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Sources And Consequences of Ecological Intraspecific Variation In The Florida Scrub Lizard (*Sceloporus Woodi*)

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Sources and Consequences of Ecological Intraspecific Variation in the Florida
Scrub Lizard (*Sceloporus woodi*)

by

Steven C. Williams

(Under the Direction of Lance D. McBrayer)

ABSTRACT

Sceloporus woodi is a small, sexually dimorphic Iguanid lizard endemic to dry xeric habitats in Florida. This species is most often found in sand-pine scrub habitats, but also inhabits relic long-leaf pine “islands” within the scrub of the Ocala National Forest in north central Florida. In the current study I investigated seasonal and sexual variation in foraging behavior of *S. woodi* and compared microhabitat use, behavior, diet, morphology, and ectoparasite load at a pine island site to *S. woodi* in scrub habitats. No variation in movement patterns existed between seasons and sexes. However significant seasonal and sexual differences did exist in the way *S. woodi* attacked prey. Using the proportion of attacks on prey made while stationary and lag sequential analysis, I found that females are more willing to move greater than one body length to attack prey items than males and both sexes are more apt to move to attack prey during the post-breeding season. These behavioral differences translated into a more diverse and higher volume diet in females during the breeding season. Even though both sexes showed the same seasonal patterns in foraging behavior, their diets changed in the opposite manner. Female diets decreased in volume and the number of prey types in the post-breeding season while male diets increased in both characteristics. Lizards at the pine island site used trees most often while lizards in the scrub used terrestrial habitats most often. Behavior was similar between habitats, but individuals did move their heads more often at the pine island site. At the pine island site lizards had significantly lower body temperatures, consumed less diverse prey, and had lower ectoparasite loads. Lizards in the long leaf pine had longer limbs than their counterparts in scrub habitats. However, only females differed in body shape between habitat types. This study has identified sources and consequences of variation in the foraging behavior of *S. woodi*. Additionally this study has shown that *S. woodi* in pine island habitats may differ ecologically from *S. woodi* in scrub habitats.

INDEX WORDS: *Sceloporus woodi*, Intraspecific variation, Behavior, Foraging, Movement patterns, Proportion attacks while stationary, Lag sequential analysis, Stomach flushing, Microhabitat, Habitat, Sand-pine scrub, Long-leaf pine island forest

Sources and Consequences of Intraspecific Variation in the Florida Scrub Lizard

(Sceloporus woodi)

by

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B.S. Stephen F. Austin State University, 2005

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DEDICATION

I would like to dedicate this thesis to my wife, Marisa, and my family who have stood by and supported me through all of the adventures I have had while completing this project.

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Chapter 1

The devil is in the details: seasonal and sexual variation in the foraging behavior of the Florida scrub lizard (*Sceloporus woodi*) not detected by quantification of movement patterns

Abstract

The foraging mode paradigm is a powerful theoretical construct which explains how many aspects of lizard ecology have evolved in concert with foraging behavior. However the foraging mode paradigm is not without its criticisms. The foraging mode paradigm has traditionally regarded foraging behavior as static within species and described foraging behavior based upon quantification of movement patterns (% time moving & rate of movements). Both of these methods have been recognized as inherent and understudied weaknesses of the paradigm. While movement patterns are often related to foraging, individuals also move for other reasons (*e.g.* mate acquisition). Such intraspecific variation in foraging behavior may not be detected via quantification of movement patterns alone. Employing detailed analyses of the behaviors lizards actually use to attack prey, such as percent of attacks on prey made while stationary (AWS) and lag sequential analysis, will reveal variation in foraging behavior missed by quantification of movement patterns. Moreover, variation in the actual foraging movements likely has subsequent ecological consequences (*e.g.* variation in diet). In this study, I examined the foraging behavior and diet of the Florida scrub lizard (*Sceloporus woodi*) between reproductive seasons and sexes. The objectives of the study were to quantify 1) the existence of intraspecific variation in foraging behavior, 2) the efficacy of metrics of movement patterns in detecting such variation, and 3) the dietary consequences any variation in foraging behavior. I found no differences in movement patterns between seasons or sexes, but males captured more prey while stationary and took smaller, less diverse prey than females during the breeding season. Lag sequential analysis revealed that both sexes fed in extended bouts during the breeding season but not during the post-breeding season. During the post-breeding season, diet showed no variation between the sexes. Comparing the new measure of attacks while stationary (AWS) with the results from the lag sequential analysis provided valuable insights on the foraging behavior of *S. woodi* and a more complete description of this species' foraging behavior than was discerned by quantifying its movement patterns alone. These results provide a cautionary note for future researchers; focusing solely on movement patterns and ignoring seasonal and sexual variation in foraging behaviors may miss ecologically relevant variation and/or skew estimates of true foraging effort.

Introduction

Foraging is an important aspect of animal behavior that has played an integral role in our understanding of ecological diversity among species of lizards. Predators have traditionally been classified into one of two general foraging modes, ambush or active foraging, based upon quantification of movement patterns (Pianka 1966; Shoener 1971; Huey and Pianka 1981). Lizards have served as an excellent model system to investigate the ecological correlates of foraging behavior over the past forty years. This work has demonstrated that sensory capacities (Cooper 1995; 2007), performance (Vitt and Price 1982; Huey *et. al.* 1984), morphology (McBrayer 2004; McBrayer and Corbin 2007), energetics (Anderson and Karasov 1981; Secor 1995), diet (Huey and Pianka 1981), and life history characteristics (Vitt and Congdon 1978; Perry *et. al.* 1990; Vitt 1990) are correlated with foraging strategies. These findings generated the “foraging mode paradigm” in which much of the variation among different clades has been linked to foraging behavior (Cooper 1995; Perry 1999; Vitt *et. al.* 2003; Miles *et. al.* 2007).

While the foraging mode paradigm is a powerful organizational construct, it is not without its criticisms. Many authors have acknowledged the inherent weakness of basing assessments of foraging behavior solely on quantifications of movement patterns that are not necessarily directly related to foraging (Cooper 2005a; Anderson 2007). Additionally, several authors have pointed out that ecologically relevant variation in foraging behavior exists at the intraspecific level and such variation is often overlooked in comparative studies (Huey and Pianka 1981; Pietruszka 1986; Perry 1996; Werner *et. al.* 2006; Anderson 2007; Verwaijen and Van Damme 2008). While these two concerns have been investigated independently (Pietruszka 1986; Jensen *et. al.* 1995; Perry 1996; Cooper *et. al.* 2001; Cooper *et. al.* 2005; Butler 2005; Werner *et. al.* 2006), no studies have determined whether assessing foraging behavior solely on quantification of movement patterns misses ecologically relevant intraspecific variation in foraging behavior.

The foraging mode paradigm defines foraging behavior principally by using two metrics of movement patterns, the percent time spent moving (PTM) and the rate of movements (moves per minute; MPM), as proxies for foraging behavior (Huey and Pianka 1981; Cooper *et. al.* 2001; Cooper 2005c). The popularity of these two metrics is due in large part to the ease of data collection that they offer (McBrayer *et. al.* 2007). However, there are some inherent drawbacks to assessing foraging behavior based solely on movement patterns. Lizards move for a variety of reasons including foraging, response to/avoidance of abiotic stresses, predator avoidance/evasion, and mate acquisition (Anderson 2007; Perry 2007). Thus, the movement

patterns recorded by researchers may not be related to foraging at all. Researchers have attempted to gather data in such a way as to minimize the influence of these other variables. However, it is often difficult (if not impossible) to know whether observed behavior is solely related to foraging. Consequently the utility of the foraging mode paradigm in accurately portraying all variation in foraging behavior has been questioned (Cooper and Whiting 1999; McBrayer *et. al.* 2007). Some authors have suggested using attack-based indices, e.g. the proportion of attacks on prey discovered while moving (PAM; Cooper and Whiting 1999; Cooper *et. al.* 2001), the proportion of attacks made while stationary (AWS; McBrayer *et. al.* 2007), or detailed analysis of behavioral sequences (Butler 2005) to more accurately describe the manner in which a predator actually locates and acquires prey (i.e. actual foraging behavior) rather than just movement patterns. PTM and MPM have performed adequately in comparative studies at higher taxonomic levels, however at the intraspecific level they may miss variation in foraging behavior that can be detected using metrics attack-based metrics.

Intraspecific variation in the foraging behavior may be related to seasonal differences in behavior between the sexes. Trivers (1972) predicted that due to differences in reproductive strategies for increasing fitness (e.g. quality offspring vs. increased mating), females and males might allocate time to foraging differently. Females should maximize foraging effort and thus energy intake (energy maximizers), while males should only spend enough time foraging to acquire enough energy to allow them to search for mates (feeding time minimizers) (Trivers 1972). Males of many taxa including lizards sacrifice foraging success to engage in reproductive behavior (stickleback fishes: Noakes 1986; lizards: Marler and Moore 1989; Durtsche 1992; Jensen *et. al.* 1995; Perry 1996; water strider insects: Sih *et. al.* 1990; orb weaving spiders: Foellmer and Fairbairn 2005). Because reproduction in many temperate species of lizards exhibits distinct seasonality, differences in foraging behavior between sexes might only exist during the breeding season. Indeed, some species have shown differences in foraging patterns consistent with these predictions (Durtsche 1992; Jensen *et. al.* 1995; Perry 1996).

Sexual differences might also lead to variation in movement patterns unassociated with foraging behavior between sexes and seasons, especially in polygynous ambush predators. Male lizards often increase their home range size and their amount of daily activity during the breeding season in order to visit the smaller home ranges of females (*Sceloporus virgatus*, Rose 1981; Marler and Moore 1989; *Sceloporus jarrovi*, Klukowski *et. al.* 2004; *Sceloporus undulatus*, Haenel *et. al.* 2003) or to patrol and defend a territory (*Anolis carolinensis*; Jensen *et. al.* 1995). As males change their movement patterns in order to acquire mating opportunities,

they may not change their foraging movement patterns or they may decrease the amount of movement associated with foraging. If males devote more movement to mate seeking in breeding season, and to foraging in the non-breeding season, then PTM and MPM will not differ between seasons. Essentially, it is possible for movement patterns to show little or no variation between seasons and sexes, but for foraging behavior to vary between seasons and sexes because metrics of movement patterns do not necessarily reflect the purpose of the movement. Such interactive effects in the ecological context of movement patterns could obscure estimates of foraging behavior if the estimates are based solely on metrics of movement.

Methodological concerns are not the only potential consequence of intraspecific variation in foraging behavior. At the intraspecific level, variation in foraging behavior could shape other intraspecific aspects of an organism's ecology, (e.g. niche partitioning, energy budgets, growth, etc.; Foellmer & Fairbairn 2005; Cox & John-Alder 2007; John-Alder & Cox 2007; Cox *et. al.* 2007; McBrayer *et. al.* 2007). In particular, differences in diet between the sexes during the breeding season are common within many species of lizards (Durtsche 1992; Preest 1994; Parmelee and Guyer 1995; Perry 1996; Saenz 1996), and these differences have been suggested to be evidence of niche partitioning (Saenz 1996; Cox *et. al.* 2007). However, niche partitioning may only be a consequence of differences in foraging behavior between the sexes since the way that an animal forages will affect the types and amounts of food that it consumes (Cox *et. al.* 2007).

Despite the breadth of the literature regarding the importance of foraging behavior in lizards (Pianka 1966; Shoener 1971; Vitt and Congdon 1978; Anderson and Karasov 1981; Huey and Pianka 1981; Vitt and Price 1982; Huey *et. al.* 1984; Perry *et. al.* 1990; Vitt 1990; Durtsche 1992; Cooper 1995, 2007; Secor 1995; Perry 1996, 1999; Vitt *et. al.* 2003; McBrayer 2004; Butler 2005; Werner 2006; Anderson 2007; McBrayer *et. al.* 2007; McBrayer and Corbin 2007; Miles *et. al.* 2007), only a few studies have focused on the intraspecific variation (Durtsche 1992; Perry 1996; Werner 2006) and none have used attack-based indices in conjunction with metrics of movement patterns to assess intraspecific variation in foraging behavior. Using attack-based indices in conjunction with metrics of movement patterns to assess intraspecific variation in foraging behavior will reveal whether the traditional methods of quantifying foraging behavior in lizards adequately captures intraspecific variation. Understanding whether diet varies concomitantly with foraging behavior within a species of lizard will help elucidate the potential ecological relevance of intraspecific variation in foraging behavior.

The objective of this study is to examine intraspecific variation in foraging behavior using both attack based indices and traditional movement patterns indices. Furthermore this study will relate variation in foraging behavior to variation in diet. To this end, I addressed the following questions: 1) does a species of lizard show seasonal and sexual variation in movement patterns as measured by percent time moving and moves per minute; 2) does a species of lizard show seasonal and sexual variation in prey attack behavior; 3) do metrics of movement patterns and attack-based indices show the same patterns of variation between seasons and sexes; and 4) do diet characteristics vary between seasons and sexes?

Methods

Study Site and Organism

The present study examined the behaviors and diet of *Sceloporus woodi* in the 154,994 hectare Ocala National Forest (ONF), Marion County, Florida from mid-March through October 2008. *Sceloporus woodi* is endemic to the xeric upland sand pine-live oak (*Pinus clausa* and *Quercus geminata*) scrub and long leaf pine-turkey oak (*Pinus palustris* and *Quercus laevis*) sand-hill habitats in Florida (Branch and Hokit 2000; McCoy *et. al.* 2004). The ONF encompasses the Mount Dora sand ridge and contains the largest remaining continuous area of scrub habitat in Florida (Myers 1990). Within the scrub habitat *S. woodi* occupies edges between young (recently cleared) and mature stands created by large fires or clear cutting (Greenberg *et. al.* 1994; Tiebout and Anderson 1997; Greenberg 2002; Fabry 2003). *S. woodi* can be found within the entire stand in sand hill habitats (*personal observation*). Both habitats provide large areas of open, well drained sand preferred by *S. woodi* (Myers 1990; Hokit *et. al.* 1999). One reason this species was chosen is because it exists in high densities (10-124 individuals/hectare) within its habitat (Jackson and Telford 1974; McCoy *et. al.* 2004). Within the ONF lizards were observed at four main sites; one sand hill site (Kerr Island, 29°21.811'N 081°49.989'W) and three scrub sites (all recently clear cut) (29°10.197'N 081°47.898'W; 29°09.403'N 081°46.609'W; 29°03.799'N 081°41.22'W).

Sceloporus woodi is a small, short lived, sexually dimorphic arthropodivorous iguanid lizard (Jackson 1972; Jackson and Telford 1974; Connant and Collins 1998; Branch and Hokit 2000). Individuals reach sexual maturity at 45-47 mm snout to vent length during the breeding season of the year following hatching (approximately 6 to 8 months) (Jackson and Telford 1974; McCoy *et. al.* 2004). The average lifespan of *S. woodi* is 12.6 months, though some individuals do live as long as 27 months (McCoy *et. al.* 2004). Based upon male testis volume cycle and female reproductive patterns, the breeding season is defined from mid-March/early April through

July, although occasional mating occurs in latter months (Jackson and Telford 1974). Lizards remain active through October but begin reducing activity in November and December (Jackson and Telford 1974). Females produce 3-4 clutches of up to 5 or 6 eggs per season (Jackson and Telford 1974; McCoy *et. al.* 2004). Males are smaller (male SVL = 51.95 ± 0.32 mm; female SVL = 57.35 ± 0.53 ; this study) and have fewer markings on their backs than females (Connant and Collins 1998). The sexes are also dimorphic in body-size corrected shape with males having relatively longer limb elements and heads than females (Jackson 1973; Pounds *et. al.* 1983). In addition to differences in morphology, males and females also differ in activity range size during the breeding season (male = 721 ± 64 m²; female = 312 ± 34 m²; Hokit and Branch 2003). The extensive sexual dimorphism and the high likelihood that individuals will only have one breeding season to reproduce suggest this species might show seasonal and sexual patterns in behavior.

Behavioral Observations

Focal observations were made using video recordings of free roaming individuals. Lizards were located by moving slowly through the habitat and scanning the ground and trees for lizards. In scrub habitats the majority of search effort was concentrated along the edges stands because *S. woodi* is most abundant and easily observed there (Fabry 2003; *personal observation*). The entire stand in the sand hill habitat was searched because lizards were fairly evenly distributed and easy to observe throughout the stand (*personal observation*). Lizards were filmed for 15 minutes (Perry 2007) using a Panasonic VDR-210 mini DVD camera from a starting distance of 5 meters after a 2 to 3 minute acclimation time in order to ensure undisturbed behavior was recorded (Cooper 2005c). Focal observations were abandoned if the lizard became engaged in social interactions with another observable lizard or the focal lizard was not visible for >2.5 minutes at a time (e.g. view of the lizard was obscured by vegetation). Care was taken to remain motionless and make as little noise as possible during filming. Drab clothing was worn during filming and when possible, films were made from behind trees or shrubs. Lizards were captured by noosing once filming concluded in order to confirm adult status and sex. All but 7 of 132 filmed individuals were captured. The sex and adult status of the 7 non-captured lizards were determined during the capture attempt and confirmed using the film. The body temperature and temperature of all substrates occupied at the time of capture were measured to ensure that behavior observed was unlikely due to thermoregulation. All lizards were then given a unique mark and released at the point of capture.

