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Tactical Escape Behavior and Performance of a Small Sceloporine Lizard in Two High Risk Habitats

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TACTICAL ESCAPE BEHAVIOR AND PERFORMANCE OF A SMALL SCELOPORINE

LIZARD IN TWO HIGH RISK HABITATS

by

SETH E. PARKER

(Under the direction of Lance D. McBrayer)

ABSTRACT

The negotiation of uneven and complex terrain has implications for many small terrestrial vertebrates. Variation in the running surface due to obstacles like woody debris or vegetation can alter escape paths and running performance. Additionally, these microhabitat features can influence behavioral tactics in complex environments. The ability to negotiate physical barriers in dense environments likely influences survivorship through important ecological tasks, such as finding mates, foraging, and evading predators. The Florida scrub lizard (*Sceloporus woodi*) is a small, rare species endemic to two distinct and structurally complex environments in Florida, i.e. sand-pine scrub and longleaf pine-wiregrass sand-hills. The differing microhabitats of scrub and longleaf pine factor into the distribution and density of lizard populations throughout the Ocala National Forest in Florida. Understanding strategies to avoid predation between these two habitats can give insight into the likelihood of population persistence, and whether one habitat may harbor a greater lizard density. Additionally, the underlying performance impacts from habitat structure (e.g. multiple obstacles) can shed light on any unique abilities in small terrestrial lizard species. In the first chapter I focus on how multiple obstacles influence running behavior and locomotor posture. Bipedal running was more efficient for crossing obstacles via faster sprint speeds and minimal foot contact with an obstacle. The second chapter investigates the populations of scrub lizards in both the scrub and longleaf habitats. I determine how risk

behaviors vary between habitats, and quantify the detectability and condition of lizards in each. Longleaf pine lizards had greater flight and detection distance than in sand pine scrub. Males showed greater risk aversion and were easier to detect than females in both habitats, indicating that they may be more sensitive to predation when conspicuously occupying open areas. Overall this study reveals areas in need of consideration with habitat management in the Ocala National Forest. Studies such as this help provide a mechanistic understanding of dispersal ability, habitat avoidance, and behavioral flexibility in this rare species, which may be useful to land managers and conservation biologists.

INDEX WORDS: Scrub lizard, *Sceloporus woodi*, Bipedal, Quadrupedal, Obstacles, Velocity, Flight distance, Microhabitat, Refuge

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by

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THE EFFECTS OF MULTIPLE OBSTACLES ON THE LOCOMOTOR BEHAVIOR AND
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ABSTRACT

The flexibility to negotiate variable terrain is important for many small terrestrial vertebrates. Variation in the running surface due to obstacles like woody debris, vegetation or rocks can alter escape paths and running performance. The ability to navigate obstacles likely influences survivorship via predator evasion success, and/or other key ecological tasks (finding mates, foraging). Earlier work established that running posture (quadrupedal, bipedal) and sprint performance are altered when organisms face an obstacle. In this study I focus on how multiple obstacles influence running behavior and locomotor posture in the Florida scrub lizard (*Sceloporus woodi)*. I predict that an increasing number of obstacles will increase the frequency of intermittent locomotion and decrease sprint velocity. I also predict that bipedal locomotion over multiple obstacles will allow a greater proportion of maximum sprint velocity to be maintained compared to quadrupedal running, thus revealing a potential advantage of this posture. Lizards were filmed with hi-speed cameras (300 frames per second) running through a racetrack containing zero, one, two, or three obstacles. Lizards using a bipedal posture with one obstacle were significantly faster than those which only utilized a quadrupedal gait. Bipedal lizards completed the trial in fewer total strides than quadrupedal lizards, yet the total number of bipedal strides decreased as the obstacle number increased. Bipedal running when facing an obstacle was also associated with increased body angle, hip height, and lowering the tail below horizontal. Overall this study sheds light on the locomotor behavior and therefore the kinematic adjustments used by lizards when interacting with multiple obstacles in their environment. By establishing a mechanistic advantage use for bipedal posture in quadrupeds, this provides further understanding as to how bipedalism persists in multiple lizard lineages.

