figure 1.3. The index for habitat thermal quality (d_e) increases in value as environmental temperatures (T_e) are further from the preferred temperature range (T_{set}). Average thermal quality of habitat (d_e) in the mornings (800-1000) and midday (1100-1300) are shown for longleaf pine and sand pine scrub habitats. In longleaf pine habitats thermal quality was the best during midday ($\chi^2_{1,42} = 14.31$; $P = 0.0002$). In sand pine scrub habitats thermal quality was highest in the mornings ($\chi^2_{1,23} = 6.31$; $P = 0.01$). Mean \pm 1 S. E. shown

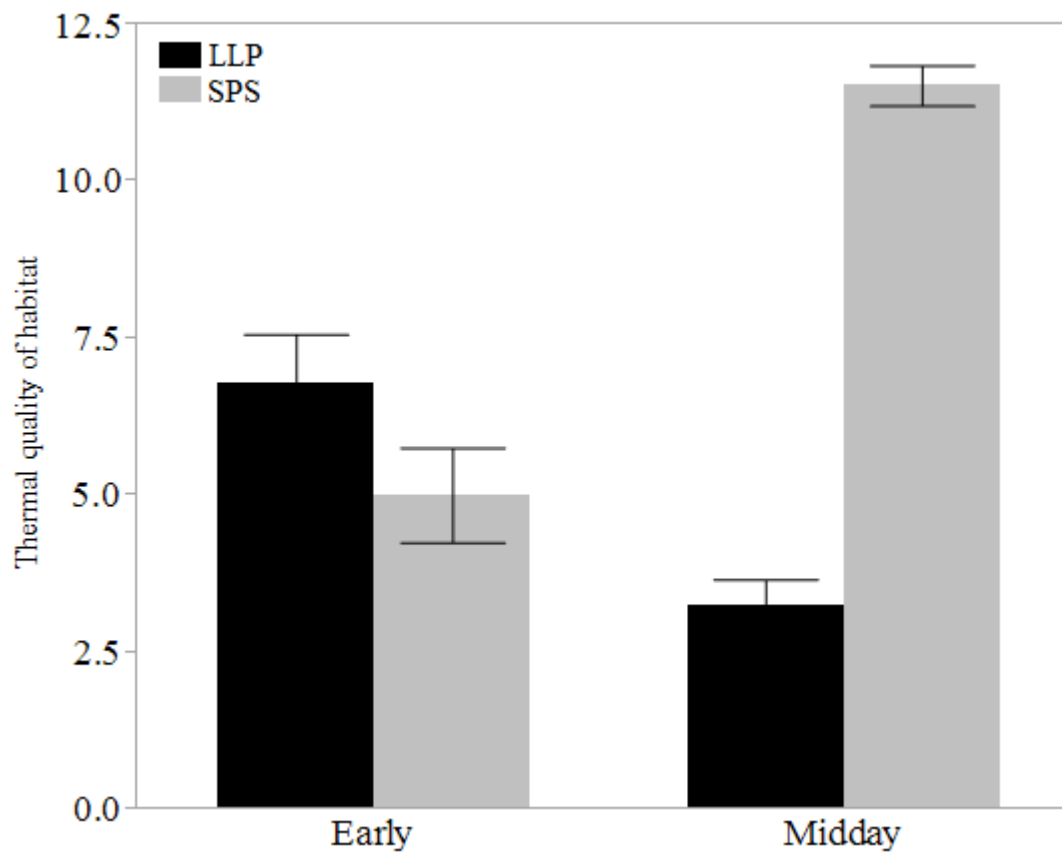


Figure 1.4. Hourly encounter data for lizards in longleaf pine and sand pine scrub habitats. Lizards were more likely to be encountered in their respective habitats when thermal quality was high (i.e., low d_e values). Lizards occupying longleaf pine habitats were more likely to be encountered midday (1100-1300). Lizards occupying sand pine scrub habitats were more likely to be encountered in mornings (800-1000). Mean \pm 1 S. E. shown

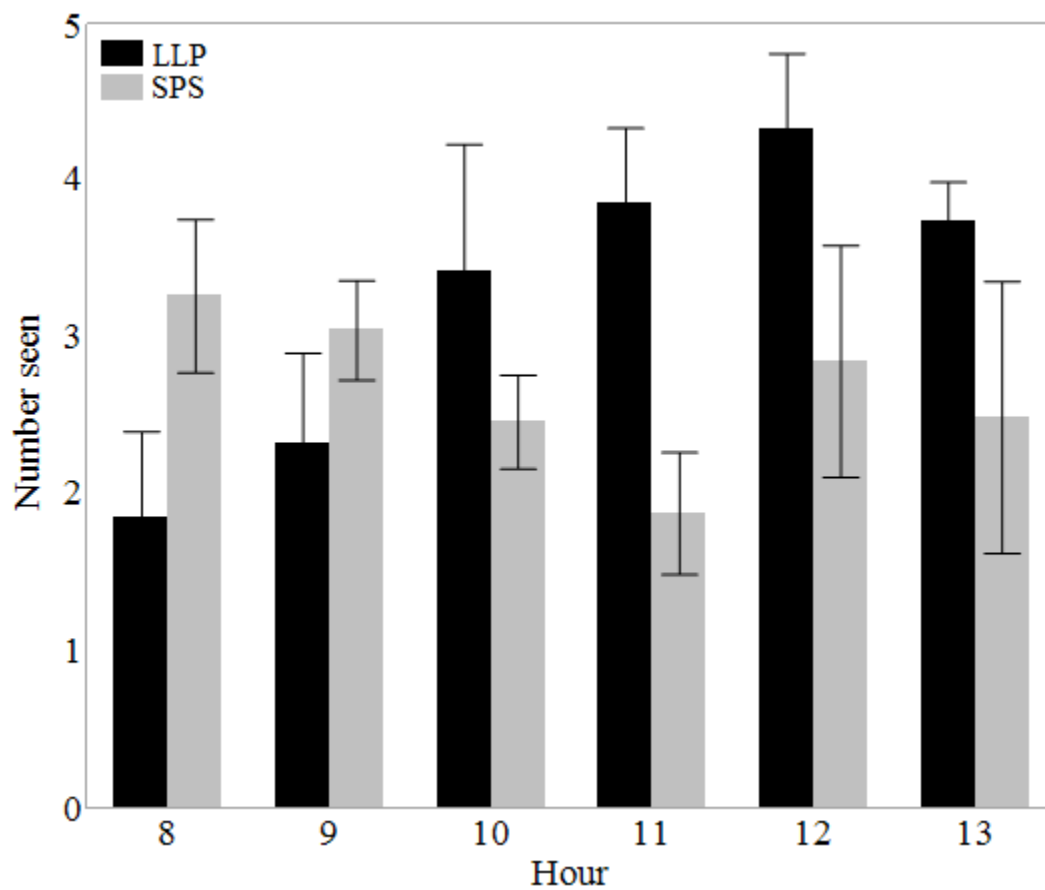


Figure 1.5. The thermoregulatory strategy of *S. woodi* when cool environmental temperatures ($T_e < T_{set}$) were experienced (A), and when warm environmental temperatures ($T_e > T_{set}$) were experienced (B). Dashed lines are linear regressions; solid lines are reference lines representing perfect thermoconformity ($M = 1$). In both cases, the slope < 1 indicating that thermoregulatory effort increases as habitat quality decreased (as d_e increased). Thermoregulatory effort increases significantly when habitat quality is poor due to high temperatures (B; $M = -0.48$) versus when habitat quality is poor due to low temperatures (A; $M = 0.33$).