The sequences and duration of behaviors were transcribed from the filmed focal observations. Focal observations shorter than 10 minutes were omitted in order to ensure acceptable levels of variance in behavioral estimates (Perry 2007). I attempted to observe similar numbers of each sex within each season (Table 1.1). The behaviors recorded were moves, jumps, periods of being stationary, displays, attacks on prey, lunges, head moves, postural adjustments, substrate licks, scratches, not visible, and other rare behaviors (Table 1.2). Continuous bouts of action were regarded as a singular behavior (*e.g.* a string of push-ups counted as a single display). The traditional metrics of foraging behavior based on rate of movements (MPM) and percentage of time spent moving (PTM) were calculated for all focal observations. In addition to metrics of movement patterns, variables more directly related to foraging were calculated for those individuals that attacked prey. The metrics of foraging behavior recorded were the rate of attacks on prey (attacks per minute; APM) and the proportion of attacks made while stationary (AWS),

Intraspecific variation in behavior was examined by making two-way comparisons of movement variables (MPM and PTM) and foraging variables (APM and AWS) with season and sex as the independent variables. Separate analyses were used to test each variable. Data for all behavioral variables were non-normally distributed (skewed right) and could not be transformed, thus non-parametric analyses were used. All statistical analyses were conducted using JMP 4.0.4 statistical analysis software (SAS Institute 2001).

Lag-sequential analysis was used to determine if there were any associations between attacks on prey and other behaviors, especially movement variables. Lag-sequential analysis is an assessment of the conditional probability of whether a target behavior occurs before a behavior of interest at a frequency significantly different from random (Butler 2005). It can therefore be used to determine what behaviors do (positive association) or do not (negative association) occur before an attack and provide a fine scale description of how an animal acquires prey. Only those focal observations in which lizards foraged ($n = 56$) were used in the sequential analysis. Individual Hochberg-Bonferroni corrected Chi-square tests with one degree of freedom were conducted to test whether any of the behaviors recorded (Table 1.2) tended to precede an attack on prey. The Phi coefficient of correlation was calculated to determine the relative strength of the association and whether it was a positive or negative association (Sokal and Rohlf 1995). Analyses were conducted for behaviors immediately preceding an attack (lag 1) and for behaviors 2 (lag 2) and 3 (lag 3) behaviors prior to the attack. I used the LAGS.SAS macro for SAS software system (Friendly 2001; SAS 2002) to calculate the lag frequencies.

One potential hazard of lag-sequential analysis is that behaviors preceding the behavior of interest by an extended time period (long lag time) can lead to spurious associations by counting sequences of behavior that are not likely associated. For instance, a lizard might scratch itself and do nothing until it attacks prey 2 minutes later. The scratch is likely not related to the attack on prey, thus this sequence should have less of an effect on the observed frequency that will be compared to the expected random frequency. Event behaviors were counted as less than one if the lag time between the behavior of interest and the target behavior was greater than the lag time of 75% (third quartile; Q3) of the sequences. Sequences with a lag time one second greater than the third quartile were assigned a weight of 0.95 and the sequence with the maximum lag time was assigned a weight of 0 (no effect on frequency). All sequences with lag times between the third quartile and the maximum were assigned a weight based upon a linear equation of a line plotted between (Q3+1, 0.95) and (max, 0). A separate weighting curve was calculated for lag 1, 2 and 3. All state behaviors received a full frequency weight of one because of the continuous nature of state behaviors.

Diet

Stomach contents were obtained from 110 lizards via gastric lavage (stomach flushing; Legler and Sullivan 1979; Pietruszka 1981). Stomach flushing is an effective and accurate means of obtaining stomach contents in lieu of killing a lizard and removing its entire digestive system (Pietruszka 1981). Of the 110 lizards that were flushed, 43 individuals were filmed foraging. Lizards were flushed the same day they were captured. Twenty to 30 milliliters of an electrolyte solution (pediatric electrolyte solution) were pushed into lizards' stomachs via a ball tipped needle passed down their throats, thereby inducing them to regurgitate their stomach contents. Contents were strained through a coffee filter and then stored in 70% ethanol. Stomach contents were sorted to functional taxonomic units. Functional taxonomic units (FTU) usually comprised the order of the prey consumed, however Hymenopterans, Coleopterans, and Lepidopterans were further subdivided to reflect major ecological differences among families (Hymenopterans) and life stages (Coleopterans and Lepidopterans). The number of FTUs, number of prey items, and the volume of prey in the stomach were recorded. Prey items were grouped together and singular body parts were counted. Volumes of prey items were determined by liquid displacement because of its high accuracy (Magnusson *et. al.* 2003) and then corrected for lizard body size via regression of volume against body size. Diets were compared between seasons and sexes using either 2-way ANOVA of transformed data (number of prey, prey volume) or the Sheirer-Ray-Hare extension of the Kruskal Wallis test (number of FTU).

Results

Behavior

I observed a total of 132 lizards for a total of 29.99 hrs, 56 of these lizards were observed foraging (Table 1.1). Sampling effort was uniform between sexes and seasons (Table 1.1). Non-parametric two-way analyses of variation between sexes and seasons revealed no differences in either focal duration or not visible time (Focal Duration: sex $H = 2.54$, $DF = 1$, $p = 0.11$; season $H = 0.59$, $DF = 1$, $p = 0.44$; interaction $H = 0.36$, $DF = 1$, $p = 0.55$; Not Visible Time: sex $H = 0.80$, $DF = 1$, $p = 0.37$; season $H = 0.01$, $DF = 1$, $p = 0.92$; interaction $H = 1.65$, $DF = 1$, $p = 0.20$; Table 1.1).

Movement patterns did not differ between seasons or sexes (PTM season: $H_{1, 0.05} = 1.39$, $p = 0.24$; sex: $H_{1, 0.05} = 0.01$, $p = 0.91$; interaction: $H_{1, 0.05} = 2.44$, $p = 0.12$; MPM season: $H_{1, 0.05} = 1.76$, $p = 0.19$; sex: $H_{1, 0.05} = 0.06$, $p = 0.81$; interaction: $H_{1, 0.05} = 3.01$, $p = 0.08$) though both showed a decreasing trend during the post-breeding season (Figure 1.1 A, B). Both sexual and seasonal differences in AWS were observed (Fig. 1.1C). Females moved before attacking prey significantly more often than males during both seasons ($H_{1, 0.05} = 4.21$, $p = 0.04$; interaction: $H_{1, 0.05} = 0.47$, $p = 0.49$). Both males and females took more prey from a stationary position during the breeding season ($H_{1, 0.05} = 4.51$, $p = 0.03$). Rate of attack (APM) showed no significant differences between seasons or sexes (season: $H_{1, 0.05} = 2.46$, $p = 0.12$; sex: $H_{1, 0.05} = 0.86$, $p = 0.35$; interaction: $H_{1, 0.05} = 0.49$, $p = 0.48$; Fig. 1.1D).

Table 1.3 summarizes the results of the lag sequential analysis. I recorded 2144 (1323 female; 821 male) sequences of behavior during the breeding season and 1788 (738 female; 1050 male) during the post-breeding season. Of the recorded two behavior sequences 197 sequences (112 female; 85 male) resulted in an attack on prey during the breeding season and 110 sequences (31 female; 79 male) during the post-breeding season. Females were not visible two behaviors before an attack significantly more often than would be expected at random during both seasons. However the significant association of not visible and attack in lag 2 may be an artifact of the overall low frequency of occurrence of 'not visible' (17/1323 behaviors during the breeding season and 14/738 in the post-breeding season) making the expected frequency of occurrence before an attack very low. That is, any more than 1 occurrence of 'not-visible' before an attack would have generated significance. However, I can not rule out the possibility that the 'not-visible' occurring two behaviors before an attack may be indicative of greater mobility of females when foraging since lizards were lost from view most often due to them moving behind shrubs and other habitat structures. Males tended to be not visible three

behaviors before an attack during the post-breeding season only; once again this was likely a statistical artifact. Lunges were the most important behaviors to immediately precede an attack on prey for both sexes in both seasons. Females moved and jumped immediately before attacking prey significantly more often than at random during the post-breeding season. During the breeding season both sexes fed in extended bouts as evidenced by ‘attack’ followed by ‘attack’ occurring at a significantly higher frequency than would be expected at random. However during the post-breeding season ‘attack’- ‘attack’ was only significant for males in the third lag only indicating that lizards did not feed in extended bouts. Females tended to not move their heads immediately before an attack on prey during the breeding season. During the post-breeding season males tended to not move their head immediately before and three behaviors before attacking prey, but there was no association between head moves and attacks on prey two behaviors before attacking prey. Display behaviors in males also showed a significant negative association with attacks on prey during the breeding season. All other behavioral sequences occurred at random frequencies.

Diet

Two way analysis of size-corrected stomach volume between seasons and sexes revealed a significant interaction ($F_{1, 0.05} = 7.20$, $p = 0.009$; Fig. 1.2) so individual t-tests with Bonferroni correction for multiple tests were carried out for males between seasons, females between seasons, and between sexes within each season. During the breeding season females had significantly higher volumes of prey in their stomachs than did males ($t_{50, 0.05} = 2.664$; $p = 0.042$; Table 1.4). Female stomach volume decreased significantly between the breeding season and post-breeding season ($t_{50, 0.05} = 2.627$; $p = 0.041$; Table 1.4). There were no significant differences in size corrected stomach volumes between sexes within the post-breeding season ($t_{55, 0.05} = -1.063$; $p = 0.999$; Table 4) or between seasons for males ($t_{55, 0.05} = -1.171$; $p = 0.988$; Table 1.4).

Females and males also had different seasonal patterns with respect to the number of prey types in their guts (season x sex interaction: $H_{1, 0.05} = 7.51$, $p = 0.006$, Fig. 1.2). Since there was a significant interaction, I performed individual Bonferroni corrected Mann-Whitney U tests. Female stomachs contained more types of prey than males ($U = 675$; $p = 0.0012$; Table 1.4). During the post-breeding season males and females consumed similar numbers of different types of prey, thus showed no significant differences ($U = 840$; $p = 0.762$; Table 1.4). Unlike the pattern seen with stomach volume across seasons, females did not show any significant decrease in number of prey types ($U = 700$; $p = 0.082$) but males showed a significant increase in the

number of different prey types consumed ($U = 810$; $p = 0.019$; Table 1.4). While there were definite seasonal and sexual patterns of prey volume and diversity, there were no significant differences between sexes in the number of prey items consumed and only a marginally significant difference between seasons (sex: $F_{1,0.05} = 0.54$, $p = 0.463$; season: $F_{1,0.05} = 3.875$, $p = 0.052$; interaction: $F_{1,0.05} = 1.62$, $p = 0.206$; Table 1.4).

Discussion

My results show that while no intraspecific differences exist in movement patterns of *Sceloporus woodi*, there are clear interseason and intersex differences in foraging behavior. During the breeding season males and females move the same amount, but males take more prey while stationary showing that the purpose of movement differs between the sexes especially in the breeding season. Anderson (2007) suggested that subtle changes in foraging behavior may arise in response to shifts in importance of the four basic autecological tasks; reproduction, acquiring energy (i.e. foraging), coping with abiotic stresses, and coping with predation. Reproductive constraints faced by *S. woodi* are likely influencing their foraging behavior, leading to differences in AWS between males and females during the breeding season (Trivers 1972; McCoy *et. al.* 2004; Foellmer and Fairbairn 2005). The seasonal and sexual variation in diet shows that the variation in foraging behavior not detected by quantifying movement patterns has important ecological consequences. Energy intake takes a back seat to mate acquisition for males of many species during the breeding season, while females seek to maximize energy intake for gestation and possibly growth (Shoener 1971, Trivers 1972). Females likely attempt to consume as large a volume of prey as possible regardless of how they capture it (Higgins and Rankin 2001). Females' attempts to consume as much large prey as possible may also predispose them to taking advantage of riskier foraging opportunities to capture larger prey items (Higgins and Rankin 2001). Indeed females experience higher mortality than males (Hokit and Branch 2003; McCoy *et. al.* 2004) which could be due to such voracious and risky feeding behavior (Higgins and Rankin 2001) and males do not attain the same maximum body size as females (Jackson 1973).

Lag analysis showed that *S. woodi* employs an ambush feeding strategy, but seasonal variation exists in foraging strategy. Lunges were the most important behaviors to precede an attack, indicating that most prey was taken while stationary. The significance of 'attack' in the breeding season lag analysis of both sexes indicates that *S. woodi* tends to feed in extended bouts during the breeding season, possibly due to the abundance of clumped prey such as swarming ants and termites. Indeed ants were much more prevalent in *S. woodi*'s diet during the breeding

season than during the post-breeding season (Table 1.5). During the post-breeding season, shifts in prey abundance (i.e. the absence of ant and termite swarms) may limit lizards' opportunity to feed in such extended bouts and consequently lead to a lack of a significant association between multiple attacks on prey. The increase in movement associated with female foraging in the post-breeding season indicated by the seasonal decrease in AWS is supported by the fact that both 'jump' and 'move' occurred immediately before an attack at significantly higher frequency than would be expected at random. Butler (2005) interpreted a lack of significance of movement preceding an attack in the chameleon *Bradypodion pumilum* to indicate it is not an ambush forager. Her interpretation makes sense in relation to the movement patterns of *B. pumilum* (PTM = 21%; MPM = 0.43). However, I do not interpret the lack of significance of 'move' in the lag analysis of *S. woodi* to indicate that this species is an active forager because PTM and MPM were low (Fig. 1). Interpretation of the lag analysis in context of the movement pattern data shows that overall both sexes of *S. woodi* employ an ambush foraging strategy, but that the specific way that prey is acquired is variable between seasons.

Lag sequential analysis and AWS are complimentary assessments of variation in foraging behavior. While the lag analysis did not detect the differences in foraging behavior shown by AWS in the breeding season, it helps put the differences in AWS into context. Interpretation of breeding season differences in AWS in the context of the lag analysis shows that although both sexes tend to remain stationary and feed on clumped prey, females are more willing to move to capture prey. Both AWS and lag analysis provide a more detailed view of the manner in which prey is captured and reveal intraspecific variation in foraging behavior. Though AWS provides some of the same information, lag analysis still provides useful insights into the specific behaviors used to complete the ecologically important task of attacking prey (Butler 2005).

Variation in diet paralleled the differences in foraging behavior. Concordant with the fact that no differences in feeding rate existed between sexes or seasons, males and females consumed the same number of prey items during both seasons. However, just as males and females differed in the way in which they captured prey, the characteristics of their diets also differed. Females captured larger and more types of prey during the breeding season than males. The consumption of larger prey items by females is inferred from their significantly larger size corrected stomach volumes in the absence of greater numbers of prey in gut and the fact that while male guts contained a greater number of ants than females, the ants in female stomachs had a higher volume (Table 1.5). During the post-breeding season the diets of males and females converged because the volume of prey consumed by females decreased and males took more

prey types. In addition to being higher in volume and more diverse than the diet of males during the breeding season, female diets are also likely more energy rich given that the small ants that make up the majority of male diets are probably the lowest energy content prey items available (Cummins and Wuycheck 1971; Tshinkel 2002). Interestingly, even though both sexes show a significant decrease in AWS during the post-breeding season, male diets increase in diversity and volume during the post-breeding season while female diets decrease in diversity and volume. This shows that seasonal shifts in behavior affect the sexes differently. Similar patterns of intersex dietary differences between seasons have been observed in other taxa as well (*Sceloporus jarrovi*, Ballinger and Ballinger 1979; *Cercopithecus* monkeys, Gautier-Hion 1980; *Uma inornata*, Durtsche 1995; *Sternotherus odoratus*, Ford and Moll 2004; Orbiculariae spiders Foellmer and Fairbairn 2005).

The fact that intraspecific variation in foraging behavior is overlooked by the traditional metrics of the foraging mode paradigm validates that quantifying foraging behavior solely on the basis of PTM and MPM is unwise (Cooper and Whiting 1999; Cooper *et. al.* 2001, 2005; Butler 2005; Anderson 2007; McBrayer *et. al.* 2007). However I do not suggest that PTM are not valuable. Indeed MPM and PTM are necessary to put attack-based indices and sequential analyses into context and thus provide a more complete, accurate, and clear quantitative description of the foraging behavior of a species. My results demonstrate the value of investing the considerable effort to calculate attack-based indices (PAM, Cooper and Whiting 1999; AWS, McBrayer *et. al.* 2007) and to conduct lag sequential analysis (Butler 2005). Attack-based indices are useful in quantifying precisely how predators acquire prey, yet require less computational effort than lag sequential analysis.

Focusing solely on movement patterns in studies of foraging behavior masks biologically relevant variation. My data shows that intraspecific variation in foraging behavior exists independent of intraspecific variation in movement patterns. The presence of seasonal and sexual differences in AWS but not in movement patterns and the similarities between seasonal and sexual differences in AWS and diet indicate complex shifts in the autecological reason for movement in response to reproductive season (Haenel *et. al.* 2003; Anderson 2007). My study adds to the growing body of evidence that intraspecific variation in foraging behavior is common (Werner *et. al.* 2006; Butler 2005; Perry 1996; Whitting 2007). For lizards, previous comparative studies of the evolution of foraging behavior and associated traits have treated species as static. However, by ignoring intraspecific variation in foraging behavior, one glosses

over highly relevant seasonal and sexual variation (Huey and Pianka 1981; Pietruszka 1986; Perry 1996; Werner *et. al.* 2006; Anderson 2007; Verwajen and Van Damme 2008; this study).