INTRODUCTION

The flexibility to exploit a range of habitats and substrates is important to the survival of terrestrial vertebrates. Limbed terrestrial animals routinely traverse variable terrain in three-dimensionally complex environments. The ability of animals to efficiently move across an array of terrains containing obstacles is important for key ecological tasks, such as escaping from predators, thermoregulation, dispersal and finding mates (Vanhooydonck *et al*., 2005). The efficiency with which these tasks are performed bear strong ecological and evolutionary implications (Clark and Higham, 2011). The physical substrate is commonly comprised of vegetation, rocks, woody debris, sand and a variety of other uneven surfaces. Variation in substrate evenness directly affects the locomotion of animals by altering the transmission of locomotor forces, which may also influence turning ability, sprinting from predators (Tulli *et al*., 2012; Higham *et al*., 2001) and dispersal, which may lead to possible habitat patch extinctions (Higham *et al*., 2001; Hokit *et al*., 1999).

Substrate rugosity, or unevenness, has substantial effects on locomotion and requires adjustments in posture and velocity (Collins *et al*., 2013; Birn-Jeffery and Daley, 2012). Toe-fringes reduce slippage in sand-dwelling lizards during acceleration, allowing them to flee from predators and capture prey despite sandy substrates which cause slippage (Carothers, 1986; Korff and McHenry, 2011). Some rock-dwelling lizard species such as *Crotaphytus bicinctores* are able to utilize kinematic adjustments to increase stability on uneven surfaces, and are therefore less sensitive to changes in the degree of substrate unevenness than smaller sand-dwelling species (Collins *et al*., 2013). This suggests that, aside from kinematic adjustments, specialized morphologies may be an important aspect of small terrestrial vertebrate locomotion in species which must deal with varied habitat structures.

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Many small terrestrial vertebrates are constrained by their abilities to navigate through, in, on and over certain vegetation or substrates. For example, sagebrush ecosystems in the western United States are rapidly changing due to the establishment of non-native cheatgrass. Dense cheatgrass impedes the sprint performance of native rodent and lizard species (Rieder *et al*., 2010). Body size, body shape, and form of movement are important factors influencing locomotion through dense cheatgrass, and may be important in sandy, rocky habitats also (Rieder *et al*., 2010; Collins *et al*., 2013). However, tradeoffs exist because body size also affects strength and stamina (Garland and Losos, 1994). Movement of a wide-bodied species may be impeded more than a slender-bodied species when moving through dense or uneven terrain. Species that occupy rocky habitats sprint and climb faster than species from leaf litter-dominated habitats, presumably because of selection for longer hind limbs (Goodman *et al*., 2008). A reduction in limb length and an elongation of the body has evolved as an adaptive response to locomotion through dense vegetation, thus revealing the important role that habitat structure plays in the evolution of morphology and performance of terrestrial organisms (Goodman, 2009; Goodman *et al*., 2008).

Obstacle negotiation has been studied among a variety of species including guinea fowl (Daley and Biewener, 2011; Clark and Higham, 2011), humans (Sparrow *et al*., 1996; Perry *et al*., 2010), cats (McFayden *et al*., 1999), cockroaches (Harley *et al*., 2009), and lizards (Kohlsdorf and Navas, 2007; Olberding *et al*., 2012; Tucker and McBrayer, 2012; Self *et al*., unpublished). Anticipatory locomotor adjustments are essential for locomotion over obstacles (McFayden *et al*., 1999). Quadrupedal animals such as cats adjust the coordination of their locomotor patterns by changing postures with the hip and ankle joints to clear an obstacle (McFayden *et al*., 1999). When approaching an obstacle (i.e. running across hurdles), humans

reorganize lower limb control using knee flexion (McFayden *et al*., 1999) because of visual anticipation of the upcoming obstacle. As obstacle height increases, the lead foot must cross earlier to allow more time to traverse the higher obstacle, implying that stride length is modified to ensure optimal foot placement (Sparrow *et al*., 1996).

Lizards must navigate various substrates and obstacles such as rocks, vegetation, woody debris, and sand in order to defend territories, find mates and flee from predators. The first level of an animal's response to change in substrate or terrain is likely to be behavioral (Ireata *et al*., 2010). For example, lizards often employ a bipedal running posture. It is not uncommon for individuals in many lizard species to switch from a quadrupedal gait to a bipedal gait during locomotion (Snyder, 1952; Snyder, 1962). Bipedal running occurs when the animal lifts its front limbs off the ground above its center of gravity, leaving only the hind limbs in contact with the substrate (Snyder, 1952). Despite that bipedalism occurs within many lizard species, the biological advantage of the posture to facultative bipeds remains unclear. A bipedal posture may allow the animal to better visualize the upcoming obstacle or terrain by elevating the head, or it may decrease energy expenditure by having only two limbs in motion (Kohlsdorf and Biewener, 2006; Snyder, 1952; Snyder, 1962), or it may simply raise the hip height and shift the center of mass (COM) of the body to overcome the obstacle. Alternatively, a bipedal posture may be due simply to the mechanical consequence of rapid initial acceleration from torques generated by the hip, causing a pitching rotation that lifts the head and trunk (Aerts *et al*., 2003; Van Wassenbergh and Aerts, 2013). Yet, for several lizard species acceleration is not a prerequisite for sustained bipedal running (Van Wassenbergh and Aerts, 2013). Active tail lifting during acceleration results in the upward rotation of the trunk through increased angular momentum of the tail, making sustained bipedal running possible at lower acceleration (Aerts *et al*., 2003; Clemente,