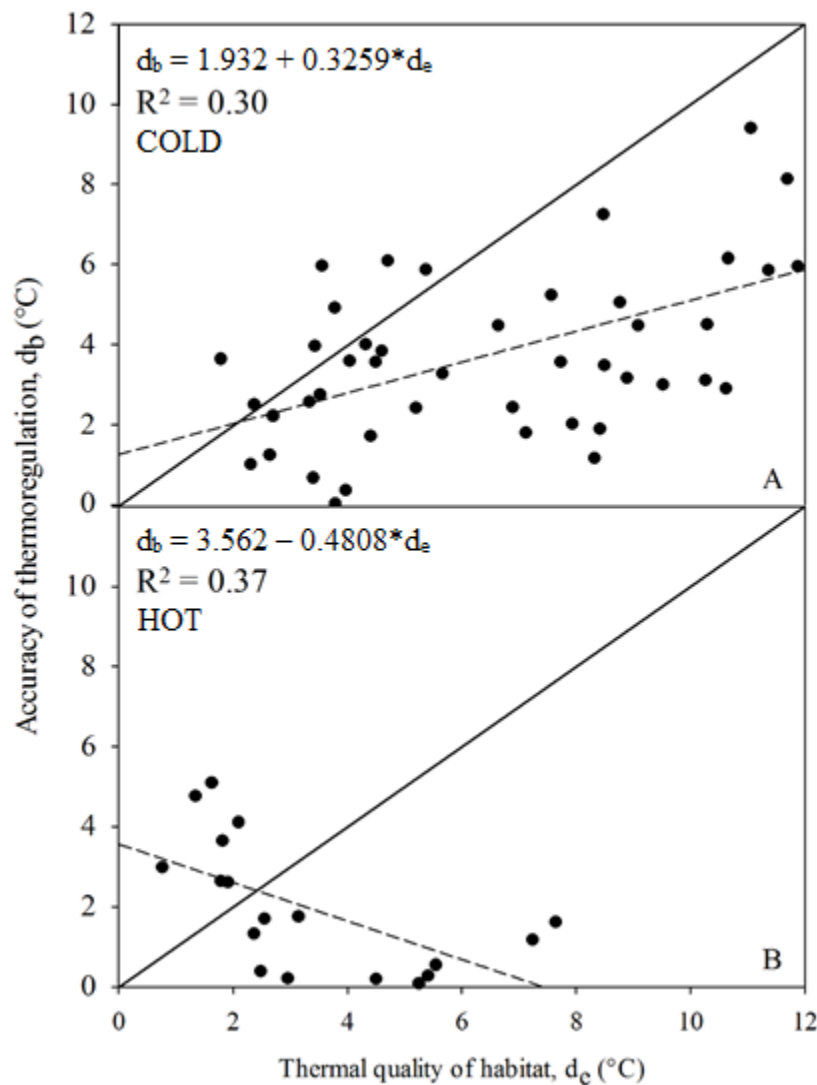
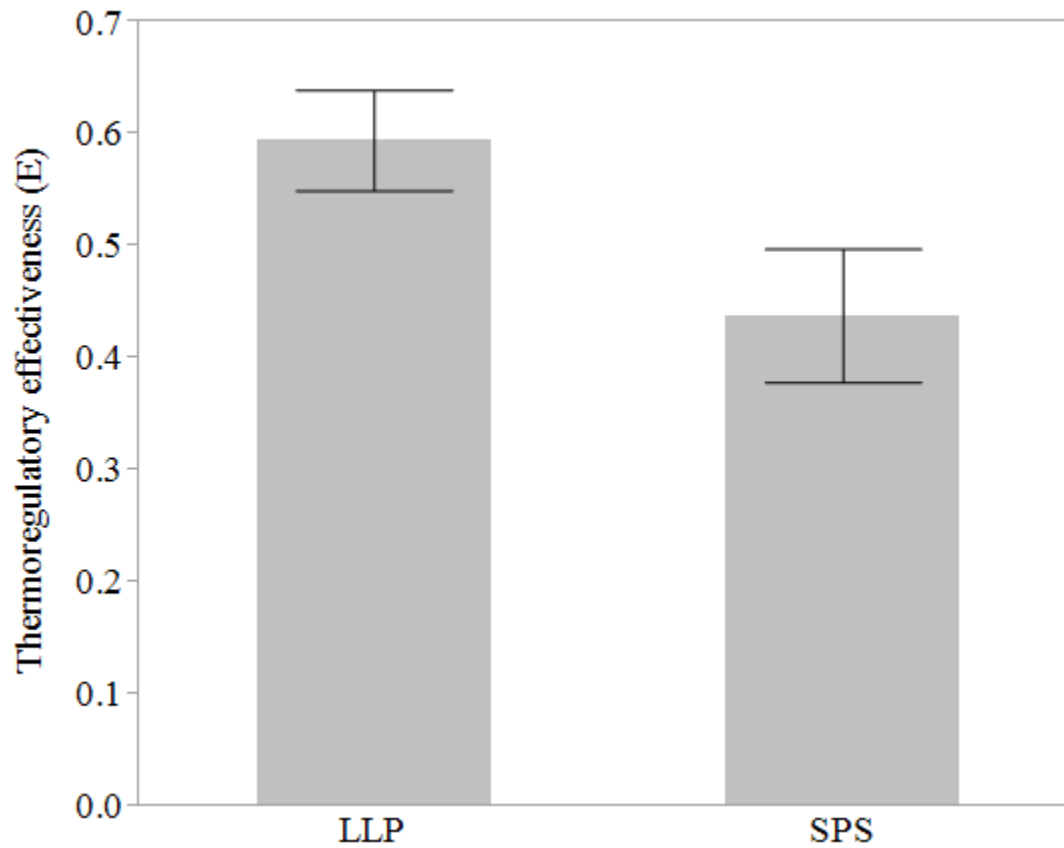


Figure 1.6. The effectiveness of thermoregulation (E) typically ranges from zero to one. Random use of thermal microclimates yield E values near zero. As animals more actively thermoregulate, E approaches one. Lizards occupying LLP habitats more actively regulated their body temperature (E: $\bar{x} = 0.61 \pm 0.04$) than lizards in SPS habitats habitat (E: $\bar{x} = 0.45 \pm 0.05$; ANOVA: $F_{1, 59} = 4.03$; $P = 0.04$). Mean \pm 1 S. E. shown



CHAPTER 2

THERMAL DEPENDENCE OF SPRINT PERFORMANCE AND CRITICAL THERMAL LIMITS IN POPULATIONS OF *SCELOPORUS WOODI* OCCUPYING ECOLOGICALLY DISTINCT HABITATS