Understanding the factors that affect foraging behavior within a species will provide deeper insights into the relationships between foraging behavior and other aspects a species' ecology (Huey and Pianka 1981). With the current focus of foraging behavior research on applying generalized concepts in a broad comparative framework, the details of intraspecific variation have been ignored. Taking seasonal and sexual differences in foraging behavior into consideration will reveal important variation often missed in comparative studies of foraging. Only by conducting analyses at both the inter- and intraspecific levels can researchers provide greater resolution and advancement of the foraging mode paradigm.

References

- Anderson, R. A. 2007. Food acquisition modes and habitat use in lizards: questions from an integrative perspective. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, ed. S. M. Reilly, L. D. McBrayer, and D. B. Miles. pp 450-490. Cambridge University Press. Cambridge, UK.
- Anderson, RA; Karasov, WH. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* 49: 67-72.
- Ballinger, R. E.; Ballinger, R. A. 1979. Food resource utilization during periods of low and high food availability in *Sceloporus jarrovi* (Sauria: Iguanidae). *The Southwestern Naturalist* 24: 347-363.
- Butler, M. A. 2005. Foraging Mode of the chameleon, *Bradypodion pumilum*; a challenge to the sit and wait versus active forager paradigm. *Biological Journal of the Linnean Society* 84: 797-809.
- Butler, M. A.; Sawyer, S. A.; Losos, J. B. 2007. Sexual dimorphism and adaptive radiation in *Anolis* Lizards. *Nature* 447: 202-205.
- Connant, R; Collins, J. T. 1998. *A Field Guide to Reptiles and Amphibians of Eastern and Central North America*. Third Edition, Expanded Houghton Mifflin Company, New York, NY, USA.
- Cooper, W. E. 2005a. Duration of Movement as a lizards foraging movement variable. *Herpetologica* 61: 363-372.
- Cooper, W. E. 2005b. Ecomorphological variation in foraging behavior by Puerto Rican *Anolis* lizards. *Journal of Zoology, London* 256: 133-139.
- Cooper, W. E. 2005c. Lizard foraging modes: global need for data, methods for data collection, and call for data. *Herpetological Review* 36: 367-369.
- Cooper, W. E. 2007. Foraging modes as suites of co-adapted movement traits. *Journal of Zoology* 272: 45-56.
- Cooper, W. E., Jr., L. J. Vitt, J. P. Caldwell, and S. F. Fox. 2001. Foraging modes of some American lizards: relationships among measurement variables and discreteness of modes. *Herpetologica* 57:65-76.
- Cooper, W. E.; Vitt, L. J.; Caldwell, J. P; Fox, S. F. 2005. Relationships among foraging variables, phylogeny, and foraging modes, with new data for nine North American species. *Herpetologica* 51: 250-259.
- Cooper, W. E.; Whiting, M. J. 1999. Foraging modes in Lacertid lizards from southern Africa. *Amphibia-Reptilia* 20: 299-311.

- Cooper, W.E. 1995. Prey Chemical Discrimination and Foraging mode in Geckonid Lizards. *Herpetological Monographs* 9:120-129.
- Cox, R. M.; John-Alder, H. B. 2007. Growing apart together: the development of contrasting sexual size dimorphisms in sympatric *Sceloporus* lizards. *Herpetologica* 63: 245-257.
- Cox, R. M.; Skelly, S. L.; John-Alder, H. B. 2005. Testosterone inhibits growth in juvenile male Eastern Fence Lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. *Physiological and Biochemical Zoology* 78: 531-545.
- Cummins, K. W.; Wuycheck, J. C. 1971. Caloric equivalents for investigations in ecological energetics. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 18: 1-158.
- Durtsche, R. D. 1992. Feeding time strategies of the fringe-toed lizard, *Uma inornata*, during the breeding and non-breeding seasons. *Oecologia* 89: 85-89.
- Durtsche, R. D. 1995. Foraging ecology of the fringe-toed lizard, *Uma inornata*, during periods of high and low food abundance. *Copeia* 1995: 915-926.
- Fabry, C. J. 2007. Spatiotemporal patterns of Florida scrub lizard abundance in young, regenerating Florida scrub. Unpublished Master's Thesis, Western Washington University, Bellingham, WA.
- Foellmer M. W. and Fairbairn D. J. 2005. Selection on male size, leg length and condition during mate search in a sexually highly dimorphic orb-weaving spider. *Oecologia* 142: 653-662.
- Ford, D. K.; Moll, D. 2004. Sexual and seasonal variation in foraging patterns in the stinkpot, *Sternotherus odoratus*, in Southwestern Missouri. *Journal of Herpetology* 38: 296-301.
- Friendly, M. 2001. Lags.sas macro for lag-sequential analysis.
<http://www.math.yorku.ca/SCS/vcd/lags.html>
- Garland, T.; Bennett, A. F.; Daniels, C. B. 1990. Heritability of locomotor performance and its correlates in a natural population of vertebrates. *Experientia* 46:530-533.
- Garland, T.; Losos, J. B. 1994. Ecological morphology of locomotor performance in Squamate reptiles. In *Ecological Morphology: Integrative Organismal Biology*, ed P. C. Wainwright and S. M. Reilly pp 240-302. University of Chicago Press, Chicago, IL, USA.
- Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology* 49: 237-269.
- Greenberg, C. H. 2002. Fire, habitat structure and herpetofauna in the southeast. In: Ford, W.; Russell, K. R.; Moorman, C. E.; Proceedings: The role of fire for non-game wildlife management and community restoration: traditional uses and new directions. Newton Square, PA: US. Dept. of Agriculture, Forest Service, Northeastern Research Station GTR-NE-288 : 91-99.

Greenberg, C. H.; Neary, D. G.; Harris, L. D. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. *Conservation Biology* 4: 1047-1057.

Haenel, G. J.; Smith, L. J.; John-Alder, H. B. 2003. Home-Range Analysis in *Sceloporus undulatus* (Eastern Fence Lizard) I: Spacing Patterns and the context of territorial behavior. *Copeia* 2003: 99-112.

Higgins, L. E.; Rankin, M. A. 2001. Mortality risk of rapid growth in the spider *Nephila clavipes*. *Functional Ecology* 15: 24-28.

Hokit, D. G.; Branch, L. C. 2003. Associations between patch area and vital rates: consequences for local and regional populations. *Ecological Applications* 13: 1060-1068.

Hokit, D. G.; Smith, B. M.; Branch, L. C. 1999. Effects of landscape structure in Florida scrub: a population perspective. *Ecological Applications* 9: 124-134.

Huey, R. B.; Bennet, A. F.; John-Alder, H.; Naggy, K. A. 1984. Locomotor capacity and foraging behaviour of Kalahari Lacertid lizards. *Animal Behaviour* 32: 41-50.

Huey, RB. 1991. Physiological consequences of habitat selection. *The American Naturalist* 137: S91-S115.

Huey, RB; Pianka, ER. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991-999.

Jackson, J. F. 1972. The phenetics of a narrow hybrid zone. *Evolution* 27: 58-68.

Jackson, J. F. 1973. Distribution and population phenetics of the Florida Scrub Lizard, *Sceloporus woodi*. *Copeia* 1973: 746-761.

Jackson, J. F. 1974. Reproductive ecology of the Florida Scrub Lizard *Sceloporus woodi*. *Copeia* 1974: 689-694.

Jensen, T. A.; Greenberg, N.; Hovde, K. A. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs* 9: 41-62.

John-Alder, H. B.; Cox, R. M.; Taylor, E. N. 2007. Proximate developmental mediators of sexual dimorphism in size: case studies from Squamate reptiles. *Integrative and Comparative Biology* 47: 258-271.

Klukowski, M; Ackerson, B; Nelson, CE. 2004. Testosterone and daily activity period in laboratory-housed mountain spiny lizards, *Sceloporus jarrovi*. *Journal of Herpetology* 38: 120-124.

Legler J. M.; Sullivan, L. J. 1979. The application of stomach-flushing to lizards and anurans. *Herpetologica* 35: 107-110.

- Magnusson, W. E.; Lima, A. P.; Alves da Silva, W.; Carmozina de Araujo, M. 2003. Use of geometric forms to estimate volume of invertebrates in ecological studies of dietary overlap. *Copeia* 2003: 13-19.
- Marler, C. A. & Moore, M. C. 1989. Time and energy costs of aggression in testosterone-implanted free-living male mountain spiny lizards. *Physiological Zoology* 62: 1334-1350.
- McBrayer, L. D. 2004. The relationship between skull morphology, biting performance, foraging mode in Kalahari Lacertid lizards. *Zoological Journal Linnean Society* 140: 403-416.
- McBrayer, L. D.; Corbin, C. L. 2007. Patterns of head shape variation in lizards: morphological correlates of foraging mode. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, ed. S. M. Reilly, L. D. McBrayer, and D. B. Miles. pp 271-301. Cambridge University Press. Cambridge, UK.
- McBrayer, L. D.; Miles, D. B.; Reilly, S. M. 2007. The evolution of the foraging mode paradigm in lizard ecology. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, ed. S. M. Reilly, L. D. McBrayer, and D. B. Miles. pp 508-521. Cambridge University Press. Cambridge, UK.
- McCoy, E. D.; Hartman, P. P.; Mushinsky, H. R. 2004. Population biology of the rare Florida Scrub Lizard in a fragmented habitat. *Herpetologica* 60: 54-61.
- Miles, D. B.; Losos, J. B.; Irshick, D. J. 2007. Morphology, performance, and foraging mode. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, ed. S. M. Reilly, L. D. McBrayer, and D. B. Miles. pp 49-93. Cambridge University Press. Cambridge, UK.
- Myers, R. L. 1990. Scrub and high pine. In *Ecosystems of Florida* pp 151-193. University of Central Florida Press, Orlando, FL, USA.
- Noakes, D. L. G. 1986. When to feed: decision making in sticklebacks, *Gasterosteus aculeatus*. *Environmental Biology of Fishes* 16: 95-104.
- Parmelee, J. R.; Guyer, C. 1995. Sexual differences in foraging behavior of an Anoline lizard, *Norops humillis*. *Journal of Herpetology* 29: 619-621.
- Perry, G. 1996. The evolution sexual dimorphism in the lizard *Anolis polylepsis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology* 74: 1238-1245.
- Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *The American Naturalist* 163: 98-109.
- Perry, G. 2007. Movement patterns in lizards: measurement, modality, and behavioral correlates. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, ed. S. M. Reilly, L. D. McBrayer, and D. B. Miles. pp 13-48. Cambridge University Press. Cambridge, UK.
- Perry, G.; Lampl, I.; Lerner, A.; Rothenstein, D.; Shani, E.; Sivan, N.; Werner, Y. L. 1990. Foraging mode in Lacertid lizards: variation and correlates. *Amphibia-Reptilia* 11: 373-384.

- Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47: 1055-1059.
- Pietruszka, R. D. 1981. An evaluation of stomach flushing for desert lizard diet analysis. *The Southwestern Naturalist* 26: 101-105.
- Pietruszka, R. D. 1986. Search tactics of desert lizards: how polarized are they. *Animal Behavior* 34: 1742-1758.
- Pounds, J. A.; Jackson, J. F.; Shively, S. H. 1983. Allometric growth of the hind limbs of some terrestrial iguanid lizards. *The American Midland Naturalist* 110: 201-207.
- Preest, M. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males. *Journal of Herpetology* 28: 292-298.
- Prenter, J.; Elwood, R. W.; Montgomery, W. I. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution* 53: 1987-1994.
- Rose, B. 1981. Factors affecting activity in *Sceloporus virgatus*. *Ecology* 62: 706-716.
- Saenz, D. 1996. Dietary overview of *Hemidactylus turcicus* with possible implications of food partitioning. *Journal of Herpetology* 30: 461-466.
- SAS Institute Inc. 2002. SAS/STAT User's Guide. Version 9.1.2. Cary, NC: SAS Institute Inc.
- Schoener, T.W. 1971. Theory of Feeding Strategies. *A Review of Ecological Systematics* 2: 360-404.
- Secor, S. M. 1995. Ecological aspects of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Herpetological Monographs* 9: 169-186.
- Siepielski, A. M.; DiBattista, J. D.; Carlson, S. M. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecology Letters* 12: 1261-1276.
- Sih, A.; Krupa, J.; Travers, S. 1990. An experimental study of the effects of predation risk and feeding regime on the mating behavior of the water strider. *The American Naturalist* 135: 284-290.
- Sokal, R. R.; Rohlf, F. J. 1995. *Biometry*. Third edition. Freeman, New York, New York, USA.
- Tiebout, H. M.; Anderson, R. A. 1997. A comparison of corridors and intrinsic connectivity to promote dispersal in transient successional landscapes. *Conservation Biology* 11: 620-627.
- Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man*, ed. B. Campell. Aldine, Chicago, IL, USA.
- Tschinkel, W. R. 2002. The natural history of the arboreal ant, *Crematogaster ashmeadi*. *Journal of Insect Science* 2: 1-15.

- Verwajen, D.; Van Dame, R. 2008. Foraging mode and its flexibility in Lacertid lizards from Europe. *Journal of Herpetology* 42: 124-133.
- Vincent, S. E.; Herrel, A. 2007. Functional and ecological correlates of ecologically-based dimorphisms in Squamate reptiles. *Integrative and Comparative Biology* 47: 172-188.
- Vitt, L. J. 1990. The influence of foraging mode and phylogeny on seasonality of tropical lizard reproduction. *Papéis Avulsos Zoologia (São Paulo)* 37:107-123.
- Vitt, L. J., and H. J. Price. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237-255.
- Vitt, L. J.; Congdon, J. D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *The American Naturalist* 112: 595-608.
- Vitt, LJ; Pianka, ER; Cooper, WE; Schwenk, K. 2003. History and global ecology of Squamate reptiles. *The American Naturalist* 162: 44-60.
- Werner, Y. L.; Takahashi, H.; Yasukawa, Y.; Ota, H. 2006. Factors affecting foraging behavior, as seen in a nocturnal lizard, *Goniurosaurus kuroiwae kuroiwae*. *Journal of Natural History* 40: 439-459.
- Whiting, M. J. 2007. Foraging mode in the African Cordylids and plasticity of foraging behavior in *Platysaurus broadleyi*. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, ed. S. M. Reilly, L. D. McBrayer, and D. B. Miles. pp 405-426. Cambridge University Press. Cambridge, UK.

Table 1.1: Sample characteristics of focal observations made during the breeding and post-breeding seasons. Mean focal duration and mean time the lizard was not visible during the focal are presented ± 1 SE. No significant differences existed among either seasons or sexes.

Season	n	Total			
		Number Foraged	Observation Time (min)	Focal Duration (min)	Time not Visible (sec)
Breeding	69	33	935.05	13.55 \pm 0.02	17.73 \pm 4.46
Female	33	17	455.05	13.73 \pm 0.28	22.70 \pm 6.44
Male	36	16	480	13.33 \pm 0.26	13.17 \pm 6.17
Post-breeding	63	23	864.68	13.73 \pm 0.11	24.48 \pm 7.45
Female	30	9	417.42	13.91 \pm 0.16	30.00 \pm 10.84
Male	33	14	447.27	13.56 \pm 0.16	19.46 \pm 10.34
Total	132	56	1799.73	13.63 \pm 0.11	20.95 \pm 4.24

Table 1.2: List of behaviors performed by *Sceloporus woodi* during filmed continuous Focal observations.

Behavior	Definition
Display	State of sexual/territorial display in which the front legs are fully extended, raising the front of the body off of the substrate and then the body is lowered or the head is quickly and repeatedly moved down and up.
Move	State of locomotion of the animal from one point to another that is >0.5 body lengths.
Jump	State of locomotion when all limbs are elevated off of the substrate while rapidly moving from one point to another, often from one structure substrate to another.
Stationary	State of occupying a single space for >1 second.
Not Visible	State in which lizard is out of view of the observer.
Attack	Event in which lizard attempts to capture prey item using either tongue or jaw prehension. Only includes actual strike on prey.
Head move	Event in which position of the head changes relative to the body.
Lick substrate	Event in which tongue protruded from mouth to touch substrate.
Lunge	Event in which body quickly pushed forward <0.5 body lengths and only front legs change position if any move at all.
Postural adjustment	Event in which position of body portions changes relative to other portions of the body (i.e. move pectoral girdle closer to pelvis) without locomotion.
Scratch	Event in which the foot is rubbed rapidly and repeatedly across the surface of body.
Other	Other rare behavior not explicitly defined including tail movements, wipes of head on the substrate, processing prey, and "yawns".

Table 1.3: Frequencies of behaviors that occurred one (Lag 1), two (Lag 2), and three (Lag 3) steps before an attack on prey for each sex within each season.