2014). However, even though bipedal running can be sustained on unobstructed trackways, it may not be maintained during obstacle negotiation by lizards. For example, the six-lined racerunner (*Aspidoscelis sexlineatus*) does not continue running with a bipedal gait after obstacle contact, despite its frequent use of bipedal posture (Olberding *et al.*, 2012).

Nevertheless, bipedal running may be an advantageous behavioral choice when negotiating obstacles such as vegetation or woody debris. Dense vegetation impacts locomotor performance of lizards by increasing the frequency of intermittent locomotion, or the extent of pausing to seek alternative routes, and/or to adjust balance between locomotor bouts (Higham *et al.*, 2011a). Since obstacles can be common in some habitats (Collins *et al.*, 2013), it is likely that the presence and size of obstacles may influence an animal's decision to move intermittently and change body posture (Tucker and McBrayer, 2012). It has been shown that lizards increase vertical limb motion and elevate the head and trunk when approaching an obstacle. This change often is coupled with a decrease in locomotor speed and an increase in the frequency of bipedalism (Kohlsdorf and Biewener, 2006). If lizards cannot sprint at (or near) maximum capacity, then their ability to elude predators would be affected (McMillan *et al.*, 2011; De Barros *et al.*, 2010; Okafor, 2010), particularly on uneven terrain containing obstacles to negotiate. While a plethora of studies have examined bipedal locomotion in lizards from an evolutionary and behavioral standpoint, this study attempts to identify a mechanistic link between bipedalism and ecologically relevant features of the habitat.

The goal of this project was to understand how multiple obstacles affect sprint performance and behavior, and how a bipedal running posture is related to each. In doing so, I will answer the following four questions: 1) Does sprint performance and locomotor posture differ between running with or without an obstacle? I predict that the frequency of bipedal running strides will be greater when lizards face an obstacle compared to those who do not. I predict that lizards will show a decrease in sprint velocity and an increase in intermittent locomotion when facing an obstacle as opposed to running without one. 2) Is bipedal posture a more efficient method of locomotion for lizards when crossing obstacles? Here, efficiency is defined as maintaining a constant velocity with minimal stumbling or stopping, and is quantified in three ways (a, b, c). I predict that lizards running with a bipedal gait while crossing obstacles will attain higher sprint velocity than lizards that only use quadrupedal running to do so (a). I predict that the frequency of intermittent locomotion will decrease when a bipedal posture is used compared to quadrupedal running because bipedalism should allow the animal to step over, not on, the obstacle (b) (Olberding *et al*., 2012; Self *et al*., unpublished). I further predict that if lizards run with a bipedal posture they will complete the trial in fewer strides than those that run with a quadrupedal gait (c).

Additionally, studies have yet to develop an understanding of how tail elevation in lizards aids in obstacle negotiation, as a horizontal tail could aid in locomotion over the obstacle (Hsieh, 2003; Self *et al*., unpublished). In the case of the water-running Basilisk lizard, holding the tail horizontally may act as a counterbalance in forward locomotion and generate thrust to propel the animal forward (Snyder, 1962; Hsieh, 2003). The horizontal tail may counterbalance the weight of the increased body angle during bipedal running, since it would position the COM of the tail