ABSTRACT

The availability of preferred microclimates within a habitat influences an ectotherm's physiological capacities and ultimately ecological performance. The Florida scrub lizard (*Sceloporus woodi*) is a ground-dwelling lizard that occupies xeric, sandy upland habitats in peninsular Florida, USA. The species is abundant in longleaf pine and Florida scrub habitats within the Ocala National Forest. These habitat types differ in their dominant vegetation, canopy cover, and availability of vertical perches and thus are ecologically, and thermally different. Thermal opportunity describes the availability of preferred temperatures within specific habitats and thus may reveal how thermal constraints influence activity time or thermoregulatory behavior. We used biophysical models to measure the available environmental temperatures in longleaf pine and sand pine scrub populations. Increased availability of favorable microclimates in longleaf pine habitats indicated higher thermal opportunity. The available temperature distribution in each environment was examined in the context of the thermal sensitivity of locomotor performance. Higher operative temperatures were observed in sand pine scrub habitats and were correlated with both higher critical thermal limits and thermal optima in these populations. The range of preferred temperatures were similar between longleaf pine and sand pine scrub, yet critical thermal limits and thermal optima were locally thereby suggesting that the thermal physiology of this species is evolutionarily labile. Thus, variation in thermal opportunity between longleaf pine and sand pine scrub stands is likely driving the divergence in thermal physiology among these populations.

INTRODUCTION

Human-induced land management has many large-scale ecological consequences, including altering species distributions, population sizes, genetic and ecosystem diversity (Flather et al., 1998; Foley et al., 2005; Haddad et al., 2015; Newbold et al., 2015). Many landscapes persist via management so that natural flora and fauna might be preserved. Yet landscape management subjects all resident species to the desired outcome of the management practices used. This outcome may, or may not, be equally beneficial to all species (Schmidt et al., 2005). Human-induced habitat alteration and management will continue to shape biotic and abiotic environments, thus understanding the behavioral and physiological responses to such changes are critical to predicting how organisms will fare in a rapidly changing world.

By definition, habitat management protocols alter the physical structure of the habitat (e.g., vegetation distribution, amount and type of ground or canopy cover, tree and shrub diversity) to some desired outcome (McDonnell et al., 1997; Dale et al., 2000; Lathrop et al., 2000; Krausman et al., 2009). Ectotherms are thought to be particularly vulnerable to variation in thermal environments as many of their fitness related behaviors are performed during relatively narrow ranges of temperatures (Gilchrist, 1995). Typically, management alters vegetation distribution and diversity. Doing so in turn, may inadvertently result in certain microhabitats being warmer or cooler than others during the day for small ectotherms (Porter et al., 1973). For example, the microclimates available to Neotropical ants are warmer in younger, more open forests as compared to closed forests (Kaspari, 1993). Thus variation in microclimates may drive intraspecific differences in thermal physiology in ectotherm populations occupying distinct environments.

Ectotherms may respond to long-term changes in thermal environments in several ways. Behavioral adjustments, such as altering daily activity times, habitat shifts, and changing basking

frequency can buffer environmental variation (Hertz and Huey, 1981; Christian et al., 1983). However, behavioral shifts alone may not be sufficient to buffer unfavorable temperatures, especially in habitats with low percentages of overhead shade (Kearney et al., 2009). Conversely, the energetic costs of behavioral thermoregulation may deter such behavior (Huey and Slatkin, 1976). Ectotherms may compensate for high cost of thermoregulating by physiologically adapting to novel environmental conditions. Such adaptation (or acclimation) may include shifting the preferred temperature range (Mayhew and Weintraub, 1971; Huey and Webster, 1975; Christian et al., 1983), field active body temperatures (Hertz, 1979), thermal optima (Hertz et al., 1983), and/or critical thermal limits (Hertz, 1979) such that these thermal parameters vary in concert with environmental temperatures. As thermal environments change, the temperatures within an organism's preferred temperature range may not be available in every habitat, or under all management protocols. Hence, many ectotherms may be forced to adapt to local climatic conditions through changes in thermal sensitivity (Angilletta, 2009).

Natural selection acts on ecologically relevant performance capabilities (Arnold, 1983; Bauwens et al., 1995). Sprint performance has been linked to fitness in numerous studies as sprinting capability can influence an organism's ability to avoid predation and forage (Bennett and Huey, 1990; Bauwens et al., 1995; Irschick and Garland, 2001; Miles, 2004; Logan et al., 2014). Thus, maximum sprint speed is an ecologically relevant index of organismal performance capacity. Thermal performance curves (TPCs) of sprint performance can be used to describe how variation in thermal environments influences physiological performance (Huey and Stevenson, 1979; Huey and Kingsolver, 1989; Kingsolver, 2009; Angilletta et al., 2010; Schulte et al., 2011; Logan et al., 2014). Several traits that describe the shape of the TPC include the predicted maximum sprint speed (P_{\max}), the temperature at which performance is predicted to be maximal (T_{opt}), and the range

of body temperatures over which an animal can sprint at least 80% of its predicted maximum or faster (B_{80}). (Huey and Stevenson, 1979; see Fig. 2.1). Numerous studies have demonstrated the capacity for ectotherm thermal physiology to respond rapidly to changes in thermal environments (Partridge et al., 1995; Kingsolver and Diamond, 2011; Logan et al., 2014). As such, TPCs are a valuable tool to use when determining how changes in available microclimates brought on by human-induced land management and climate change may affect organismal performance.

The Florida scrub lizard (*Sceloporus woodi*) occupies xeric, sandy upland habitats in peninsular FL, USA. The species is found in both longleaf pine and sand pine scrub habitats within the Ocala National Forest. In the Ocala National Forest (ONF) longleaf pines are managed via prescribed burns, whereas habitats are managed by clear-cut logging (Anderson and Tiebout, 1993; Tiebout and Anderson, 1997; Litt et al., 2001). In regenerating sand pine scrub habitats, lizards are restricted to the ground as mature trees have been removed. Due to the lack of vertical perching options and the more open structure of the sand pine scrub, activity levels of lizards occupying scrub sites may be altered, especially as operative temperatures approach critical thermal limits. Conversely, populations occupying longleaf pine stands are likely to have cooler, vertical perches on mature trees. Studies have shown that lower perches have higher operative temperatures and lower wind speeds (Stevenson, 1985), thereby suggesting a gradient of cooler microclimates on higher perches, to hotter microclimates on level substrate. In the ONF, lizards perch on the lower 1.5m of longleaf pine trees when ground microclimates become unfavorably hot (Kaunert and McBrayer, 2015). Thus, longleaf pine and sand pine scrub habitats differ in microclimate (Chapter 1), which subsequently likely leads to variation in thermal opportunity and/or thermoregulatory behavior. As such, management practices in longleaf pine and sand pine scrub provide an ideal system to investigate the effects of small-scale microclimatic variation on organismal performance

and thermal biology of small ectotherms like *S. woodi*. The environmental heterogeneity caused by variation in land management practices may result in differing etho-physio-morphotypes in each habitat type.