Breeding Season		Lag 1		Lag 2		Lag 3		Male		Lag 1		Lag 2		Lag 3		
Behavior	Overall Frequency	Observed Frequency	ϕ	Observed Frequency	ϕ	Observed Frequency	ϕ	Overall Frequency	Observed Frequency	ϕ	Observed Frequency	ϕ	Observed Frequency	ϕ	Observed Frequency	ϕ
Adjust Posture	0.091	0.027	-0.066	0.063	-0.030	0.063	-0.027	0.084	0.024	-0.072	0.082	0.004	0.059	-0.027	0.059	-0.027
Attack	0.085	0.214*	0.142	0.223*	0.151	0.188*	0.115	0.104	0.247*	0.153	0.329*	0.233	0.212*	0.112	0.212*	0.112
Display	0.011	0.000	-0.031	0.000	-0.031	0.009	-0.003	0.085	0.012	-0.087	0.000*	-0.099	0.094	0.018	0.094	0.018
Jump	0.015	0.000	0.008	0.009	-0.014	0.018	0.009	0.013	0.024	0.033	0.012	-0.001	0.012	-0.036	0.012	-0.036
Lunge	0.014	0.134*	0.322	0.009	-0.011	0.045*	0.085	0.011	0.106*	0.319	0.012	0.006	0.024	0.047	0.024	0.047
Move	0.076	0.107	0.039	0.054	-0.023	0.116	0.049	0.097	0.141	0.057	0.035	-0.064	0.047	-0.051	0.047	-0.051
Move Head	0.546	0.402	-0.095	0.518	-0.022	0.446	-0.071	0.362	0.376	0.002	0.353	-0.004	0.471	0.075	0.471	0.075
Not Visible	0.013	0.000	-0.034	0.045*	0.089	0.009	-0.009	0.013	0.000	-0.039	0.000	-0.038	0.000	-0.038	0.000	-0.038
Other	0.026	0.027	0.004	0.000	-0.049	0.036	0.022	0.035	0.012	-0.041	0.000	-0.062	0.000	-0.062	0.000	-0.062
Pause	0.101	0.063	-0.037	0.080	-0.018	0.071	-0.026	0.151	0.047	-0.094	0.141	0.006	0.059	-0.077	0.059	-0.077
Scratch	NA	NA	NA	NA	NA	NA	NA	0.002	0.012	0.057	0.000	-0.016	0.012	0.066	0.012	0.066
Tongue Flick	0.011	0.009	-0.006	0.000	-0.032	0.000	-0.032	0.026	0.000	-0.054	0.012	-0.026	0.000	-0.052	0.000	-0.052
Post Breeding Season		Lag 1		Lag 2		Lag 3		Male		Lag 1		Lag 2		Lag 3		
Behavior	Overall Frequency	Observed Frequency	ϕ	Observed Frequency	ϕ	Observed Frequency	ϕ	Overall Frequency	Observed Frequency	ϕ	Observed Frequency	ϕ	Observed Frequency	ϕ	Observed Frequency	ϕ
Adjust Posture	0.077	0.129	0.034	0.097	0.010	0.097	0.016	0.070	0.038	-0.035	0.051	-0.019	0.025	-0.007	0.025	-0.007
Attack	0.042	0.129	0.089	0.065	0.021	0.000	-0.043	0.075	0.089	0.005	0.165	0.086	0.304*	0.245	0.304*	0.245
Display	0.008	0.000	-0.019	0.000	-0.019	0.032	0.052	0.019	0.000	-0.039	0.013	-0.012	0.000	-0.039	0.000	-0.039
Jump	0.011	0.097*	0.176	0.032	0.044	0.000	-0.021	0.007	0.025	0.066	0.013	0.022	0.013	0.022	0.013	0.022
Lunge	0.007	0.129*	0.316	0.000	-0.017	0.000	-0.017	0.040	0.494*	0.666	0.013	-0.038	0.089	0.074	0.089	0.074
Move	0.062	0.226*	0.145	0.129	0.060	0.065	-0.004	0.042	0.076	0.050	0.025	-0.022	0.013	-0.041	0.013	-0.041
Move Head	0.653	0.258	-0.173	0.516	-0.059	0.645	-0.001	0.593	0.241*	-0.204	0.557	-0.020	0.354	-0.142	0.354	-0.142
Not Visible	0.019	0.000	-0.029	0.097*	0.121	0.032	0.016	0.008	0.000	-0.025	0.000	-0.025	0.038*	0.102	0.038*	0.102
Other	0.019	0.000	-0.029	0.000	-0.029	0.032	0.022	0.056	0.025	-0.038	0.089	0.041	0.127*	0.091	0.127*	0.091
Pause	0.088	0.032	-0.040	0.065	-0.016	0.097	0.010	0.072	0.000	-0.079	0.076	0.007	0.000	-0.079	0.000	-0.079
Scratch	NA	NA	NA	NA	NA	NA	NA	0.003	0.000	-0.015	0.000	-0.015	0.000	-0.015	0.000	-0.015
Tongue Flick	0.003	0.000	-0.012	0.000	-0.011	0.000	-0.011	0.002	0.013	0.071	0.000	-0.012	0.000	-0.012	0.000	-0.012

Behavior = behavior scored

Overall frequency = frequency of each behavior observed during the focal for each season-sex combination

Observed frequency = frequency of occurrence of the behavior scored preceding an attack on prey

ϕ = coefficient of correlation; values approaching 1.0 indicates strong relationship; (+) values indicate behaviors that are likely to precede an attack on prey while (-) values indicated those behaviors which likely will not precede an attack on prey

* indicates sequence occurs at a frequency significantly different from random at $\alpha = 0.05$

Table 1.4: Mean \pm SE stomach content variables of male and female *S. woodi* during the breeding and post-breeding season.

Season	n	Volume (ml)	# Prey Items	# Prey Types
Breeding	52	0.24 \pm 0.03	15.79 \pm 2.09	3.02 \pm 0.18
Female	25	0.33 \pm 0.03	17.60 \pm 3.23	3.88 \pm 0.39
Male	27	0.16 \pm 0.03	14.11 \pm 2.72	2.22 \pm 0.24
Post-breeding	58	0.021 \pm 0.02	13.95 \pm 2.58	2.97 \pm 0.18
Female	28	0.20 \pm 0.03	10.75 \pm 2.29	2.93 \pm 0.26
Male	30	0.22 \pm 0.03	15.20 \pm 4.53	3.00 \pm 0.24
Total	110	0.22 \pm 0.02	14.35 \pm 1.68	2.99 \pm 0.15

Table 1.5: Total numbers and volumes of the most important prey types consumed by all individuals that were stomach flushed in the breeding and post-breeding seasons.

	Female		Male	
	Total volume			
Breeding Season	Total Number	(ml)	Total Number	Total volume
Ants	300.00	2.88	352.00	2.53
Beetles	16.00	0.96	7.00	0.42
Beetle Larvae	8.00	0.46	4.00	0.23
Grass Hoppers	6.00	0.55	5.00	0.40
Spiders	19.00	0.98	6.00	0.72
Percent of Total	87.03	66.86	92.80	77.03
Post-breeding Season				
Ants	172.00	2.20	268.00	2.60
Beetles	16.00	0.71	23.00	0.94
Beetle Larvae	31.00	0.20	10.00	0.92
Grass Hoppers	13.00	1.70	3.00	0.20
Spiders	13.00	0.80	11.00	0.74
Percent of Total	81.67	68.54	82.03	59.66

Figure 1.1 Movement patterns (A & B) and foraging behavior (C & D) compared among seasons and sexes. Data are presented as means (± 1 SE). Within each panel columns with different numbers of asterisks are significantly different (Kruskal-Wallis 2-way ANOVA). Only AWS was significantly different among seasons and sexes. Females moved before attacking prey more often than males. Lizards took more prey from stationary posts during the breeding season. Panels A & B include 132 focal observations, panels C & D include the 56 focal observations in which lizards attacked prey.

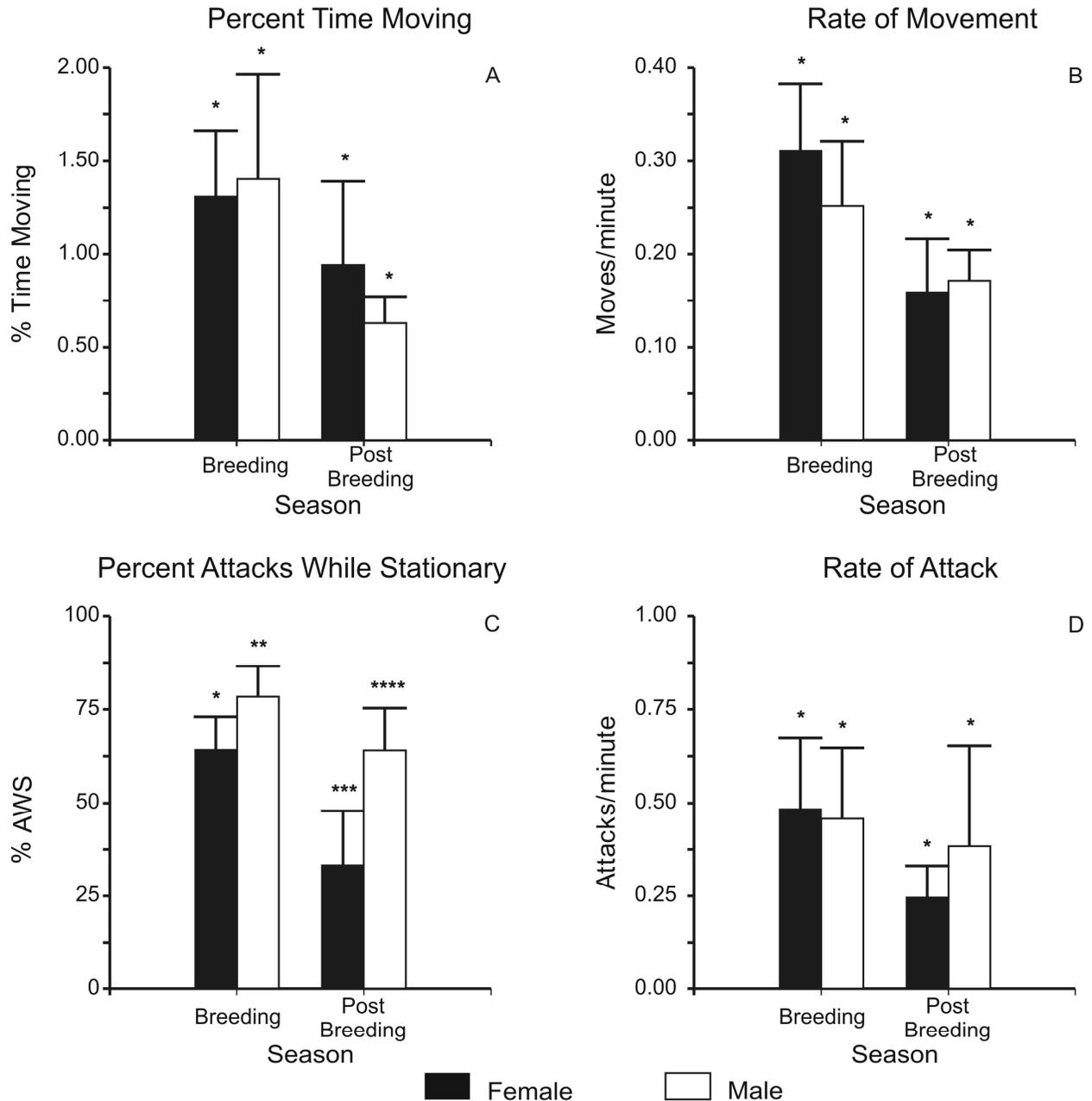
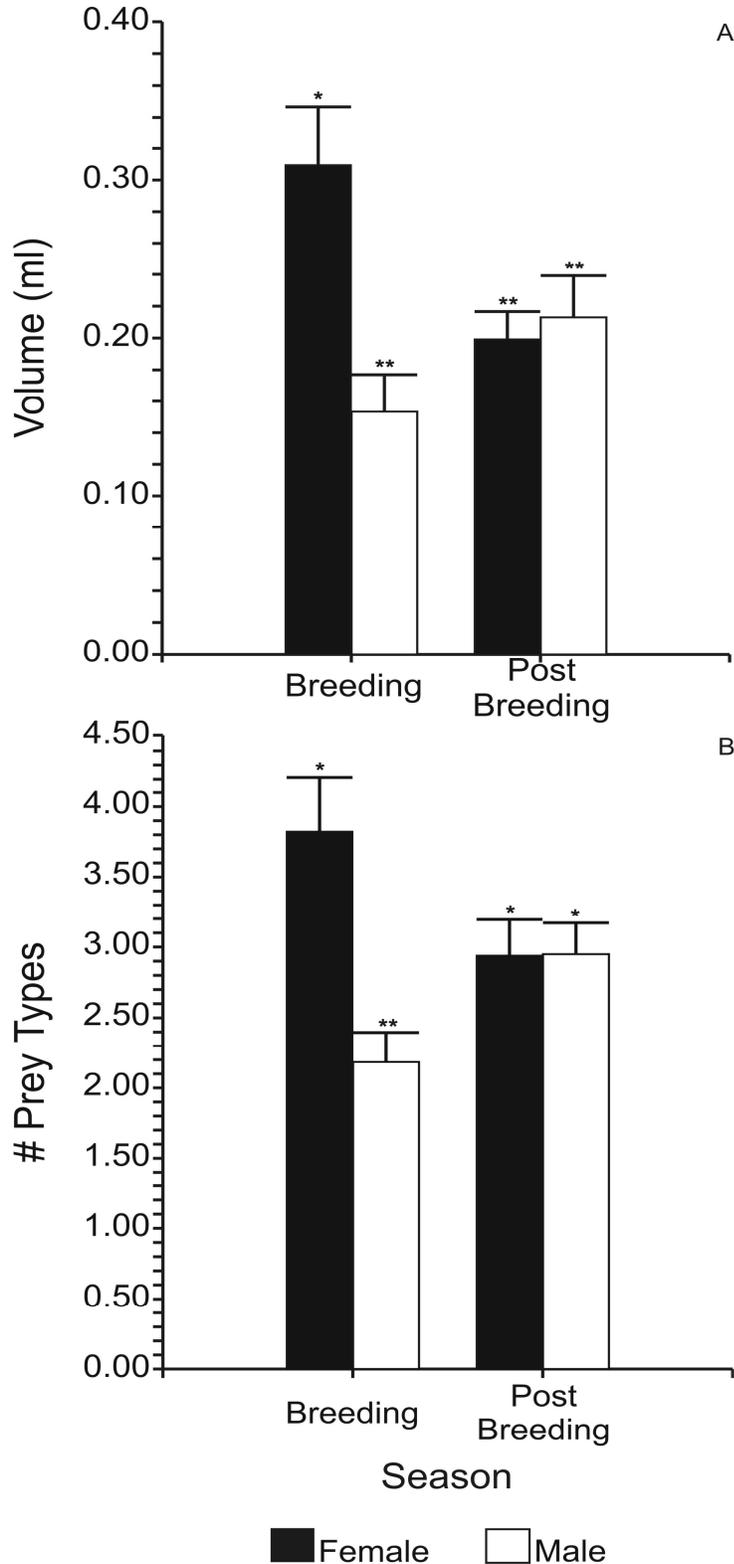


Figure 1.2 Characteristics of stomach contents compared among seasons and sexes. Data are presented as means (± 1 SE). Within each panel columns with different numbers of asterisks are significantly different (Kruskal-Wallis 2-way ANOVA). Females consumed significantly larger volumes of prey and more prey types during the breeding season. Females consumed significantly lower volumes of prey during the post breeding season. Males consumed significantly more types of prey during the post breeding season.



Chapter 2

Characteristics of the Florida scrub lizard (*Sceloporus woodi*) in a long-leaf pine island habitat

Abstract

Habitats with different structures provide individuals with different microhabitat options which expose them to different abiotic (thermal environments) and biotic stresses (risk of parasitism, prey availabilities, competition). Consequently the structure of the habitat occupied by a population of lizard has a great deal of influence on the processes which determine behavioral and morphological phenotypes. Thus habitat structure may play an important role in generating intraspecific variation. *Sceloporus woodi* in the Ocala National Forest inhabits sand-pine scrub and long-leaf pine island habitats which differ in vegetation structure and composition. Little is known about the ecology of *S. woodi* in long-leaf pine islands. In the present study I describe microhabitat use, behavior, diet, ectoparasite load, and morphology of *S. woodi* in a long-leaf pine island in comparison to *S. woodi* in scrub habitats in the Ocala National Forest in Florida. Microhabitat use was significantly different among habitats. Lizards at the pine island site used trees most often while lizards in the scrub used terrestrial habitats. Foraging behavior was similar between habitats, but lizards did move their heads more often at the pine island site. At the pine island site lizards had significantly lower body temperatures, consumed less diverse prey, and had lower ectoparasite loads than lizards at scrub sites. Also, the more arboreal lizards in the long leaf pine had longer limbs. Interestingly, only females differed in body shape. The differences in ecology between *S. woodi* in the pine island and scrub habitats may be due to differences in the vegetation structure of the two habitats, but further research is needed to elucidate the consequences of such variation.

Introduction

The Florida scrub lizard (*Sceloporus woodi*) is a small iguanid endemic to xeric scrub habitats in central and coastal Florida (Jackson 1973). Much of Florida's scrub habitat has been lost to urban expansion and conversion to agriculture (McCoy and Mushinsky 1992; Clark *et. al.* 1999; Hokit and Branch 2003). The largest remaining contiguous area of Florida scrub is in the Ocala National Forest (ONF) where *S. woodi* thrives along the edges of mature and young sand pine (*Pinus clausa*) scrub forests (henceforth 'scrub') created during large scale disturbances (*e.g.* stand clearing fires or clear cutting; Laessle 1958; Myers 1990; Greenberg 2003; Tiebout and Anderson 1997; Fabry 2007). While *S. woodi* most commonly uses the relatively ephemeral scrub it can also be found throughout isolated long leaf pine–turkey oak (*Pinus palustris* – *Quercus laevis*) sand hill forests (henceforth 'pine island') in the ONF (Jackson 1973). A great deal is already known about *S. woodi* biology, however most of the research to date has focused on populations of this species in scrub habitat (Jackson 1972, 1973; Jackson and Telford 1974; DeMarco 1989; DeMarco 1992; McCoy and Mushinsky 1992; Tiebout and Anderson 1997, 2001; Hokit *et. al.* 1999; Clark *et. al.* 1999; Hokit and Branch 2003; Branch *et. al.* 2003; Greenberg 2003) and no effort has been made to compare the ecology of *S. woodi* in the pine island habitat.