as far as possible from the center of the hip (Irschick and Jayne, 1999b), thus providing a potential benefit for lizards using a bipedal running posture. In contrast, a tail elevated 12° above a horizontal plane allows lizards to sustain bipedal running at lower accelerations (Van Wassenbergh and Aerts, 2013; Aerts *et al*., 2003; Clemente, 2014), however studies have yet to show that bipedal running can be sustained when lizards negotiate obstacles (Olberding *et al*., 2012). 3) Based on this, I ask will bipedal running occur with an elevated or lowered tail just before crossing an obstacle. I predict the tail will be lowered below horizontal to provide the greatest stability for lizards crossing obstacles using a bipedal posture. In addition, I predict that a bipedal posture will be associated with a greater body angle and hip height than a quadrupedal posture when crossing obstacles. 4) Finally I ask if sprint performance and intermittent locomotion vary between lizards running across a single versus multiple obstacles. I predict that multiple obstacles will result in a decrease in sprint velocity compared to a single obstacle. I also predict that the frequency of intermittent locomotion will be greater when there are multiple obstacles compared to only a single obstacle. While the effects of a single obstacle on performance and behavior are well studied, the effect of multiple obstacles on terrestrial vertebrate locomotion has not, yet is worthy of exploration because many habitat types may be replete with different types of obstacles that lizards would need to negotiate in order to survive.

Study species

  This study focused on locomotor behavior and performance in the Florida scrub lizard *Sceloporus woodi*, a species restricted to the sand pine scrub habitat in central Florida (Jackson, 1973). The scrub lizard is a diurnally active, ground-dwelling lizard which uses flat, open sandy areas to sprint away from predators (Hokit *et al*., 1999; Tucker and McBrayer, 2012), and is capable of acceleration to near maximum sprinting speed over a short distance (0.4m; McElroy

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and McBrayer, 2010). This species has a demonstrated capacity for sprinting on a narrow trackway, making them ideal for performance studies on obstacle negotiation and sprint velocity (Bonine *et al*., 2001; Bonine *et al*., 2005; Higham *et al*., 2011b). An important behavioral strategy used by the scrub lizard is the ability to adjust body posture and employ a bipedal gait while sprinting over obstacles (Tucker and McBrayer, 2012). This species also shows a decrease in maximum velocity, and increased pausing, when moving on a vertical surface (Higham *et al*., 2011a), such as a tree branch or rock. The Florida scrub lizard is considered rare and potentially threatened, and thus been used as a model to study habitat fragmentation for its conservation (Tiebout and Anderson, 2001; Hokit *et al*., 1999; Hokit and Branch, 2003; Clark *et al*., 1999; Heath *et al*., 2012; McCoy *et al*., 2004). Disturbance and habitat fragmentation are major impediments on scrub lizard locomotion, dispersal, and survival. This ground-dwelling species encounters various obstacles and substrates that result from forest management practices (clear-cut logging). During logging, tree de-limbing and chipping, considerable amounts of coarse woody debris (CWD) are generated (Tiebout and Anderson, 2001). Scrub lizards prefer shaded open sand substrates, and avoid CWD which may be thermally stressful and impede locomotion (Tiebout and Anderson, 2001). As the scrub habitat is frequently disturbed, lizards must seek new suitable sites. Given this, studying running performance and obstacle negotiation is relevant from a mechanistic and an ecological standpoint. This study will examine how obstacles, which resemble those found in the disturbed scrub system, impact the locomotor behavior of the Florida scrub lizard.

METHODS

Field collection

Field work was conducted within the Ocala National Forest located in Marion County, Florida. The ONF covers over 180,000 hectares in central Florida and contains the largest remaining continuous area of scrub habitat (Greenberg *et al*., 1994). Scrub lizards were collected in the ONF throughout a single field season from May to August 2013. Animals were captured within recently disturbed sand pine scrub stands, as well as in longleaf pine islands. Lizards were captured via slip noose made from monofilament fishing line threaded through the tip of a fishing pole, and temporarily housed in numbered cloth bags in a cool environment. Field active temperature was measured via cloaca thermometer immediately upon capture to ensure each lizard's body temperature during performance trials was similar to those experienced naturally (Collins *et al*., 2013). Only adult males were used since females alternate in gravidity throughout the season, and this affects their locomotor performance (Sinervo *et al*., 1991; Ireata *et al*., 2010). After performing trials (see below), each lizard was released to the original point of capture; potential recaptures were avoided because each lizard was given paint markings. Individuals were subjected to running trials within 24 hours of capture.