The purpose of this study is to describe the operative temperatures available to *S. woodi* in longleaf pine and sand pine scrub habitats. Subsequently, I quantify thermal tolerance range and thermal sprinting sensitivity to test if either is optimized for each habitat. I test the following hypotheses. 1) Since management alters microhabitat structure and availability, then management must also alter the thermal environments experienced by small ectotherms. 2) If the thermal environment available to *S. woodi* is different, then populations should exhibit shifts in thermal physiological traits to optimize performance. I predict that the higher environmental operative temperature in sand pine scrub populations will result in increased thermal tolerance (CT_{max}) and thermal optima (T_{opt}) in those populations. If so, then sprint performance should either shift to a higher thermal optima in sand pine scrub populations, or the thermal performance breadth (B_{80}) should be broader in these populations.

METHODS

I sampled male lizards from three longleaf pine populations and two sand pine scrub populations in the Ocala National Forest, FL during May and July 2016. Sand pine scrub populations were characterized by regenerating (0-7 years) sand pine (*Pinus clausa*) and a variety of understory oaks (*Quercus* spp.), crookedwood (*Lyonia ferruginea*), and palmetto (*Serenoa* spp.) shrubs (Greenberg et al., 1994). Longleaf pine populations were dominated by longleaf pine (*Pinus palustris*), as well as scattered turkey oaks and wiregrass (*Aristida beyrichiana*) in the understory (Campbell and Christman, 1982; Hokit et al., 1999). Scrub lizards prefer open, shady sand substrates interspersed with leaf litter and scattered vegetation. Such microhabitats are found in longleaf pine stands where prescribed fire is applied on biannual basis to maintain the understory (Campbell and Christman, 1982; Tiebout and Anderson, 2001). These microhabitat characteristics are not readily found in sand pine scrub habitats (Tiebout and Anderson, 2001). In sand pine scrub habitats, mature stands are logged in place of the historic fire disturbance. This process results in less open sand patches that as a habitat specialist, the species needs to survive (Tiebout and Anderson, 1997). Longleaf pine and sand pine scrub habitats are ecologically distinct as they differ in their dominant vegetation, canopy cover, and perch availability (Pringle et al., 2003).

Habitats were sampled by haphazardly walking through sites. Once spotted, lizards were captured in the field using a slip noose, and were temporarily stored in cloth bags in a cool environment. Immediately upon capture, field active body temperature (T_b) was measured using a Schultheis rapid reading cloacal thermometer. Lizards were then transferred to the animal care facility at Georgia Southern University to measure sprinting thermal sensitivity and thermal tolerance ranges. Experimental trials were performed April, May, and July 2016.

Field Operative Temperatures

To quantify the thermal environment in longleaf and sand pine scrub habitats, we used operative temperature models (OTMs). The OTMs were made of cylindrical PVC equipped with Thermochron iButtons adhered on the end and inside of the model. The OTMs were sized to match adult male snout vent length (50-55 mm). The OTMs were painted grey to match the solar spectral absorptance of the Florida scrub lizard (Bakken and Gates, 1975; Bakken, 1992). The OTMs were calibrated against live animals prior to data collection to ensure their accuracy (Bakken and Gates, 1975; Dzialowski, 2005). The iButtons recorded temperature at 15 minute intervals. On each day of sampling, 16 OTMs recorded operative temperatures at one longleaf pine population, while 16 additional OTMs recorded temperatures at one sand pine scrub population. Four models were placed in full sun, four models were placed in dappled sun, and 4 models were placed in full shade at each site for five hours between 800-1300. The OTMs were also placed at random locations covering the greatest area possible within a site. Lizards were sampled in sites on the same day as OTMs logged temperatures. All models were placed on the ground in sand pine scrub sites. In longleaf pine sites, models were placed on the ground and in locations 0-1.5 m up the base of a tree because lizards will perch on the bases of both turkey oak and longleaf pine trees (Williams and McBrayer, 2011). This protocol was repeated at each of the four longleaf pine, and four sand pine scrub populations.

Sprinting thermal sensitivity

Lizard sprint speed was quantified at five ecologically relevant temperatures (28°, 31°, 34°, 37°, and 39.5°C) that span the critical thermal limits of the Florida scrub lizard. Prior to each sprinting trial, lizards were placed in an incubator for one hour to ensure the desired body temperature was reached. Lizards were removed from the incubator and coerced to sprint down a

2m racetrack. Infrared photocells lined the track and calculated sprint velocity (Bauwens et al., 1995; Angilletta et al., 2002; Miles, 2004). Each lizard was run 3-4 times at each temperature so that a maximum value of sprint performance could reliably be retained for analysis (Anderson et al., 2008). Lizards were sprinted at the same temperature on the same day and the order of temperature trials was randomized. Between the various temperatures trials, lizards were kept in terraria within their preferred temperature range for 24+ hours between sampling days to minimize stress and ensure lizards are ready for the next sprint trial at a different temperature.

The thermal performance curve (TPC) of each individual lizard was estimated by fitting a set of left-skewed parabolic equations to the raw sprint data using the program TableCurve 2D (Systat Software, Inc.) (Angilletta, 2006; Logan et al., 2014). Equations were chosen based on the typical left-skewed shape of ectotherm TPCs, which are thought to be structured by the thermodynamics of enzyme function (Somero, 1978). A line of best fit for the data for each individual was selected using Akaike's Information Criterion (AIC; Akaike, 1987; Logan et al., 2014). When two equations did not significantly differ in their AIC score, the equation with the fewest parameters was chosen. When curves did not differ in AIC score or the number of parameters, the curve with the highest r^2 value was chosen. The TPCs were anchored with the critical thermal limits for an individual. The critical thermal limits were described as the highest/lowest temperature at which a lizard lost its righting response. The loss of a righting response would clearly hinder locomotor performance, and thus this measure makes biological sense to incorporate into the TPCs for sprint performance.

The TPCs were used to estimate three traits associated with thermal performance. First, the predicted maximum sprint speed (P_{\max}) is estimated from each curve. Second, the thermal optima (T_{opt}), or the temperature at which performance is predicted to be maximal is estimated for

each individual from their TPC. Finally, the range of body temperatures over which the lizard can run at least 80% of its P_{\max} or faster (B_{80}), is estimated for each individual via the TPC. These three traits are all used to describe and compare the shapes of the thermal performance curve (Huey and Stevenson, 1979; see Fig. 2.1).

Measuring thermal tolerance

Critical thermal maxima (CT_{\max}) and critical thermal minima (CT_{\min}) are indices of the highest and lowest temperatures at which an animal loses basic locomotor function (Lutterschmidt and Hutchison, 1997) and define tolerance limits in ectotherms (Huey and Bennett, 1987; Huey, 1987; Angilletta, 2002). To measure CT_{\max} , lizards were placed in a deep container under heat lamps so the temperature increased at a constant rate ($\sim 1^{\circ}\text{C}/\text{min}$). Animals were placed in the container with a small thermocouple taped to the venter to continuously measure ventral body temperature. Every minute, a lizard's "righting response" was checked by gently flipping the lizard onto its back, and observing whether the lizard could regain an upright position. If the lizard flipped over within 15 seconds, the trial continued. The temperature at which an animal lost its righting response was recorded as CT_{\max} . For CT_{\min} trials, lizards were cooled on an icepack and righting response was checked each minute. The temperature an animal lost its righting response was recorded as the CT_{\min} .