Although both scrub and pine island habitats are similar xeric, pine dominated habitats with sandy soil, they are unique and differ markedly in vegetation structure and ecology (Laessle 1958). The scrub habitats most populations of *S. woodi* occupy in the ONF (Tiebout and Anderson 1997; Fabry 2007) consist of a dense scrubby sand pine forest bordered by a recently cleared (naturally or anthropogenically) and regenerating scrub. The mature forest has a dense canopy dominated by sand pine, a crowded understory of large evergreen shrubs, and ground covering of lichens and debris (Laessle 1958; Myers 1990; Greenberg 2003). The regenerating scrub provides the open sand preferred by *S. woodi* (Tiebout and Anderson 2001; Hokit and Branch 2003) between woody shrubs (mostly scrub oaks *Quercus chapmanii*, *Quercus geminate*, and *Quercus myrtifolia*) and palmettos (*Serenoa repens* and *Sabal etonia*) (Greenberg 2003). *Sceloporus woodi* primarily utilizes the edge between the two seral stages (Fabry 2007). Historically sand pine scrub was maintained in a matrix of uneven aged stands by high intensity stand clearing fires which occurred every 10-20 years (Myers 1990). Individuals of *S. woodi* colonize the newly created edges from other nearby young stands, thrive while the sand pine canopy is regenerating and patches of open sand are abundant, and then decline as the canopy closes in and shrubs expand to cover exposed sand (Hokit *et. al.* 1999; Fabry 2007).

Pine island sand hills in the ONF are relic forest stands left behind following sea level changes during the Pliocene and Pleistocene eras (Myers 1990). These forests consist of an overstory of widely spaced long leaf pine trees interspersed with turkey oak with an understory of clump grasses (mostly wire grass *Aristida stricta*), forbs, and a few woody shrubs with patches of exposed sand between plants (Laessle 1958; Myers 1990). To maintain its open structure and diversity, frequent, low intensity, prescribed fires are applied to pine islands to reduce the understory growth and mimic the historical fire cycle (Litt *et. al.* 2001). *Sceloporus woodi* can be found throughout the pine island forest (*personal observation*) and presumably has a fairly stable population.

Habitats with different physical structures (e.g. distribution of vegetation, amount and type of ground cover, and other physical attributes) provide individuals with different microhabitat options which expose them to different abiotic (thermal environments; Adolph and Porter 1993, 1996; Anderson 2007) and biotic stresses (risk of mite infestation; Clopton and Gold 1993; Baldwin 1999; prey availabilities; Durtsche 1995; Smith 1998; Anderson 2007). Consequently the structure of the habitat lizards occupy has a great deal of influence their biology (Smith and Ballinger 2001 and references therein). The conditions lizards experience in different habitat types has been shown to influence important ecological aspects of lizard biology such as physiology (Huey 1991), locomotion (Pounds 1988; Losos 1990; McElroy 2007; Melville 2007), morphology (Williams 1972; Harmon *et. al.* 2005; Calsbeek *et. al.* 2007) and behavior (Karasov and Anderson 1984; Martin and Lopez 1995; Cooper 2005; Asbury and Adolph 2007; Johnson *et. al.* 2008). Given this, it seems likely that *S. woodi* inhabiting pine island habitats may differ from their counterparts in the scrub in some of the same aspects.

The purpose of this study is to quantify the microhabitat use, behavior, diet, mite load, and morphology of a population of *S. woodi* inhabiting pine island habitat as compared to populations in scrub habitats.

Methods

Study Site and Timing

Populations of *Sceloporus woodi* inhabiting pine island and scrub (scrub) habitats in the Ocala National Forest, Marion County, Florida were observed during the 2008 activity season. The ONF encompasses 383,000 acres along the Mount Dora sand ridge. During a complimentary study (Chapter 1), some aspects of the feeding behavior of *S. woodi* were observed to differ between the reproductive and non-reproductive seasons. The characteristics of male and female diets were also observed to differ markedly during the breeding season, but not

in the post-breeding season. Consequently, I restricted analysis of microhabitat use, behavior, and diet to the post-breeding season (August to October) so that variation related to the habitat could be isolated from other effects. Morphological data were collected over the entire activity season (Mid March to October) because overall morphological patterns likely do not vary over such a short time period.

One major pine island site and three scrub sites were used. Kerr Island (KI) is a relic long leaf pine forest in the northern portion of the ONF (29°21.811'N 081°49.989'W). The scrub stands were located in 1-3 year old clear cuts southern and central portions of the ONF (Site 1 (near Mill Dam): 29°10.197'N 081°47.898'W; Site 2 (near FS 13) 29°09.403'N 081°46.609'W; Site 3 (near Blue Sink); 29°03.799'N 081°41.22'W). Three scrub sites and one long leaf pine site were used because individual scrub sites presented less searchable area than the long leaf pine site. All measurements from the scrub sites were pooled because previous studies revealed minimal variation in habitat structure between individual stands (Laessle 1958; Fabry 2007).

Microhabitat Use

The microhabitat use of 174 (76 in the long leaf pine; 98 in the scrub) individual *S. woodi* was recorded. I recorded the substrate type occupied by lizards encountered while slowly moving through habitat. Half of the lizards were captured for measurement, dietary analysis and marking. Marked lizards were only included once in all analyses. For non-captured and non-marked lizards, I attempted to only use those individuals which were observed in sites where lizards had not previously been observed. For the lizards I captured (n = 87), I measured body temperature using a cloacal thermometer within 30 seconds and recorded the temperature of perch substrate using an infrared thermometer within 5 minutes. Air temperature was measured using a quick read thermometer held one meter above the ground. The temperature of each substrate type in shade and sun was measured in the immediate vicinity of lizards filmed for behavioral analysis. The perch height and circumference, when appropriate, were also recorded for captured lizards.

Behavior

I video recorded the behavior of 63 lizards (n = 32 in long leaf pine; n = 31 in scrub) for 15 minutes in order to analyze the behavior *S. woodi* in the pine island and scrub. Behaviors were transcribed from the videos. The complete methodology and definitions of behaviors are described in chapter 1. From the transcribed behaviors I calculated rates of movements (MPM), rate of attacks on prey (APM), postural adjustments (PAPM), and head moments (HMPM). I

also calculated the proportion of time lizards spent moving (PTM) and the proportion of attacks on prey made while the animal was stationary (AWS). Only the individuals that attacked prey during filmed focal observations (n = 23) were used to calculate APM and AWS.

Prey Consumption

Diet was assessed via analysis of stomach contents collected from 74 lizards (n = 35 in pine island; n = 39 in scrub). I collected stomach contents using stomach flushing (Legler and Sullivan 1979; Pietruszka 1981). Stomach flushing allowed me to collect stomach contents without harming any lizards. Upon collection, stomach contents were stored in 70% ethanol. I sorted prey items by type and measured volume by liquid displacement. Prey types correspond to taxonomic order except for Lepidoptera and Coleoptera which have distinct larval and adult forms and Hymenoptera because ants are mostly terrestrial while the rest of the order is comprised of mostly winged forms. I compared number of prey items in gut, number of prey types in gut, and volume of stomach contents between habitats. I also calculated Shannon's diversity (H) and evenness (J) indices for the stomach contents of lizards captured in each habitat.

Morphology

External morphology was quantified for a large sample of lizards from each habitat. Since lizards using different microhabitats might be exposed to different foraging opportunities and hence move in different ways (i.e. climbing vs. running on flat ground), I measured 11 features associated with feeding and locomotion. Using dial calipers and a ruler I measured snout to vent length (SVL), head length (HL), head height (HH) and head width at the orbit (HW), width of the pectoral girdle (PCW), width of the pelvic girdle (PVW), intergirdle length (IGL), femur length (FL), tibia length (TL), hind foot length (HFL), the length of the longest hind toe (HTL), and tail length (51 mutilated animals were excluded). To quantify variation in body size between the two habitats, SVL was compared (n = 80 lizards from pine island, n = 112 in scrub). A subset of this sample (140 lizards; 58 from pine island, 83 from scrub) was used to quantify variation in the 11 features of body shape. Since males and females show significant sexual size dimorphism (Jackson 1973), all analyses of morphology were conducted separately for males and females.

Ectoparasite Load

Ectoparasitic mites (*Eutrombicula sp.*) were counted on 78 lizards (n = 38 in pine island; n = 40 in scrub) captured in the post-breeding season. I only assessed mite load in the post-breeding season because of the potential confounding effects of intersex differences during the

breeding season (Klukowski and Nelson 2001). I examined lizards for the presence of mites and counted the mites using a 10X jeweler's lens. Mites were most abundant behind the auricular openings on either side of the lizard's head and in the posterior side of the hind limb.

Statistical Analyses

Air and substrate temperatures were compared between habitats using standard t-tests. Body temperatures were compared between habitats using standard t-tests. I used a Chi square test of a 2 x 5 contingency table to determine if *S. woodi* uses different substrates in pine island and scrub. Perch height and circumference were compared using non-parametric Mann-Whitney U tests. Behavioral variables were compared using the Sheirer-Ray-Hare extension of Kruskal-Wallis test (non-parametric 2-way ANOVA; Sokal and Rohlf, 1995) using sex and habitat as grouping factors. I took sex into account when analyzing behavior because I wanted to reduce any confounding effects of sex on comparisons of behavior between habitats. Diet variables were compared between habitat types using Mann-Whitney U tests. Morphological variables were corrected for size by using the residuals of linear regressions of the 11 log transformed measurements on log SVL for all analyses. Principle components analysis was used to condense the 11 size corrected shape variables into 3 major axes that described variation in body shape of females and males respectively. The scores of the three principle components were used in comparisons between habitats using t tests. SVL was compared between habitats using Mann-Whitney U-tests. I used two-way analysis of variation with habitat and sex as dependent variables to determine if mite load differed between habitats while taking potential sexual differences into account. All statistical analyses were carried out using JMP 4.0.

Results

Perch Use

Patterns of microhabitat use differed between the pine island and scrub habitats. The substrate type used most often by *S. woodi* is contingent upon the major habitat type occupied by a population ($X^2_{(4, 0.05)} = 35.143$; $p < 0.0001$). Of the lizards I observed in the pine island, 61.84% were on trees, 14.47% were on downed wood, 14.47% were on sand, and 9.21% were on leaf litter (Fig. 2.1). In the scrub habitat 35.71% of lizards were observed on sand, 28.57% were observed on debris, 20.41% were observed on trees, 14.08% were observed on downed wood, and 1.02% (1 individual) were observed in shrubs (Fig. 2.1). Though *S. woodi* in the pine island perched on trees more often than in scrub, lizards that did perch on trees in scrub perched significantly higher than lizards in the pine island ($U = 414.5$; $p_{(0.05)} = 0.007$; Fig. 2.3). However the trees *S. woodi* used in the pine island were significantly larger in circumference ($U = 438$;

$p_{(0.05)} < 0.0001$; Fig. 2.2). Interestingly, all lizards observed perching on trees in the pine island used hardwood species while lizards in the scrub used sand pine.

Air temperature in the pine island was significantly cooler than in the scrub ($t_{df=81} = -3.77$; $p_{(0.05)} < 0.001$; Fig 2.3). There were no significant differences in substrate temperatures between habitats (Table 2.3). In both habitats, debris was the warmest substrate in the sun and downed wood was the warmest substrate in the shade (Table 2.3). In the pine island, trees were the coolest substrate in the sun. In scrub, both trees and sand were the coolest substrates in the sun (Table 2.3). In both habitat types, average temperature of all shaded substrate types were within 1°C of each other and debris and downed wood were the warmest substrates (Table 2.3). Lizards used significantly cooler perches in the pine island than in scrub habitats ($f_{(79)} = 5.04$; $p_{(0.05)} = 0.028$) and subsequently had significantly cooler body temperatures ($f_{(79)} = 4.56$; $p_{(0.05)} = 0.036$; Fig. 2.3).

Behavior

Patterns of behavior were similar between habitats. Lizards were sedentary and took half of their prey while stationary (Table 2.2). The only significant difference in behavior between habitats was that lizards in the pine island scanned the surrounding habitat (moved their head) more often than lizards in scrub ($t_{(61)} = 3.69$; $p_{(0.05)} < 0.001$; Table 2.2).

Prey Consumption

Individual t-tests showed little variation in the amount of prey consumed between habitats (Fig. 2.4). In both scrub and the pine island lizards consumed a similar number of prey items ($U = 861.5$; $p = 0.053$) and volume of prey consumed ($U = 786.5$; $p = 0.261$). However, lizards in the scrub consumed significantly more different types of prey ($U = 885$; $p = 0.028$; Fig. 2.4). Diets were more diverse and even in the scrub ($H = 2.84$, $J = 0.91$) than in the pine island ($H = 1.61$; $J = 0.57$). A total of 23 different types of prey were consumed by lizards in scrub and 17 types consumed in the pine island. Ants made up the majority of prey items consumed in both scrub and the pine island, but were considerably more important in the pine island than in scrub; ants comprised 74.26% of the prey items consumed (46.63% by volume) in the pine island versus 50.17% of the prey items consumed (12.32% by volume) in scrub. Volumetrically the same prey types were important in both habitats (Table 2.3).

Morphology

Only females showed significant body shape differences between habitats. Mann-Whitney U tests of SVL between habitats revealed that females in scrub habitats are significantly larger than in the pine island ($U = 1222.5$; $p = 0.005$) but showed no significant interhabitat

differences in male SVL ($U = 1574.5$; $p = 0.170$; Fig. 2.5). For females, the three major axes described head shape (PC 1), hind limb length and tail length (PC 2), and a positive relationship between IGL and FL (PC 3; Table 2.4). Male characters loaded very similarly on the three major axes with PC1 describing hind limb length, PC2 describing head shape, and PC3 describing an inverse relationship between PCW and both IGL and tail length (Table 2.4). None of the principle component axes describing male morphology differed between habitats (Table 2.5; Fig. 2.6). Females only differed in PC 2 between habitats with lizards in the pine island scoring significantly higher along the axis than lizards in scrub (Table 2.5; Fig. 2.6). In the scrub lizards tended show greater diversity in morphology than in the pine island (Fig. 2.6)

Mite Load

Two way ANOVA of mite load between sexes and habitats revealed no significant interaction ($F_{(1)} = 1.21$; $p_{(0.05)} = 0.276$) and no significant sexual differences ($F_{(1)} = 1.45$; $p_{(0.05)} = 0.232$). However, significant interhabitat differences did exist in mite load ($F_{(1)} = 73.36$; $p_{(0.05)} < 0.0001$). The average number of mites infesting 38 lizards in the pine island was 9.39 ± 6.05 and 50.95 ± 5.89 infesting 40 lizards in scrub (Fig 2.7).

Discussion

Microhabitat use of *S. woodi* is dependent upon the major habitat type occupied by an individual. Microhabitat use by *S. woodi* in scrub habitats is consistent with previous reports (Jackson 1972; Tiebout and Anderson 2001). Lizards most often occupy terrestrial sites and used sand more often than other substrates. In the scrub, *S. woodi* uses open sand near large woody shrubs (the dominant vegetation; Myers 1990) because shrubs provide refugia from predators and thermal extremes. The sandy open areas are important for foraging and social interactions. The structure of scrub habitat consists of a mosaic of large patches of sand interspersed between large woody evergreen shrubs (mostly scrub oak). *S. woodi* feeds heavily on ants (Jackson 1972; *personal observation*) which nest in the open patches in scrub (DeMers 1993; Burrow *et. al.* 2001; *personal observation*). Consequently lizards spend much of their time on open sand foraging on ants. However such exposure puts individuals at risk of predation or thermal stress. Shrubs provide lizards with refuge from which to scan open patches of sand for prey and to retreat to in order to avoid predators and thermal extremes. Indeed many of the lizards sighted in scrub habitats were either underneath the edge or within a short distance of a shrub and would run to the shrub for cover upon my approach. Another benefit is that the shrubs serve as another source of prey since many arthropods inhabit the foliage and litter underneath shrubs (Durtsche 1992, 1995). This effectively allows *S. woodi* to continue foraging

through midday when high ambient and soil temperatures make venturing into the open dangerous.

While trees are abundant in the scrub (mostly sand pines), they are tightly clustered within the mature forest which borders young open stands of regenerating scrub. Suitable warm microhabitats are not available in mature forests (Tiebout and Anderson 1997; Fabry 2007), although the dense edges provide deep shade during the warmest portion of the day. Larger trees at the scrub edge are appealing to *S. woodi* during the warmest times of day because they are cooler than the sandy substrate, yet are still near *S. woodi*'s field active body temperature ($\approx 36^{\circ}\text{C}$). This pattern of use of arboreal perches during high ambient temperatures was observed in this study and in earlier work (Tiebout and Anderson 2001).