Trials were conducted in a field laboratory. A rectangular, wooden - racetrack (2.4m length x 1m width x 0.4m height) with high speed cameras mounted above was used to measure sprint performance and record body posture and behavior (Appendices; Figure 1A, 2B). Trials were performed with a ½ inch of packed sand inside the racetrack. One of four obstacle treatments was randomly selected for each group of lizards run each day; treatments contained 0, 1, 2, or 3 obstacles. Lizards ran without an obstacle as a control (trial 0). One rectangular obstacle was placed in a perpendicular orientation to the running path of the lizard 0.4m from the

starting point for trial 1. *Sceloporus woodi* can reach near maximum acceleration by 0.4m (McElroy and McBrayer, 2010) hence the obstacle was place at this distance. Trial 2 consisted of two rectangular obstacles of equal dimensions placed at 0.4m and 0.8m for the start position. The two obstacles were 0.4m apart so that the lizards would not be able to jump from one obstacle to the other, and might reach maximum acceleration once again. Trial 3 contained three obstacles placed at 0.35m, 0.6m, and 0.85m. This alternative spacing for 3 obstacles was required in order to fit within the 1 meter field-of-view of the cameras. Obstacle height and width was standardized to 35% of the average hind limb length for each lizard in each trial. This size was used to allow continuous locomotion (Self *et al*., unpublished). Obstacles were long enough to fit flush with sidewalls in the track so that lizards could not hide or maneuver around the obstacle.

Trials were filmed with two CASIO[©] EXILIM hi-speed digital cameras at 300 frames per second. Both cameras filmed dorso-laterally from above the track, each had a 0.5m field-of-view and captured a mirrored view and dorsolateral view of the running lizard (Appendices; Figure 2B). The mirror was angled at 50° to ensure that the lateral side of the lizard would be in view. It was placed against the wall opposite to the cameras. Lizards were warmed to 34-38°C in an incubator for one hour prior to running. Each individual was placed at the starting position with forelimbs oriented in a forward direction and subsequently released. Using light tail-taps or loud hand-clapping, lizards were coerced to run down the track to a dark refuge where they were immediately captured and placed at the start for a second run. A trial was considered successful if a lizard completed the 1-meter distance in a continuous run. If a lizard paused, ran into the mirror, or reversed direction, then the trial was not used in performance analysis, although these observations were recorded to describe locomotor behavior.

Morphological Measurements

Prior to performance testing, three morphological measurements were taken on each individual using a ruler or dial caliper accurate to 0.01m (Appendices; Figure 3C). Hind limb length was measured from the hip joint to the tip of the longest toe with a caliper, and averaged between both hind limbs. Snout-to-vent length and tail length (original tail and newly regenerated) were measured using a ruler. These measurements were necessary for determining proper obstacle height for each lizard, as well as in other ongoing studies. Only adult males with a snout-vent length of at least 42mm were included in trials.

Video Analysis and statistics

Only trials in which the lizard ran straight, did not pause, or run into the sidewalls, etc. were included in analyses. Each video was digitally clipped and converted to a compressed file (.AVI) using Adobe Premiere© Pro Elements software. These files were then viewed in DLTdv5, a video digitization program within MATLAB© software (Hedrick, 2008). Videos were calibrated using a custom 30-point calibration cube. A scale bar with 10cm increments was visible on the racetrack; it was digitized in order to standardize the distance (in pixels) for each video. Prior to performance trials, five anatomical landmarks were painted on each lizard using non-toxic white paint (Appendices; Figure 3C). A single mark on the top of the head, posterior to the pineal eye, was used as a landmark to calculate sprinting velocity (m/sec). To reduce variation due to digitization error, velocity data was reviewed and single, very large values (≥ 3.5 m/sec) were replaced by averaging these outliers with sequential values in the data set. This species, and a few others, are not known to sprint over 3m/sec, hence this cutoff is justifiable. Obstacle crossing posture (bipedal or quadrupedal) was quantified at the last full stride before coming in contact with the first obstacle. Obstacle crossing behavior was determined by whether

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a hind foot touched (on) the obstacle, or whether the animal cleared (i.e. stepped over) the

obstacle with no contact. The frequency of bipedal and quadrupedal running was measured as the

number of full strides completed using each posture, while total strides were quantified as the

total number of combined strides within each trial (bipedal + quadrupedal strides). Strides were

defined as the initial footfall of the hind-limb and a subsequent footfall of the same hind-limb. If

a stride was completed with no contact from the front limbs, then it was classified as bipedal.

Alternatively, the total number of strides of each posture was quantified by counting the total

number of strides completed with a bipedal posture, versus the total number of strides using a

quadrupedal posture. Intermittent locomotion (frequency of pausing within the run) was also

quantified.