To statistically determine the relationship between environmental temperature and traits associated with physiological performance in longleaf pine and sand pine scrub habitats, a combination of ANOVA and nonparametric alternatives were used. When data met assumption of normality, ANOVA tests were used. When data did not meet assumptions of parametric tests, Nonparametric Wilcoxon tests were used. All statistical tests were performed using JMP Pro[©] v 12.0 (Cary, NC, USA) for all statistical analyses. I reported all means ± 1 SE. All protocols were

approved by the Georgia Southern University Institutional Animal Care and Use Committee (protocol I15011 and I5012), the State of Florida Fish and Wildlife Conservation Commission (permit #LSSC-15-00027), and the U.S. Forest Service (USFS permit #SEM540).

RESULTS

Thermal variation among habitats

The distribution of operative temperatures differed between longleaf pine and sand pine scrub habitats (Nonparametric Wilcoxon: $\chi^2_{1, 1250} = 13.06$; $P = 0.0003$). Mean operative temperature in sand pine scrub was 1.2 °C higher than the mean operative temperature in longleaf pine (SPS $\bar{x} = 35.60 \pm 0.31^\circ\text{C}$; LLP $\bar{x} = 34.44 \pm 0.31^\circ\text{C}$; Fig. 2.2). Lizard body temperatures were the same across the two habitat types (SPS $\bar{x} = 33.51 \pm 0.37^\circ\text{C}$; LLP $\bar{x} = 33.71 \pm 0.24^\circ\text{C}$; ANOVA; $F_{1, 92} = 0.08$; $P = 0.76$).

Operative temperatures were higher on the ground compared to temperatures on trees (Nonparametric Wilcoxon; $\chi^2_{1, 6205} = 7.6557$; $P = 0.005$). Temperatures on the ground averaged 2.8°C warmer than those on trees (ground $\bar{x} = 35.1 \pm 0.3^\circ\text{C}$; tree $\bar{x} = 32.2 \pm 0.4^\circ\text{C}$; Fig. 2.3).

Thermal performance curves

The performance breadth of lizards did not differ between longleaf pine and sand pine scrub populations (ANOVA: $F_{1, 55} = 0.108$; $P = 0.74$). The performance breadth in longleaf pine populations spanned 35.17 - 40.07°C. The performance breadth in sand pine scrub populations spanned 34.25 - 39.37°C (Table 2.1). The upper limit of the performance breadth was significantly higher in sand pine scrub than longleaf pine populations (Nonparametric Wilcoxon: $\chi^2_{1, 55} = 9.06$; $P = 0.002$). The lower limit of the performance breadth was not different between habitat types (ANOVA: $F_{1, 55} = 1.80$; $P = 0.18$).

The thermal optimum for sprinting (T_{opt}) was higher in sand pine scrub populations ($\bar{x} = 39.2 \pm 0.28^\circ\text{C}$), than in longleaf pine populations ($\bar{x} = 38.3 \pm 0.21^\circ\text{C}$) (Nonparametric Wilcoxon: $\chi^2_{1,55} = 6.72$; $P = 0.009$; Fig. 2.4). The upper critical thermal limit (CT_{max}) was also significantly higher in sand pine scrub populations ($\bar{x} = 41.17 \pm 0.23^\circ\text{C}$; Fig. 2.4) than in longleaf pine populations ($\bar{x} = 40.37 \pm 0.18^\circ\text{C}$; Nonparametric Wilcoxon: $\chi^2_{1,54} = 10.42$; $P = 0.002$). The lower critical thermal limit (CT_{min}) did not differ between habitat types, although the CT_{min} in sand pine scrub populations was 0.8°C higher than in longleaf populations (ANOVA: $F_{1,53} = 2.80$; $P = 0.10$; Fig. 2.4). The predicted maximum sprint speed (P_{max}) did not differ between habitat types (Nonparametric Wilcoxon: $\chi^2_{1,55} = 0.85$; $P = 0.35$).

The critical thermal maximum (CT_{max}) appears to have evolved in concert with the thermal optima (T_{opt}). Thermal optima were correlated with CT_{max} in sand pine scrub populations ($F_{1,20} = 4.38$; $P = 0.049$; Fig. 2.5). Thus, in sand pine scrub populations, lizards with higher thermal optima sprinted over a wider range of temperatures than lizards with lower thermal optima. No trend was present for CT_{min} or CT_{max} in longleaf pine populations.

DISCUSSION

Thermal environments are rapidly changing due to anthropogenic effects such as habitat fragmentation, management, and global climate change (Deutch et al., 2008; Tuff et al., 2016). Land management is known to influence the overall structure and composition of habitats (Rieman et al., 2001; Beschta et al., 2004; Shochat et al., 2004; Woltz et al., 2012), and variation in land-use intensity also alters habitat structure (Bestelmeyer and Wiens, 1996). Furthermore, population density may vary based on management. Natural forests and forests managed by retaining canopy trees, are known to have significantly higher bird abundances than habitats managed with clear-cut logging (Hansen et al., 1995). Thus, management may substantially alter habitat structure and species abundances, yet few studies empirically linked land management to the alteration of the thermal environment in natural systems. This present study demonstrates that differing land management protocols influence the microclimate experienced by small ectotherms, and as such may have consequences for the residence species.

Environmental operative temperatures were higher in sand pine scrub habitats, where forests are managed with clear-cut logging in place of prescribed burning (Fig. 2.2). Populations occupying sand pine scrub habitats resultantly exhibited higher thermal tolerance and thermal optima than populations occupying the cooler, longleaf pine habitats (Table 2.1; Fig. 2.4; Fig. 2.6). Further evolutionary correlations were detected in sand pine scrub populations as critical thermal maxima were co-adapted with optimal temperatures, but not with critical thermal minima (Fig. 2.5). Similar results have been shown in *Drosophila*, where critical thermal maxima, but not minima, were correlated with optimal temperatures (Huey and Kingsolver, 1993). Thus, some but not all aspects of thermal sensitivity may be co-adapted. Interestingly, I did not find such trend in longleaf pine populations. This may be attributed to the increased

range of temperatures available to lizards in longleaf pine habitats. Numerous studies suggest that ectotherms can adapt to thermal variation along latitudinal/altitudinal clines (Van Berkum, 1986; Wilson, 2001), or when introduced to novel, warmer environments (Logan et al., 2014). My data suggest that ectotherms can also adapt to thermal variation caused by habitat land management, and do so on a relatively small geographic scale.