Conversely in the pine island, *S. woodi* occupied trees more often than terrestrial areas. The trees in the pine island provide *S. woodi* with larger useable microhabitat than can be found in open sand on the ground. The ground in the pine island is a mosaic of small patches of open sand separated by clumps of bunch grasses (mostly wire grass) which offer poor refuge from thermal extremes and predators (Burrow *et. al.* 2001; Green *et. al.* 2001; Tchabovsky *et. al.* 2001; Smith and Ballinger 2001). Consequently clumps of grass in the pine island hamper lizards' ability to flee from predators, especially highly maneuverable aerial predators (Burrow *et. al.* 2001). The tightly spaced grasses also obstruct lizards' view of the habitat, reducing their ability to detect potential prey and predators (Jackson 1972; Green *et. al.* 2001). Elevated perches provide lizards a better vantage point to scan for prey on the bole of the tree and on the ground. Tiebout and Anderson (2001) attributed the preference of open sand in *S. woodi* to thermoregulatory needs. Trees in the pine island provide a thermal environment similar to that of open sand while granting lizards easy access to refuge from both thermal extremes and predators on the opposite side of the tree. Interestingly all of the adult lizards observed on trees ($n = 47$) in the pine island used hardwoods over the long leaf pine. This could be due to the stickiness and toxic compounds found in long leaf pine sap that has been shown to adversely affect pine bark beetles and other reptiles such as rat snakes (*Elaphe spp.*) (Jackson and Telford 1974; Hodges *et. al.* 1979; Rudolph *et. al.* 1990; Conner and Rudolph 1995).

The most immediate consequence of the differences in *S. woodi*'s microhabitat use between pine island and scrub habitats is a difference in body temperature. Lizards in the pine island have significantly lower body temperatures than those in scrub. The body temperature differences likely reflect the differences in air temperature between habitats and in opportunities for thermoregulation throughout the day in conjunction with greater exposure of lizards perched

on trees to wind. Because lizards are ectotherms, they are very sensitive to different thermal environments and thus choose habitats conducive to thermoregulation (Adolph 1990; Huey 1991; Adolph & Porter 1993, 1996; Smith & Ballinger 2001; Asbury and Adolph 2007). Trees are self shaded during mid day and thus reduce heating in lizards perched on trees during the warmest part of the day (Huey 1991; Asbury and Adolph 2007). Wind is known to affect the thermoregulatory ability of some lizards (*e.g. Dipsosaurus dorsalis*; Weathers 1970). In scrub, shrubs act as wind breaks for lizards and thus may reduce the amount of evaporative cooling lizards experience (Weathers 1970) in comparison to *S. woodi* in the pine island which have no direct protection from wind. The net effect of the different conditions *S. woodi* experience in the two habitats results in the significant difference in mean body temperature (1.04 °C) mirroring the significant difference in air temperature (1.19 °C) and perch temperature (0.83 °C) between the two habitats. The differences in body temperature between habitats could result in different physiological performance capacities in individuals (Huey 1991) in these habitats but this remains to be tested.

Habitat structure has been shown to influence the behavior of some animals (Braña 1993, 2003; Smith and Ballinger 2001; Lima 1992; Mauer and Whitmore 1981; Adolph 1990; Tchabovsky *et. al.* 1991; VanderWerf 1994). In pine islands, *S. woodi* move their heads more often than lizards in scrub likely because the trees they perch on limit the amount of their immediate surroundings encompassed by their line of sight. Similarly, downy woodpeckers (*Picoides pubescens*) increase vigilance behaviors with increasing trunk size and potentially greater perceived risk (Lima 1992). In addition to predator detection, increased head movement by lizards in the pine island is likely also important for prey detection. Even though shrubs might obstruct some sight lines in scrub, lizards do not have to worry about threats or prey approaching from below their plane of vision. The cover offered by shrubs like in scrub have been shown to reduce vigilance in other species like the fat sand rat (*Psammomys obesus*) in the wadis of the Negev desert (Tchabovsky *et. al.* 2001).

The differences in dietary diversity between the pine island and scrub may be due to differences in prey availability. While shrubs in scrub provide access to essentially three sources of different prey (shrub, litter, open sand), trees in the pine island only offer *S. woodi* two sources (boles of trees and open sand) of very similar prey. In addition to providing lizards a place to scan open patches for ants, grasshoppers and other passing prey, shrubs in scrub harbor a unique community of arthropods in their foliage (Hemipterans, flies, spiders) and the litter underneath them (grubs, roaches, and spiders; Durtsche.1992, 1995) In contrast, the boles of

trees offer lizards a very similar array of prey as is available in open sand (e.g. ants, grasshoppers, beetles, and flying insects; Durtsche.1992, 1995; Izhaki *et. al.* 2003). The reduced diversity of prey available to *S. woodi* in the pine island observed here may be due to fire; the site was burned at the beginning of the study (16 February 2008). Low intensity fires in long-leaf pine sand-hills kill soil arthropods reducing arthropod diversity and abundance on the ground leaving trees as reserves of potential prey for *S. woodi* following burns (Hanula *et. al.* 2003; Rieske-Kinney 2006). Ants which made up much of *S. woodi*'s diet are not adversely affected by fires in long-leaf pine forests, and some species actually show an increase in abundance immediately following fires (Pearse 1943; Izhaki *et. al.* 2003). Consequently the fire that burned through the pine island site may have had considerable influence on the dietary differences observed in *S. woodi* in this study. Dietary differences between scrub and pine island habitats may not be as pronounced in non-burn years.

Like dietary diversity, the difference in mite load between habitats is likely tied to fire regime of the habitats and microhabitat use in those habitats. The obvious reason for the lower mite loads in the pine island is that mites inhabit shaded leaf litter, a microhabitat which lizards do not use very often (Clopton and Gold 1993; Baldwin 1999; Klukowski and Nelson 2001; Klukowski 2004). Additionally, frequent managed burning of pine islands reduces litter and the number of large shrubs, so even when lizards do occupy terrestrial substrates they are not exposed mites (Baldwin 1999; Klukowski and Nelson 2001; Klukowski 2004). The higher mite loads *S. woodi* encounters in the scrub could impose a physiological burden on lizards (Baldwin 1999; Klukowski & Nelson 2001). In the lizard *Lacerta vivipara*, high ectoparasite loads have been shown to increase maternal investment at first reproduction (Sorci & Clobert 1995). This was interpreted to be a mechanism to mitigate the detrimental effects of parasitism on fecundity (Moller 1990; Sorci and Clobert 1995). If ectoparasite load affects life history the same way in *S. woodi*, the differences in ectoparasite load between scrub and pine island habitat may also lead to differences in life history between habitats. *Sceloporus woodi* in the scrub and pine island presents an opportunity to explore the effects ectoparasites have on a species of lizard that inhabits different habitats

The differences body size and limb length between habitats shows that the differences in ecology faced by *S. woodi* between habitat types are biologically important. As a result of morphological differences, *S. woodi* may subsequently differ in performance capabilities between habitats (Losos 1990; Garland and Losos1994; Garland 1999). Microhabitat has been shown to affect locomotion performance and subsequently select for different morphologies in

other groups of lizards (Arnold 1983; Losos 1990; Beutell and Losos 1999; McElroy *et. al.* 2007; Calsbeek and Irschick 2007). The longer limbs and smaller bodies of the pine island lizards may enhance climbing speed and agility on broad surfaces (Pounds 1988; Losos 1990). In contrast the larger individuals with a more generalized shape in the scrub may run well on open sand and be able to maneuver through the dense, thin stems and branches of shrubs (Pounds 1988; Losos 1990). However the fact that only females differ indicates that the selection pressures acting on *S. woodi* between habitats may be sex specific as has been suggested by other authors (Shine 2003; Butler *et. al.* 2000; Butler 2007; Lailvaux 2007). Consequently selection pressures on locomotion may be acting to differentiate female morphology between habitats (Losos *et. al.* 1994; Lailvaux 2007). The sexual patterns may be linked to ecological differences between the sexes due to reproduction (Trivers 1972; Butler *et. al.* 2000; Shine 2003; Lailvaux 2007). Further research incorporating more pine island sites and reproductive behavior would help elucidate the role of habitat structure in generating morphological diversity.

Habitat is known to have a myriad of ecological consequences for lizards (Smith and Ballinger 2001). However many of the previous studies of interpopulational variation in ecology of lizards have used populations living in different habitats separated by geography (Adolph and Porter 1993, 1996; Niewiarowski & Roosenburg 1993; Asbury and Adolph 2007) or have focused on thermal differences between habitats (Adolph 1990). The two habitat types occupied by *S. woodi* in the ONF differ in vegetation structure and composition (Laessle 1958; Myers 1990) but not major climatological patterns, geographic location, or altitude. Even the herpetofaunal community is similar between the two habitats (Greenberg 2002). The differences in microhabitat use, body temperature, behavior, diet, ectoparasite load, and morphology highlighted here demonstrate that differences in habitat structure between scrub and pine island may affect the ecological pressures faced by populations in different habitats. The differences in morphology show that differences in ecology between the two habitats have the potential to drive population divergence (Pounds 1988; Smith and Ballinger; Cooper 2005; Calsbeek *et. al.* 2007; Irschick *et. al.* 2007 Johnson *et. al.* 2008). However the body shape differences between the habitats may only be a plastic response (Gothar & Nylin 1995). Understanding whether any genetic differences exist and the degree of gene flow between habitats would help clarify whether the morphological variation observed in *S. woodi* is simply a plastic response to differences in ecology between habitats or the result of long term selection. Future work investigating the relationships between the ecology of *Sceloporus woodi* in the ONF and habitat structure may help to better elucidate the role of habitat in phenotypic divergence.

References

- Adolph, S. C. 1990. Influence of Behavioral Thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71: 315-327.
- Adolph, S. C.; Porter, W. P. 1993. Temperature, activity, and lizard life histories. *The American Naturalist* 142: 273-295.
- Adolph, S. C.; Porter, W. P. 1996. Growth Seasonality and lizard life histories: age and size at maturity. *Oikos* 77: 267-278.
- Anderson, R. A. 2007. Food acquisition modes and habitat use in lizards: questions from an integrative perspective. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*, ed. S. M. Reilly, L. D. McBrayer, and D. B. Miles. pp 450-490. Cambridge University Press. Cambridge, UK.
- Arnold, S. J. 1983. Morphology, performance and fitness. *American Zoologist* 23: 347-361.
- Asbury, D. A.; Adolph, S. C. 2007. Behavioral plasticity in an ecological generalist: microhabitat use by western fence lizards. *Evolutionary Ecology Research* 9: 801-815.
- Baldwin, K. S. 1999. The effects of mites on the physiology and performance of the Florida scrub lizard (*Sceloporus woodi*). Unpublished Dissertation, University of Florida, Gainesville, FL .
- Bauwens, D.; Garland, T.; Castilla, A. M.; Van Damme, R. 1995. Evolution of sprint speed in Lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49: 848-863.
- Beutell, K, Losos, J. B. 1999. Ecological morphology of Caribbean Anoles. *Herpetological Monographs* 13: 1-28.
- Braña, F. 1993. Shifts in body temperature and escape behaviour of female *Podacris muralis* during pregnancy. *Oikos* 66: 216-222 .
- Braña, F. 2003. Morphological correlates of burst speed and field movement patterns: the behavioral adjustment of locomotion in wall lizards (*Podacris muralis*). *Biological Journal of the Linnean Society* 80: 135-146.
- Branch, L. C.; Clark, A.-M.; Moler, P. E.; Bowen, B. W. 2003. Fragmented landscapes, habitat specificity, and conservation genetics of three lizards in Florida scrub. *Conservation Genetics* 4: 199-212.
- Burrow, A. L.; Kazmaier, R. T.; Hellgren, E. C.; Ruthven III, D. C. 2001. Microhabitat selection by Texas horned lizards in southern Texas. *Journal of Wildlife Management* 65: 645-652.

- Butler, M. A. 2005. Foraging Mode of the chameleon, *Bradypodion pumilum*; a challenge to the sit and wait versus active forager paradigm. *Biological Journal of the Linnean Society* 84: 797-809.
- Butler, M. A. 2007. Vive le difference! Sexual dimorphism and adaptive patterns in lizards of the genus *Anolis*. *Integrative and Comparative Biology* 47: 272-284.
- Butler, M. A.; Schoener, T. W.; Losos, J. B. 2000. The relationship between sexual size dimorphism and habitat use in greater Antillean *Anolis* lizards. *Evolution* 54: 259-272.
- Calsbeek R.; Irschick D. J. 2007. The quick and the dead: Locomotor performance and natural selection in island lizards. *Evolution*. 61:2493–2503.
- Calsbeek, R.; Smith, T. B.; Bardeleben, C. 2007. Intraspecific variation in *Anolis sagerei* mirrors the adaptive radiation of Greater Antillean anoles. *Biological Journal of the Linnean Society* 90: 189-199.
- Clark, A. M.; Bowen, B. W.; Branch, L. C. 1999. Effects of natural fragmentation on an endemic scrub lizard (*Sceloporus woodi*): an historical perspective based on mitochondrial DNA gene genealogy. *Molecular Ecology* 8: 1093-1104.
- Clopton, R. E.; Gold, R. E. 1993. Distribution and seasonal and diurnal activity patterns of *Eutrombicula alfreddugesi* (Acari: Trombiculidae) in a forest edge ecosystem. *Journal of Medical Entomology* 30:47-53.
- Conner, R. N.; Saenz, D.; Rudolph, D. C.; Coulson, R. N. 1998. Southern pine beetle-induced mortality of pines with natural and artificial red-cockaded woodpecker cavities in Texas. *Wilson Bulletin* 110: 100-109.
- Cooper, W. E. 2005. Ecomorphological variation in foraging behavior by Puerto Rican *Anolis* lizards. *Journal of Zoology, London* 256: 133-139.
- Cummins, K. W.; Wuycheck, J. C. 1971. Caloric equivalents for investigations in ecological energetics. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 18: 1-158.
- Demarco, V. G. 1989. Annual variation in the seasonal shift in egg size and clutch size in *Sceloporus woodi*. *Oecologia* 80: 525-532.
- Demarco, V. G. 1992. Embryonic development times and egg retention in four species of *Sceloporine* lizards. *Functional Ecology* 6: 436-444.
- DeMers, M. N. 1993. Roadside ditches as corridors for range expansion of the western harvester ant (*Pogonomyrmex occidentalis* Cresson). *Landscape Ecology* 8: 93-109.
- Fabry, C. J. 2007. Spatiotemporal patterns of Florida scrub lizard abundance in young, regenerating Florida scrub. Unpublished Master's Thesis, Western Washington University, Bellingham, WA.

- Garland, T. 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour* 58: 77-83.
- Garland, T.; Losos, J. B. 1994. Ecological morphology of locomotor performance in Squamate reptiles. In *Ecological Morphology: Integrative Organismal Biology*, ed P. C. Wainwright and S. M. Reilly pp 240-302. University of Chicago Press, Chicago, IL, USA.
- Gothar, K.; Nylin, S. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74: 3-17.
- Green, G. A.; Livezey, K. B.; Morgan, R. L. 2001. Habitat selection by Northern Sagebrush Lizards (*Sceloporus graciosus graciosus*) in the Columbia Basin, Oregon. *Northwestern Naturalist* 82: 111-115.
- Greenberg, C. H. 2002. Fire, habitat structure and herpetofauna in the southeast. In: Ford, W.; Russell, K. R.; Moorman, C. E.; Proceedings: The role of fire for non-game wildlife management and community restoration: traditional uses and new directions. Newton Square, PA: US. Dept. of Agriculture, Forest Service, Northeastern Research Station GTR-NE-288 : 91-99.
- Greenberg, C. H. 2003. Vegetation recovery and stand structure following a prescribed stand replacement burn in sand pine scrub. *Natural Areas Journal* 23: 141-151.
- Hanula, J. L.; Franzreb, K. E.; Pepper, W. D. 2000. Longleaf pine characteristics associated with arthropods available for Red-cockaded woodpeckers. *The Journal of Wildlife Management* 64: 60-70.
- Hanula, J. L.; Wade, D. D. 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flat-woods ecosystems. *Forest Ecology and Management* 175: 163-184.
- Hodges, J. D.; Elam, W. W.; Watson, W. F.; Nebeker, T. E. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. *Canadian Entomology* 111: 889-896.
- Hokit, D. G.; Branch, L. C. 2003. Habitat patch size affects demographics of the Florida scrub lizard (*Sceloporus woodi*). *Journal of Herpetology* 37: 257-265.
- Hokit, D. G.; Smith, B. M.; Branch, L. C. 1999. Effects of landscape structure in Florida scrub: a population perspective. *Ecological Applications* 9: 124-134.
- Hudson, P. J.; Dobson, A. P.; Newborn, D. 1998. Prevention of population cycles by parasite removal. *Science* 282: 2256-2258.
- Huey, RB. 1991. Physiological consequences of habitat selection. *The American Naturalist* 137: S91-S115.
- Irschick D. J.; Garland T. Jr. 2001. Integrating function and ecology in studies of adaptation: Investigations of locomotor capacity as a model system. *Annual Reviews of Ecology and Systematics* 32:367-396.