Tail elevation, body angle, and hip height were measured at mid-stance of the last full

stride before reaching the obstacle at 0.4m. Runs without an obstacle could be compared, given

that the first obstacle was placed at 0.4m. To determine tail elevation, paint marks were placed at

the base of the tail and 40% of the tail length from the tail base (Appendices; Figure 3C). Tail

elevation was calculated as the vertical distance between both tail points and the substrate

directly below each tail point. Positive values indicate the tail was elevated above the pelvis, and

negative values indicate that the tail was below the pelvis and towards the substrate. Body angle

was quantified by calculating the angle between marks on the shoulder and the hip (ilium)

relative to two horizontal points on the substrate (Appendices; Figure 3C). Positive values

indicate the body angle is elevated, while negative values indicate the body is angled toward the

substrate. Hip height was measured as the distance from the hip mark to the substrate in

centimeters. Data was analyzed with 1-way ANOVAs with Tukey-Kramer post hoc, Welch's

ANOVA, Kruskal-Wallis, Mann-Whitney U, and Chi Square tests (Appendices; Table 1D). All

statistical tests were performed using JMP Pro$^©$ v10.0 software; alpha was the standard p < 0.05. Forty eight percent of all trials (68/141) were analyzed for the study, though data from all trials (N=141) was used to test predictions regarding intermittent locomotion.

<center>RESULTS</center>

Performance, posture and behavior between trials with and without an obstacle

I measured the sprint velocity and behavior of 68 adult males (mean snout-to-vent length [SVL] 47.2 ± 0.18mm; mean hind-limb length [HLL] 39.8 ± 0.14mm). Mean velocity over the 1m track was not significantly different between all trials with obstacles (trial 1+2+3) and without (trial 0) ($F_{1,68}$ = 0.0017; p = 0.97). For trials without an obstacle, velocity was not significantly different between trials containing bipedal running and those containing only quadrupedal running ($F_{1,15}$ = 0.49; p = 0.49) (Figure 1.1). There was also no difference in velocity of bipedal running with an obstacle compared to bipedal running without obstacle ($F_{1,46}$ = 0.10; p = 0.75). However, the frequency of the use of bipedal posture prior to the obstacle was significantly greater with obstacles present than without ($\chi^2_{1,28}$ = 9.72; p = 0.0018). Lizards averaged 7.04 ± 0.16 total strides along the 1m track when facing an obstacle, compared to 6.9 ± 0.27 total strides without an obstacle ($U_{1,68}$ = 1714.5; N_1 = 15; N_2 = 53; p = 0.926) (Table 1.1). Lizards averaged 1.5 ± 0.2 bipedal strides over the 1m run when an obstacle was present, and 1.6 ± 0.4 bipedal strides without an obstacle ($\chi^2_{1,68}$ = 0.02; p = 0.88) (Table 1.1). Hence, neither the total number of strides, nor the number of bipedal strides used with an obstacle was different. An alternative stride analysis was also used to tease apart trials containing bipedal running. Here the total stride number was quantified between lizards using a bipedal posture at any point during the 1 meter run and those using only quadrupedal running throughout the 1m run. All trials (0-3) were combined in this analysis; low sample sizes and variation in obstacle spacing made it

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impossible to compare among each obstacle trial. Lizards using a bipedal posture completed the 1-meter run in significantly fewer total strides (6.8 ± 0.16) than those using only a quadrupedal posture (7.5 ± 0.23) ($\chi^2_{1,68} = 7.34$; $p = 0.0067$) (Figure 1.3, Table 1.1). Finally, there was no significant difference in the frequency of pausing with obstacles vs. without ($\chi^2_{1,55} = 1.98$; $p = 0.1589$).

Bipedal vs. quadrupedal locomotion over obstacles

The frequency of each posture used was analyzed independently within each obstacle trial to see if increasing obstacle number would elicit the same behavioral change. Posture was quantified during the last full stride prior to crossing each obstacle. In trial 1, the observed frequencies of bipedal and quadrupedal posture before the 1st obstacle were not different (50% Q; 50% B; $\chi^2_{1,20} = 0.0$; $p = 1.0$). In trial 2, the frequency of a given posture was not different before the 1st obstacle (64% Q; 36% B; $\chi^2_{1,14} = 1.2$; $p = 0.3$), however a quadrupedal posture was used significantly more before the 2nd obstacle (93% Q; 7% B; $\chi^2_{1,14} = 12.2$; $p = 0.0005$). In trial 3, a quadrupedal posture was used with a greater frequency than a bipedal posture before the 1st obstacle (74% Q; 26% B; $\chi^2_{1,19} = 4.4$; $p = 0.04$), the 2nd obstacle (100% Q; 0% B; $\chi^2_{1,19} = 26.3$; $p < 0.0001$), and before the 3rd obstacle (95% Q; 5% B; $\chi^2_{1,19} = 18.5$; $p < 0.0001$).