For ectotherms, being able to exhibit adaptive (or acclimatization) responses to thermal variation is critical to maintaining maximal performance in rapidly changing environments. In the ONF, longleaf pine populations have increased thermal opportunity, as they have greater access to thermally preferred microclimates (Chapter 1). In longleaf pine, lizards can rely on behavioral thermoregulation to buffer unfavorably high environmental temperatures. In many environments, terrestrial microhabitats are warmer than arboreal perches during midday (Porter et al., 1973). In sand pine scrub habitats, the clear-cutting management practices eliminate the cooler, arboreal perching options on trees. This constrains activity levels midday (Chapter 1). Yet, access to open sand allows lizards in sand pine scrub to warm up early in the day. Conversely, the management protocol for longleaf in the ONF allow greater access to cooler microclimates on trees midday (Williams and McBrayer, 2015), less constrained activity times (Chapter 1), and lower predation rates (Orton, unpublished data). The behavior and physiology of populations occupying sand pine scrub habitats appear to be constrained in activity time, perch use, diet (Williams and McBrayer, 2015), and thermal physiology. While populations are still common in managed sand pine scrub in the ONF, the management of the sand pine scrub generates a thermal environment with greater costs for thermoregulation. Given this, it is likely that management might be linked to the lower population densities observed in sand pine scrub (Kaunert and McBrayer, 2015)

My results show that subtle differences in management practices can yield large effects on ectotherm behavior and physiology, specifically thermal tolerance range and thermal optima. Understanding adaptive responses to novel thermal variation is key to predicting how ectotherms may fare under various climate change models. While some studies suggest that certain ectotherms may actually benefit from projected climate warming events (Logan et al., 2013), studies also suggest that ectotherms may lack the ability to adapt to increasing environmental temperatures, this is especially true for ectotherms occupying tropical and sub-tropical latitudes (Deutch et al., 2008; Tewksbury et al., 2008; Huey et al., 2009; Sinervo et al., 2010). When facing novel thermal variation organisms have two options: seek out thermally favorable environments or adapt to novel conditions (Van Berkum, 1986; Bennett and Huey, 1990; Angilletta et al., 2002; Berg et al., 2009; Somero, 2010). Here, I show that land management may introduce additional variation in microclimates and thereby effect how they escape from predators and/or spend their daily activity cycle. Much still remains unknown regarding ectotherm adaptive capabilities. Thus, the prospects of ectotherms in light of future warming scenarios remains a complex topic. However in addition to climate change, land management has now been found to introduce additional variation to the microclimates available to small ectotherms. Therefore, land management could exacerbate ectotherm population declines.

Table 2.1. Thermal performance and critical thermal limits in *Sceloporus woodi*. Mean \pm 1 S. E. shown (sample sizes: LLP = 34; SPS = 22).

Trait	Longleaf pine		Sand pine scrub	
	Value	SE	Value	SE
T _{opt} - Temperature at which performance is predicted to be maximal	38.3	0.21	39.2	0.27
P _{max} - The predicted maximum sprint speed	1.2	0.05	1.3	0.07
B ₈₀ - Range of temperatures at which an individual is predicted to achieve at least 80% of P _{max}	34.3 - 39.4	0.09	35.2 - 40.1	0.12
CT _{min} - Lower critical thermal limit	18.9	0.32	19.9	0.38
CT _{max} - Upper critical thermal limit	40.4	0.18	41.1	0.24

Figure 2.1. Hypothetical thermal performance curve with the characteristic thermal performance traits labeled. The thermal optimum is the temperature (T_{opt}) at which sprint speed is predicted to be maximal (P_{max}). The thermal performance breadth (B_{80}) is the range of body temperatures over which performance is 80% of P_{max} or faster. Critical thermal limits (CT_{min} and CT_{max}) are also labeled below. (Redrawn from Huey and Stevenson, 1979).

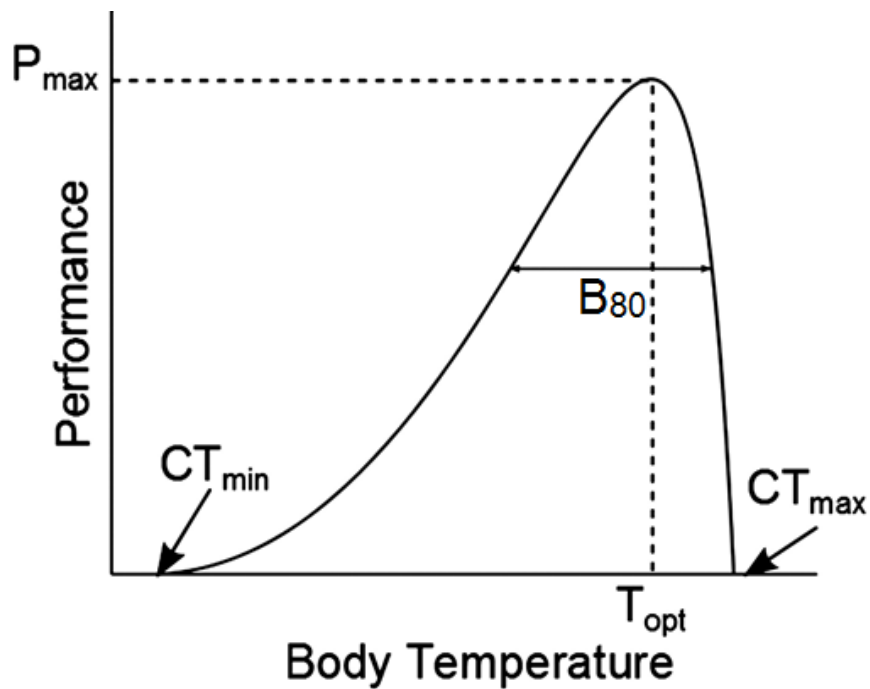


Figure 2.2. Frequency distribution of environmental temperatures at longleaf pine (top) and sand pine scrub habitats (bottom). Vertical solid lines represent the lower (CT_{min}) and upper (CT_{max}) critical thermal limits. The thermal optimum for sprinting (T_{opt}) is labeled with a dashed line (LLP $\bar{x} = 38.3 \pm 0.21$; SPS $\bar{x} = 39.2 \pm 0.27$).