- Irschick, D. J.; Ramos, M.; Buckley, C.; Elstrott, J.; Carlisle, E.; Lailvaux, S. P.; Bloch, N.; Herrel, A.; Vanhooydonck, B. 2006. Are morphology-performance relationships invariant across different seasons: A test with the green anole lizard (*Anolis carolinensis*). *Oikos* 114: 49-59.
- Irshick, D. J.; Losos, J. B. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean Anolis lizards. *Evolution* 52: 219-226.
- Izhaki, I.; Levey, D. J.; Silva, W. R. 2003. Effects of prescribed fire on an ant community in Florida pine savanna. *Ecological Entomology* 28: 439-448.
- Jackson, J. F. 1972. The phenetics of a narrow hybrid zone. *Evolution* 27: 58-68.
- Jackson, J. F. 1973. Distribution and population phenetics of the Florida Scrub Lizard, *Sceloporus woodi*. *Copeia* 1973: 746-761.
- Jackson, J. F.; Telford, S. R. 1974. Reproductive ecology of the Florida Scrub Lizard. *Sceloporus woodi*. *Copeia* 1974: 689-694.
- Johnson, M. A.; Leal, M.; Schettino, L. R.; Lara, A. C.; Revell, L. J.; Losos, J. L. 2008. A phylogenetic perspective on foraging mode evolution and habitat use in West Indian Anolis lizards. *Animal Behavior* 75: 555-563.
- Klukowski, M. 2004. Seasonal changes in abundance of host-seeking chiggers (Acari: Trombiculidae) and infestations on fence lizards, *Sceloporus undulatus*. *Journal of Herpetology* 38: 141-144.
- Klukowski, M.; Nelson, C. R. 2001. Ectoparasite loads in free-ranging northern fence lizards, *Sceloporus undulatus hyacinthinus*: effects of testosterone and sex. *Behavioral Ecology and Sociobiology* 49: 289-295.
- Laessle, A. M. 1958. The origin and successional relationship of sand-hill vegetation and Sand-pine scrub. *Ecological Monographs* 28: 361-387.
- Lailvaux, S. P. 2007. Interactive effects of sex and temperature on locomotion in reptiles. *Integrative and Comparative Biology* 47: 189-199.
- Lima, S. L. 1992. Vigilance and foraging substrate: anti-predatory considerations in a non-standard environment. *Behavioral Ecology and Sociobiology* 30: 283-289.
- Litt, A. R.; Provencher, L.; Tanner, G. W.; Franz, R. 2001. Herpetofaunal responses to restoration treatments of longleaf pine sand-hills in Florida. *Restoration Ecology* 9: 462-474.
- Lope, F.; Moller, A. P.; Cruz, C. 1998. Parasitism, immune response and reproductive success in the house martin *Delichon urbica*. *Oecologia* 114: 188-193.
- Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian Anolis lizards: an evolutionary analysis. *Ecological Monographs* 60: 369-388.

- Losos, J. B.; Irschick, D. J.; Schoener, T.W. 1994. Adaptation and constraint in the evolution of specialization of Bahamian Anolis lizards. *Evolution* 48: 1786-1798.
- Losos, J. B.; Sinervo, B. 1989. The effects of morphology and perch diameter on sprint performance of Anolis Lizards . *Journal of Experimental Biology* 145: 23-30.
- Maurer, B. A.; Whitmore, R. C. 1981. Foraging behavior of five bird species in two forests with different vegetation structure . *Wilson Bulletin* 93: 478-490.
- McCoy E. D.; Mushinsky H. R. 1992. Rarity of organisms in the sand pine scrub habitat of Florida. *Conservation Biology* 6: 537-548.
- McElroy, E. R.; Meyers, J. J.; Reilly, S. M.; Irshick, D. J. 2007. Dissecting the effects of behaviour and habitat on the locomotion of a lizard (*Urosaurus ornatus*). *Animal Behaviour* 73:359-365.
- Moller, A. P. 1990. Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. *Ecology* 71: 2345-2357.
- Myers, R. L. 1990. Scrub and high pine. In *Ecosystems of Florida* pp 151-193. University of Central Florida Press, Orlando, FL, USA.
- Niewiarowski, P. H.; Roosenburg, W. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* 74: 1992-2002.
- Pearlstine, E. V.; Thompson, D. B. 2004. Geographic variation in morphology of four species of migratory raptors. *Journal of Raptor Research* 38: 334-342.
- Pearse, A. S. 1943. Effects of burning over and raking off litter on certain soil animals in the Duke Forest. *American Midland Naturalist* 29: 406-424.
- Pounds, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland Anolis community. *Ecological Monographs* 58: 299-320.
- Rieske-Kinney, Lynne K. 2006. Do fire and insects interact in eastern forests . In: Dickinson, Matthew B., ed. 2006. *Fire in eastern oak forests: delivering science to land managers, proceedings of a conference; 2005 November 15-17; Columbus, OH. Gen. Tech. Rep. NRS-P-1. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 152-157.*
- Rudolph, D. C.; Kyle, H; Conner, R. N. 1990. Red-cockaded woodpeckers vs. rat snakes: the effectiveness of the resin barrier. *Wilson Bulletin* 102: 14-22.
- Shine, R. 2003. Locomotor speeds of gravid lizards: placing 'costs of reproduction' within an ecological context. *Functional Ecology* 17: 526-533.
- Siepielski, A. M.; DiBattista, J. D.; Carlson, S. M. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecology Letters* 12: 1261-1276.

- Smith, G. R.; Ballinger, R. E. 2001. The ecological consequences of habitat and microhabitat use in lizards: a review. *Contemporary Herpetology* 2001: 398-26.
- Smith, G. R. 1998. Habitat-associated life history variation within a population of the striped plateau lizard, *Sceloporus virgatus*. *Acta Oecologica* 19: 167-173.
- Sokal, R. R.; Rohlf, F. J. 1995. *Biometry*. Third edition. Freeman, New York, New York, USA.
- Sorci, G.; Clobert, J. 1995. Effects of maternal ectoparasite load on offspring life-history traits in the common lizard (*Lacerta vivipara*). *Journal of Evolutionary Biology* 8: 711-723.
- Tchabovsky, A. V.; Krasnov, B. R.; Khokhlova, I. S.; Shenbrot, G. I. 2001. The effect of vegetation cover on vigilance and foraging tactics in the fat sand rat *Psammomys obesus*. *Journal of Ethology* 19: 105-113.
- Tiebout, H. M.; Anderson, R. A. 1997. A comparison of corridors and intrinsic connectivity to promote dispersal in transient successional landscapes. *Conservation Biology* 11: 620-627.
- Tiebout, H. M.; Anderson, R. A. 2001. Mesocosm Experiments on Habitat Choice by an Endemic Lizard: Implications for Timber Management. *Journal of Herpetology* 35: 173-185.
- Tinkle, D. W.; Ballinger, R. E. 1972. *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* 53: 570-584.
- VanderWerf, E. A. 1994. Intraspecific variation in Elepaio foraging behavior in Hawaiian forests of different structure. *The Auk* 11: 917-932.
- Williams, E. E. 1972. The ecology of faunas: evolution of lizard congeners in a complex island fauna - a trial analysis. *Evolutionary Biology* 6: 47-89.

Table 2.1: Thermal characteristics of substrates under different lighting conditions. Data presented as mean \pm 1 SE. Substrate temperatures did not differ significantly among habitat types. There were no significant differences between habitats.

Substrate	n	Pine Island	Scrub Edge
Sand Sun	79	36.18 \pm 0.83	34.59 \pm 0.84
Sand Shade	77	29.53 \pm 0.45	30.20 \pm 0.47
Coarse Debris Sun	77	39.76 \pm 1.25	39.54 \pm 1.27
Coarse Debris Shade	78	30.09 \pm 0.44	31.01 \pm 0.45
Tree Sun	59	35.30 \pm 0.69	34.59 \pm 0.75
Tree Shade	67	29.45 \pm 0.39	30.39 \pm 0.46
DWD Sun	76	38.48 \pm 1.18	38.82 \pm 1.24
DWD Shade	74	30.58 \pm 0.49	31.17 \pm 0.51

Table 2.2: Comparison of behavior between habitats. Data presented as mean \pm 1 SE.

Behavior	n	Pine Island	Scrub
Attacks while Stationary	23	51.15 \pm 12.54	53.33 \pm 13.29
Rate of Movements	63	0.135 \pm 0.045	0.197 \pm 0.045
Rate of Attacks	23	0.411 \pm 0.222	0.229 \pm 0.524
% Time Moving	63	0.541 \pm 0.321	1.012 \pm 0.327
Rate of Posture Adjustments	63	0.271 \pm 0.050	0.256 \pm 0.051
Rate of Head Movements	63	2.700 \pm 0.312*	1.518 \pm 0.317

* indicates behaviors which are significantly different between habitats.

Table 2.3: Percent of items eaten and volume of the most important prey types consumed by all lizards sampled in pine island and sand pine scrub habitats.

Habitat	Prey Type	% Prey	
		Eaten	% Volume
Pine Island	Araneae	1.98	6.89
	Coleoptera adult	6.68	9.48
	Coleoptera larvae	7.43	1.71
	Hymenoptera Formicidae	74.26	46.63
	Lepidoptera larvae	2.23	5.82
	Orthoptera Acrididae	1.73	12.01
Total		94.31	82.55
Scrub Edge	Araneae	5.73	10.87
	Coleoptera adult	4.30	9.88
	Coleoptera larvae	3.94	10.87
	Hymenoptera	11.83	9.55
	Hymenoptera Formicidae	50.18	12.32
	Orthoptera Acrididae	3.58	12.14
Total		79.57	65.62

Table 2.4: Principle components of size corrected body shape measurements of *Sceloporus woodi*.

Male PCA			
77 individuals			
	PC1	PC2	PC3
Head Width	0.078	0.576*	-0.062
Head Height	0.130	0.556*	0.061
Head Length	0.206	0.355*	0.096
Inter-girdle Length	0.105	-0.141	0.511*
Pectoral Width	0.204	-0.044	-0.597*
Pelvic Width	0.409*	0.137	-0.279
Femur Length	0.405*	-0.220	0.225
Tibiofibula Length	0.432*	-0.033	-0.070
Hind-foot Length	0.382*	-0.338	-0.086
Longest Hind Toe Length	0.429*	-0.048	0.106
Tail Length	0.186	0.163	0.462*
EigenValue	2.944	2.386	1.364
Percent	26.760	21.687	12.403
Cumulative Percent	26.760	48.447	60.850

Female PCA			
63 individuals			
	PC1	PC2**	PC3
Head Width	0.463*	-0.168	-0.199
Head Height	0.432*	-0.104	-0.092
Head Length	0.401*	-0.045	-0.087
Inter-girdle Length	0.233	-0.076	0.560*
Pectoral Width	0.293	-0.059	-0.307
Pelvic Width	0.378	0.247	0.063
Femur Length	0.197	0.164	0.570*
Tibiofibula Length	0.239	0.472*	-0.208
Hind-foot Length	-0.110	0.450*	0.217
Longest Hind Toe Length	-0.118	0.585*	-0.305
Tail Length	0.183	0.306*	0.155
EigenValue	3.412	1.629	1.204
Percent	31.02	14.81	10.95
Cumulative Percent	31.02	45.83	56.78

* indicates most important components of principle components.

** indicates Principle components that are significantly different between habitats.

Table 2.5: Results of comparisons of principle components describing body shape between habitats.

Sex	PC Axis	t	p(0.05)
Female (n = 63)	PC1	-1.614	0.112
	PC2*	2.784	0.007
	PC3	0.697	0.489
Male (n = 77)	PC1	0.715	0.477
	PC2	1.058	0.293
	PC3	-0.684	0.496

* Indicates significantly different.

Figure 2.1 Percent of lizards sighted occupying each microhabitat type.

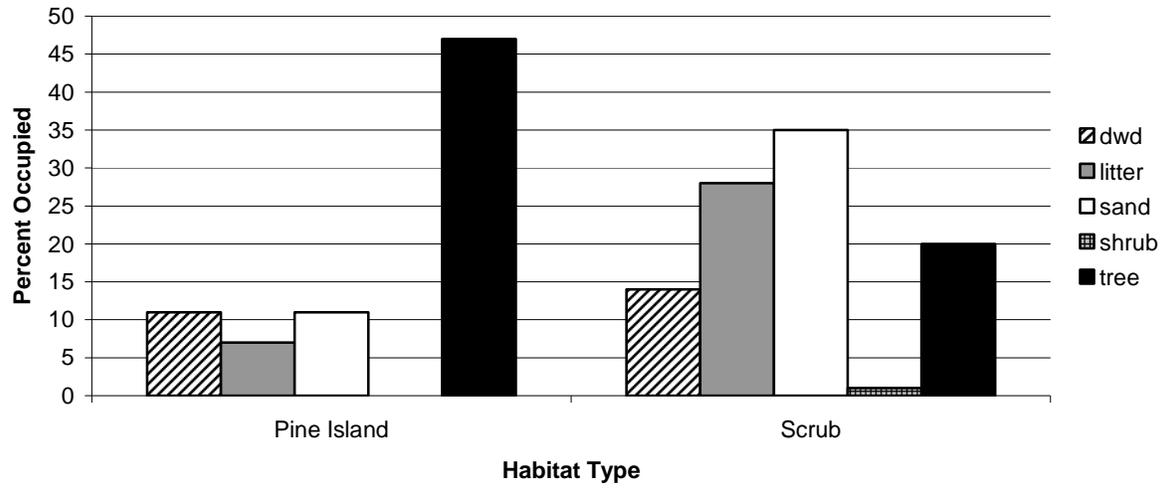
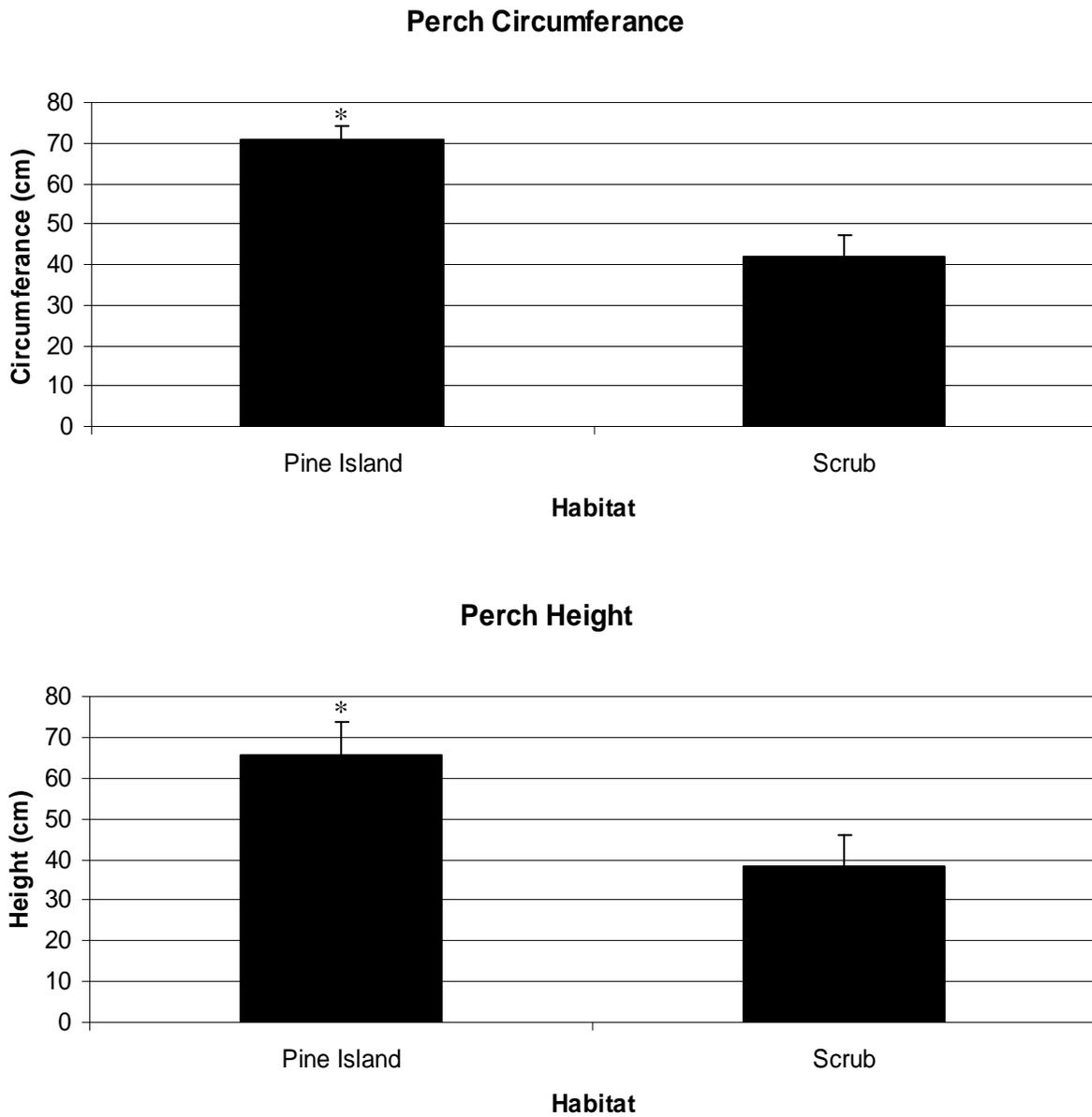
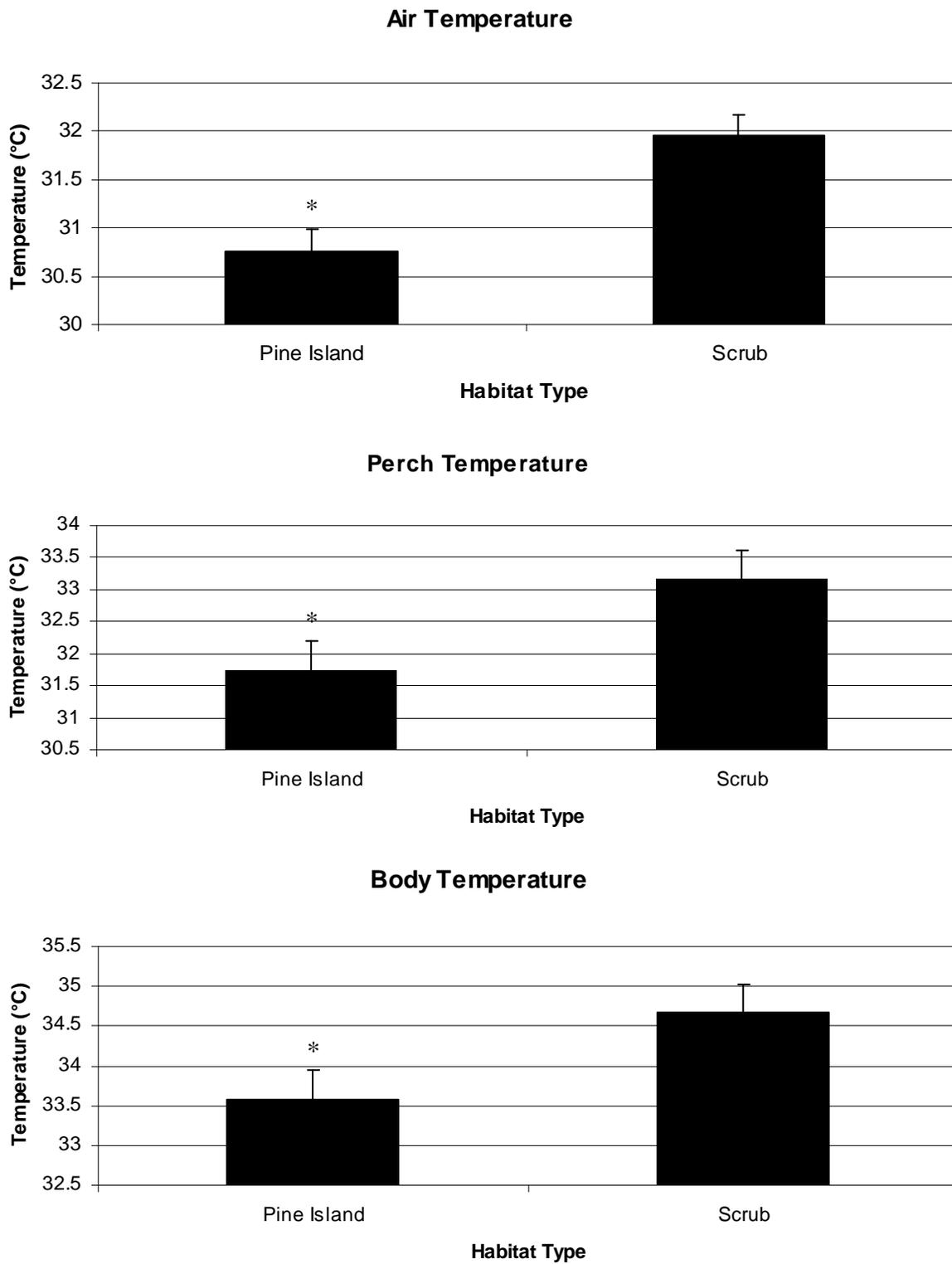