Mean velocity and the frequency of each posture were analyzed between obstacle crossing behaviors (stepping on vs. stepping over the obstacle) among all trials. This analysis examined whether stepping over an obstacle using a bipedal posture was faster than stepping over with a quadrupedal posture. No significant difference in velocity between postures were found among obstacle crossing behaviors (stepping on vs. over) ($F_{3,53} = 2.08$; $p = 0.114$). Among obstacle trials (1-3), lizards stepped on the obstacle significantly more when using a quadrupedal posture ($\chi^2_{1,17} = 7.72$; $p = 0.0055$) (Figure 1.2, Table 1.1). No difference in the frequency of

bipedal or quadrupedal posture was found when stepping over (no limb contact) the first obstacle ($\chi^2_{1,36} = 0.45$; p = 0.5045). However, lizards that stepped over an obstacle using a bipedal posture were significantly faster than lizards that stepped over using a quadrupedal posture ($\chi^2_{1,36} = 6.1662$; p = 0.013) (Figure 1.1, Table 1.1). Pausing was significantly less frequent when a bipedal posture was used compared to sole use of a quadrupedal posture ($\chi^2_{1,141} = 34.9$; p $\leq$ 0.0001) (Figure 1.4).

Bipedal kinematics of tail elevation, body angle and hip height

Tail elevation was significantly lower among lizards running with a bipedal posture; 86% had held the tail below horizontal in the stride prior to the obstacle compared to 14% that elevated the tail (above horizontal) ($\chi^2_{1,28} = 15.8$; p < 0.0001). The tail was held below horizontal significantly more with an obstacle present than without, regardless of posture ($\chi^2_{1,51} = 17.5$; p < 0.0001). Body angle in the stride prior to reaching the obstacle was not significantly greater with an obstacle than without ($\chi^2_{1,68} = 0.067$; p = 0.79) and was not different among obstacle trials ($F_{3,64} = 1.49$; p = 0.23). However, in all trials (0-3), body angle was significantly greater with a bipedal posture (15.035 $\pm$ 2.9 degrees) than with a quadrupedal posture (5.66 $\pm$ 2.0 degrees) (Table 1.2). Body angle was significantly different between postures in trial 0 ($F_{1,15} = 13.6$; p = 0.0027), trial 1 ($\chi^2_{1,20} = 5.49$; p = 0.0191), trial 2 ($\chi^2_{1,14} = 7.47$; p = 0.0063) and trial 3 ($F_{1,19} = 10.9$; p = 0.0041). Hip height did not differ between running with and without an obstacle ($F_{1,68} = 0.13$; p = 0.72) or among obstacle trials ($F_{3,68} = 0.05$; p = 0.97). Bipedal hip height was significantly greater than quadrupedal hip height in trial 0 ($F_{1,15} = 5.08$; p = 0.043), trial 1 ($F_{1,20} = 19.2$; p = 0.0004) and trial 3 ($\chi^2_{1,19} = 3.7$; p = 0.051); there was no difference in trial 2 ($\chi^2_{1,14} = 1.96$; p = 0.16) (Table 1.2).

Performance and intermittent locomotion between single and multiple obstacles

Mean velocity was significantly greater over one obstacle (trial 1; 2.9 ± 0.09 m/sec) than two obstacles (trial 2; 2.5 ± 0.07 m/sec); this was also true for velocity over one obstacle compared to three obstacles ($F_{3,68} = 3.75$; $p = 0.015$). In both instances lizards had the fastest velocity when running over one obstacle, and experienced a decrease in velocity over two and three obstacles (Figure 1.1, Table 1.1). Bipedal running lizards in the one, two, or three obstacle trials showed significantly higher velocity than lizards which only ran quadrupedal ($F_{1,53} = 5.57$; $p = 0.022$) (Figure 1.1, Table 1.1). However, when testing for differences in velocity by posture within each of the obstacle trials (1-3), mean velocity was only significantly greater with a bipedal posture in the one obstacle group (trial 1; $F_{1,20} = 8.06$; $p = 0.0109$) (Table 1.1). There was also no significant difference in the total number of bipedal strides taken among obstacle groups ($\chi^2_{3,68} = 3.41$; $p = 0.333$). The total number of strides within the 1-meter run did not differ significantly among obstacle trials ($\chi^2_{3,68} = 6.63$; $p = 0.0845$), although a trend was evident (Figure 1.3, Table 1.1). Finally, lizards did not use intermittent locomotion more or less frequently in any particular obstacle trial ($\chi^2_{3,141} = 5.29$; $p = 0.1515$).