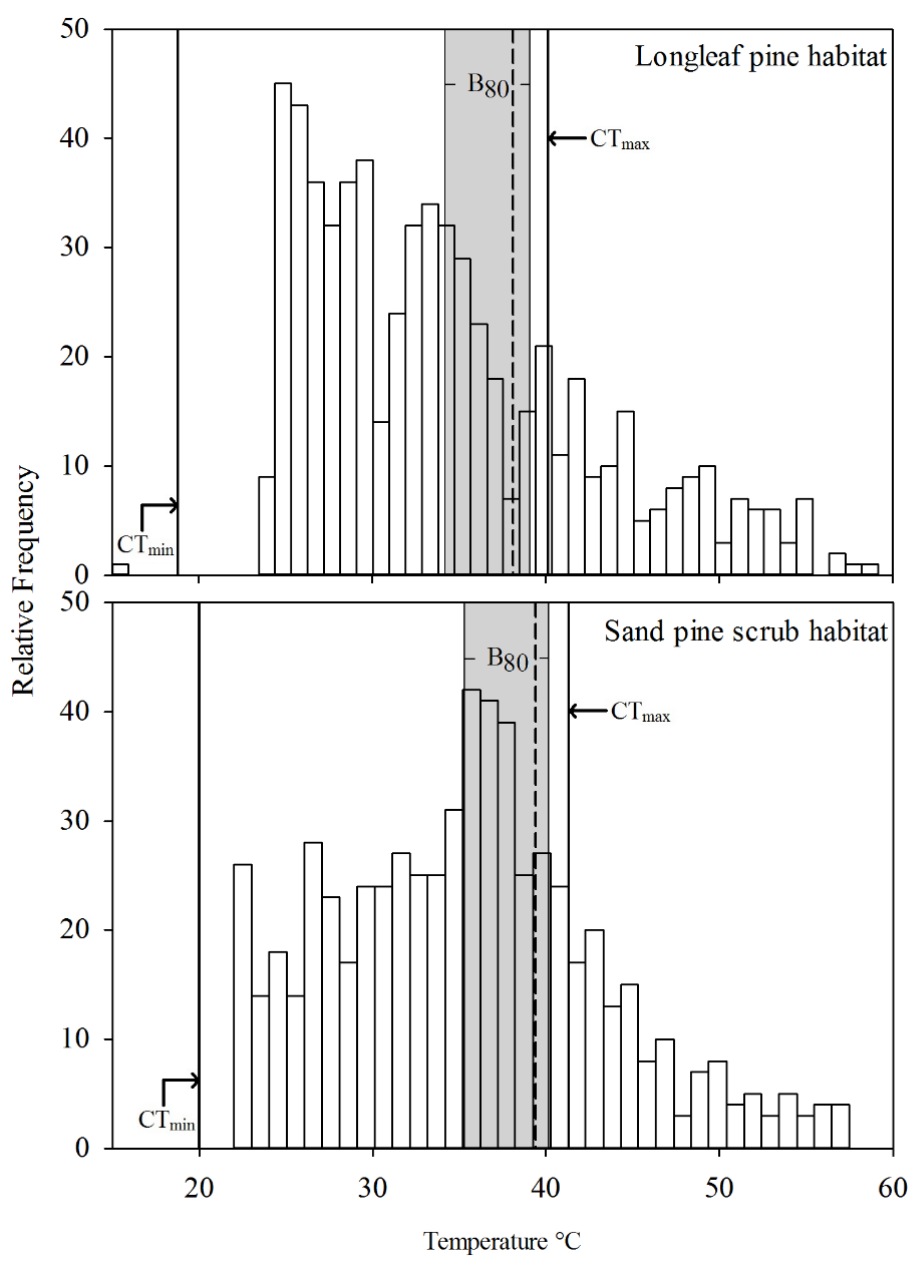


Figure 2.3. Average hourly temperature recorded by thermal models on the ground versus adhered to vertical perching sites in longleaf pine habitats. Mean \pm 1 S. E. shown

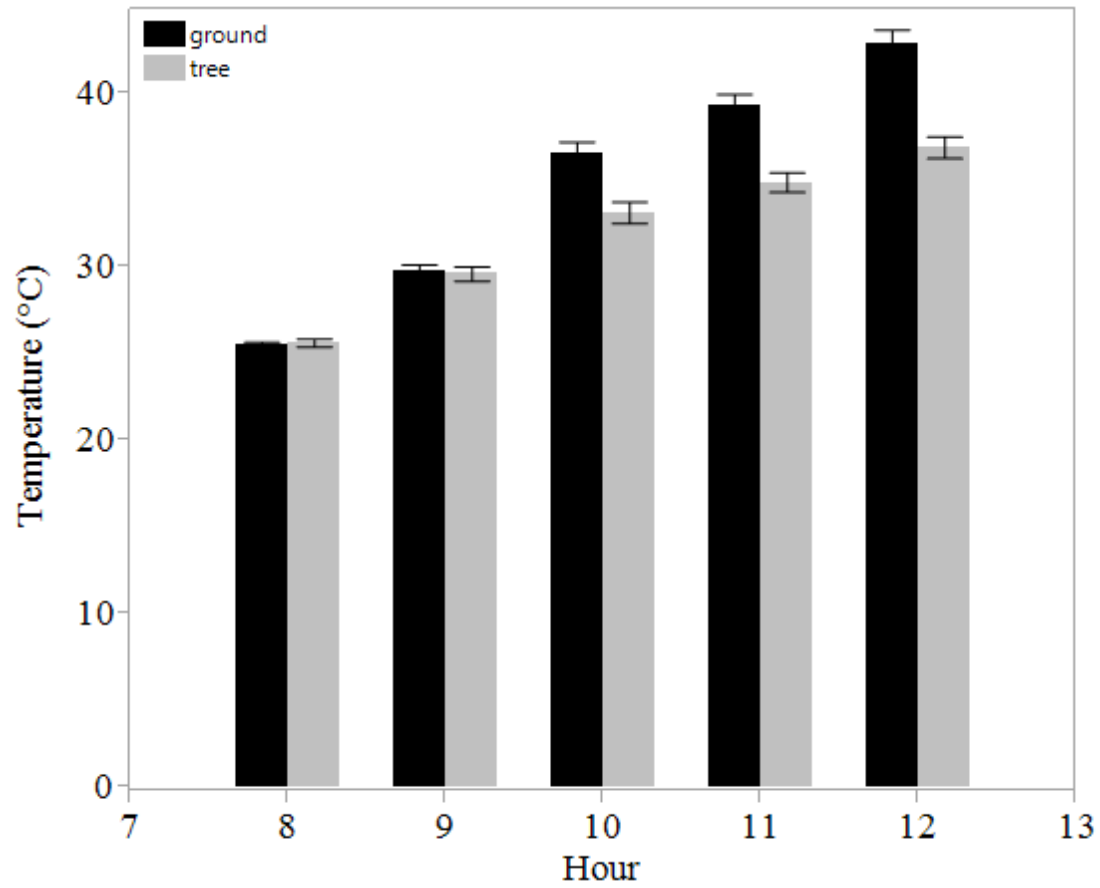


Figure 2.4. Critical thermal minima (CT_{min}), maxima (CT_{max}), and thermal optima (T_{opt}) in longleaf pine (LLP) and sand pine scrub populations (SPS). Mean \pm 1 S. E. shown