Figure 2.2 Perch characteristics compared between pine island and scrub habitats. Data presented as mean (± 1 SE). Lizards that perched on trees in pine island habitats used trees with significantly larger circumference and perched significantly higher than lizards in scrub.



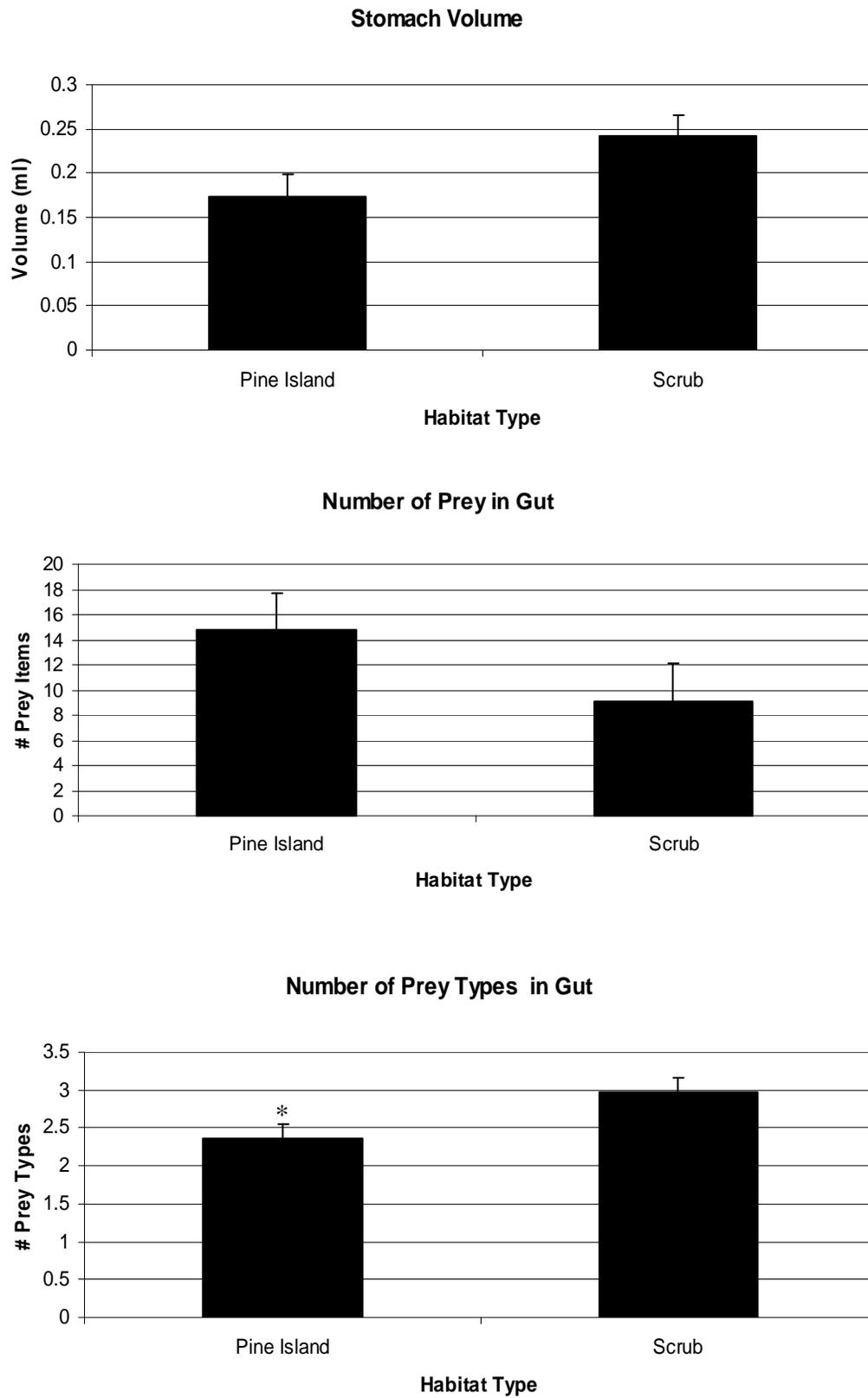
* Indicates that column is significantly different from other the column in Mann-Whitney U test.

Figure 2.3 Comparison of temperature between habitats. Data presented as mean (\pm 1 SE). All temperatures were significantly lower in pine island habitats



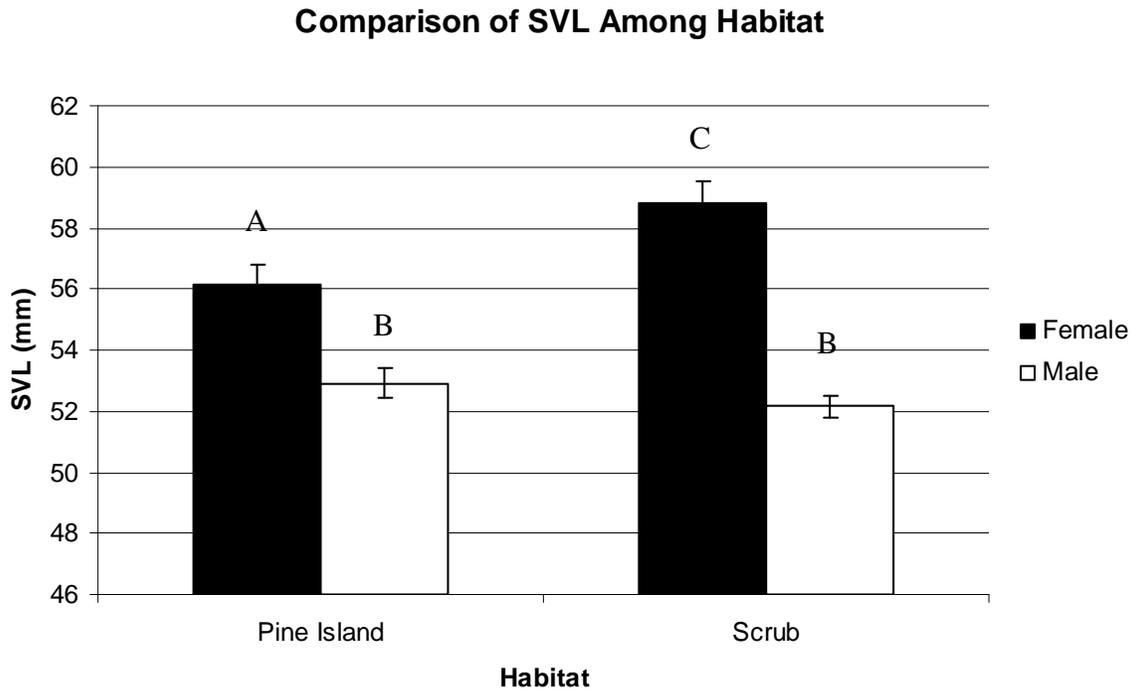
* Indicates that column is significantly different from other the column in t-test or Mann-Whitney U test.

Figure 2.4 Comparison of prey consumption between habitats. Data presented as mean (\pm 1 SE). Only the number of prey types consumed was significantly different between habitats.



* Indicates that column is significantly different from other the column in Mann-Whitney U test.

Figure 2.5 Comparison of mean SVL (\pm 1 SE) between habitats. Females in the scrub are significantly larger than lizards in the pine island habitat. Males are not significantly different in body size between habitats.



Columns with the same letter were not significantly different in Mann-Whitney U tests. Comparisons were conducted for each sex separately and the sexes were not compared

Figure 2.6 Scatter plot of principle component scores for the two most important axes of body shape variation showing 95% confidence limits for pine island (hollow circles) and scrub edge habitats (closed circles). Small ellipses with a cross approximate the centroid of each group.

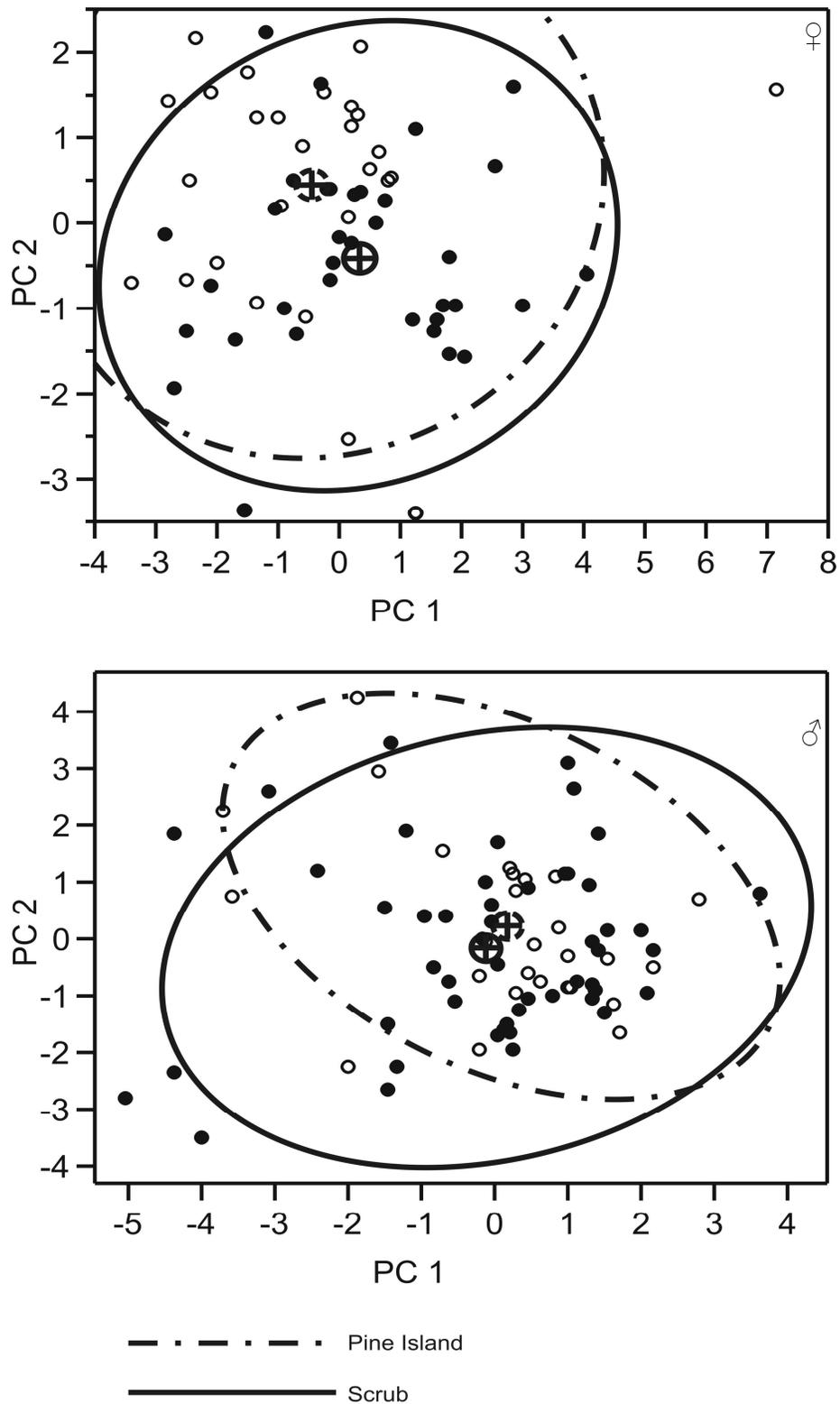
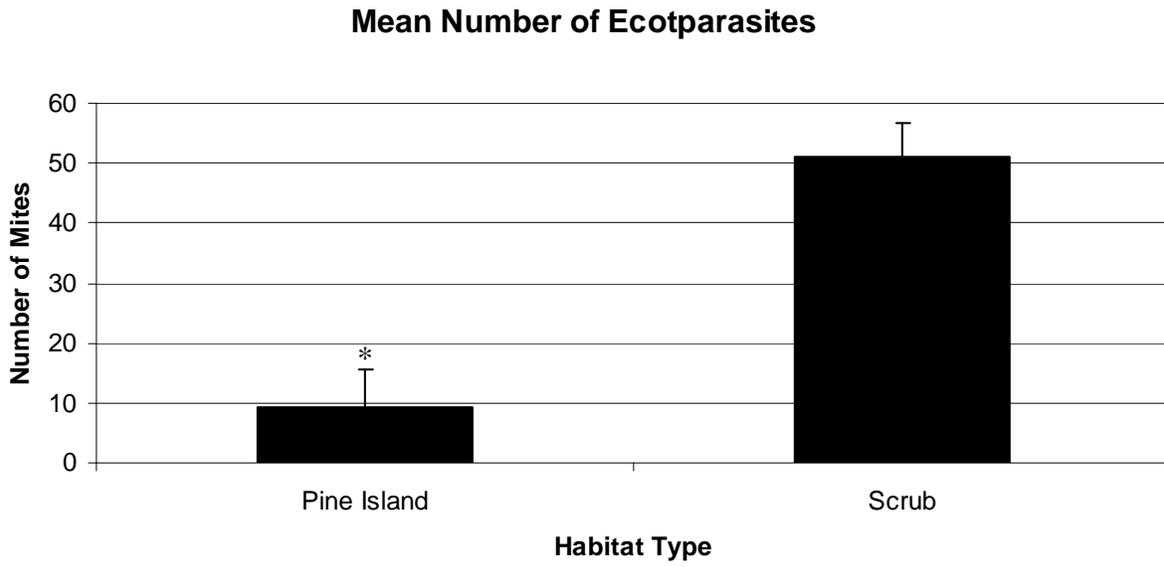


Figure 2.7 Comparison of mean ectoparasite load (\pm 1 SE) between pine island and scrub habitats. Lizards in the pine island habitat had significantly fewer ectoparasites than their counterparts in the scrub.



* Indicates that column is significantly different from other the column in ANOVA.