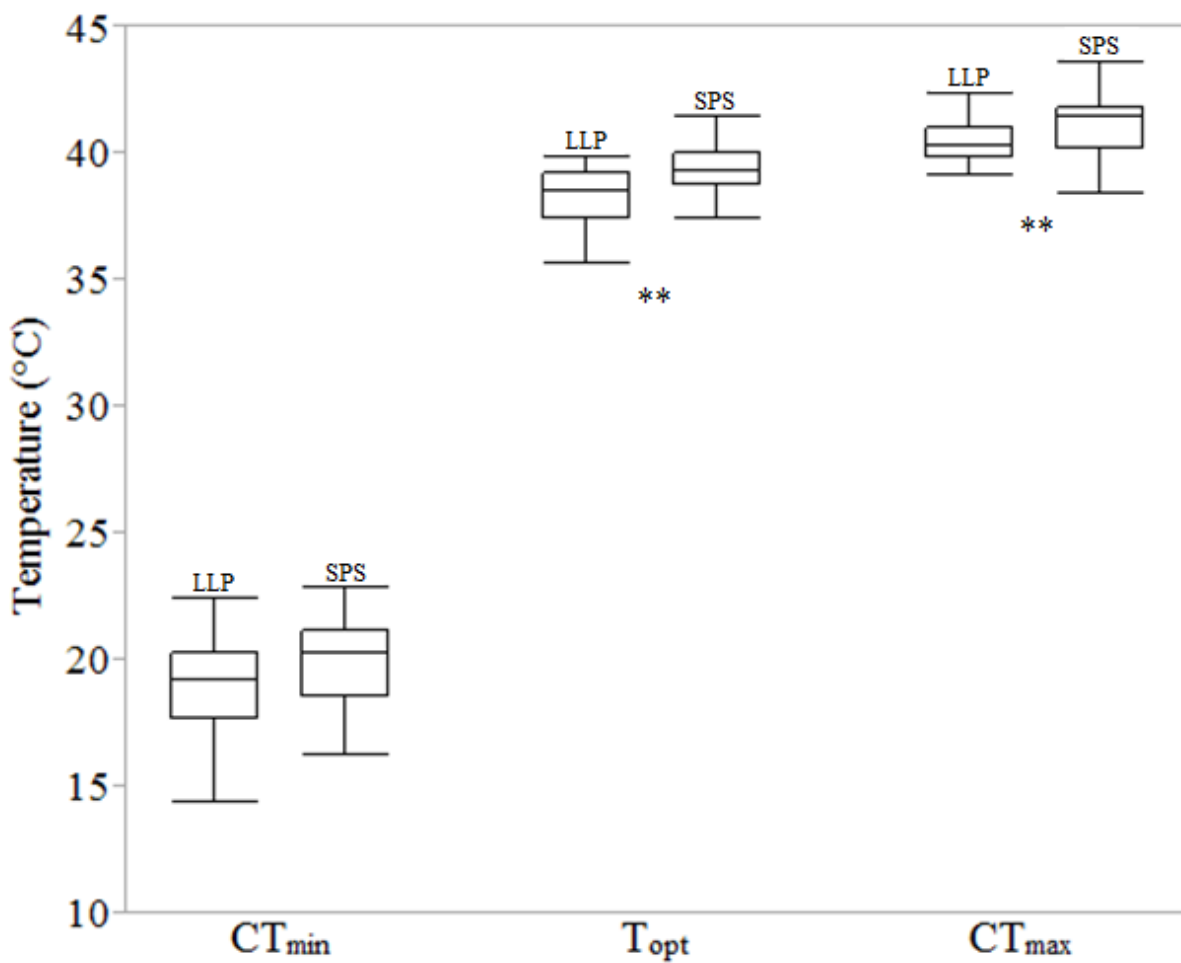


Figure 2.5. The critical thermal maximum is positively correlated with the thermal optimum for sprinting in sand pine scrub habitats ($F_{1, 20} = 4.38$; $P = 0.049$). Critical thermal maxima are co-adapted with optimal temperatures but not with critical thermal minima. Thus, some but not all aspects of thermal sensitivity are co-adapted in sand pine scrub populations. No such trend was present in longleaf pine habitats.

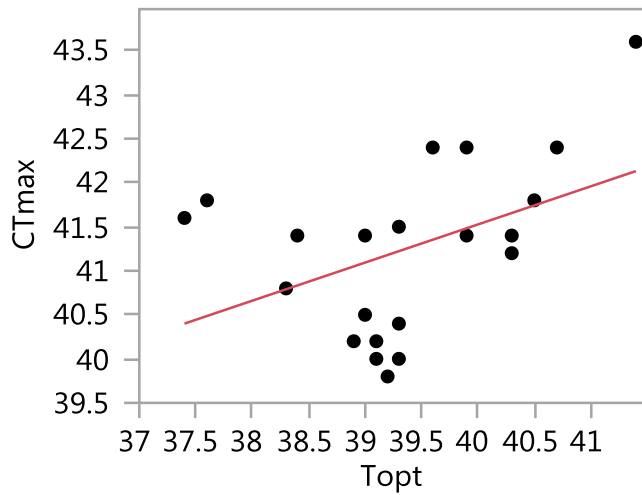
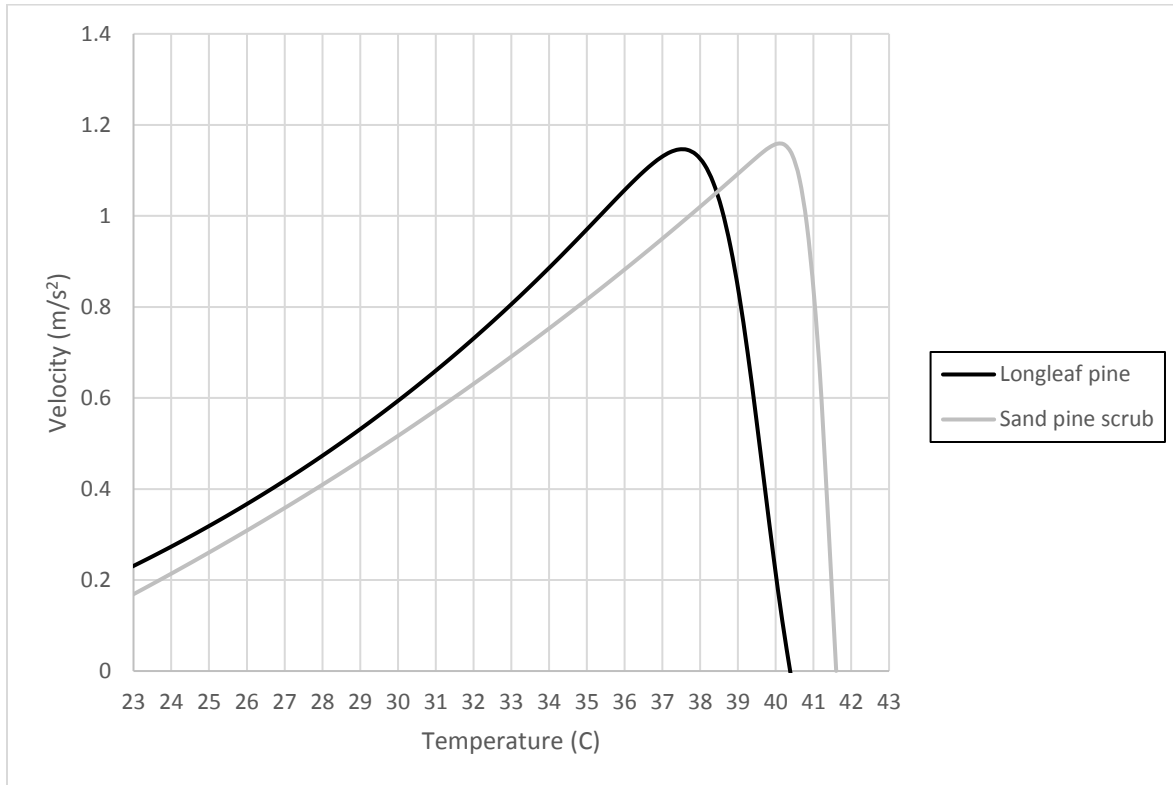


Figure 2.6. Representative thermal performance curve for a typical longleaf pine lizard (black) and a sand pine scrub lizard (grey).



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