DISCUSSION

Bipedal locomotion may enhance environmental perception in the presence of physical barriers, and may enlarge the animal's visual field by elevating the trunk above the obstacle before crossing (Kohlsdorf and Biewener, 2006; Tucker and McBrayer, 2012). For quadrupeds crossing obstacles, bipedality also enables locomotion to continue without disrupting the body COM (Olberding *et al*., 2012). The goal of this study was to compare how multiple obstacles affect sprint performance, posture, and locomotor behavior. I predicted that multiple obstacles would decrease velocity, increase bipedal running, and promote intermittent locomotion

(pausing). Mean velocity decreased with multiple obstacles as predicted, but pausing did not vary. However, lizards were less likely to pause or touch on obstacle when using a bipedal posture. Body angle and hip height were greater during bipedal running in anticipation of obstacle crossing. Furthermore, the tail was more likely to be lowered below horizontal just before crossing the obstacle, presumably to maintain an upright bipedal posture. This finding contrasts past reports showing an elevated tail during unobstructed bipedal running (Van Wassenberg and Aerts, 2013; Aerts *et al*., 2003). This study demonstrates that bipedal running is advantageous for negotiating a single obstacle by increasing relative velocity, but bipedal running posture is not necessarily advantageous for multiple obstacles in close proximity. Multiple obstacles have a significant impact on small vertebrate locomotion, yet these negative effects may be offset via use of bipedal running.

Performance and behavior with and without obstacles

Running over an obstacle significantly decreases sprint speed of quadrupedally running lizards (Kohlsdorf and Biewener, 2006; Self *et al*., unpublished), as obstacles are physically and visually obtrusive using this posture (Tucker and McBrayer, 2012). Yet contrary to my prediction, there was no change in sprint speed from running without obstacles to running with an obstacle. Unexpectedly, lizards showed a 5.6% increase in mean velocity from 0 to 1 obstacle, perhaps due to a use of bipedal running (Figure 1.1, Table 1.1). This is supported by the fact that lizards used a bipedal posture with one obstacle more frequently than without any obstacle present (Table 1.1). A similar pattern has been observed among four other lizard species (Self *et al*., unpublished). With an obstacle present, bipedalism is used more often when approaching the obstacle compared to no obstacle, but the number of bipedal strides did not increase over the 1m track (Table 1.1). Additionally, most lizards were observed switching to a quadrupedal posture

when preparing to cross the 2nd and 3rd obstacles. This finding indicates that lizards rely less on bipedal running *after* crossing an obstacle, which likely explains why mean forward speed does not change. For lizards that encounter additional obstacles, use of bipedal running does not appear to have the same benefit because velocity slowed in both the two and three obstacle trials.

Is bipedal locomotion more efficient than quadrupedal locomotion?

Complex or cluttered habitats can prove difficult for maintaining a straight path of travel and speed during movement, requiring a behavioral repertoire to negotiate barriers within these arenas (Rieder *et al*., 2010; Garber and Pruetz, 1995; Tucker and McBrayer, 2012). Quickly maneuvering on or over obstacles can play a vital role in predator evasion in complex habitats (Kohlsdorf and Navas, 2007; Tucker and McBrayer, 2012). When facing a single obstacle, lizards experienced a 13.8% faster velocity running with a bipedal posture compared to quadrupedal running (Figure 1.1, Table 1.1). However, six-lined racerunners were unable to continue running with a bipedal gait after obstacle contact (Olberding *et al*., 2012), suggesting a tradeoff where some species may forego a bipedal posture to maintain stability after crossing a barrier. The results of Olberding *et al.* (2012) differ from those here in that six-lined racerunners did not experience any change in performance with a single obstacle present (Olberding *et al*., 2012). Given that six-lined racerunners have a much higher velocity over obstacles (4.7±0.5 m/sec; Olberding *et al*., 2012) than *S. woodi* (2.5±0.06 m/sec; Table 1.1), bipedalism may be less stable crossing obstacles at high velocity.

Stability may be gained by switching to a quadrupedal gait, yet this posture is associated with shorter stride length (Irschick and Jayne, 1999a) and a slower velocity on one obstacle (Figure 1.1, Table 1.1). Higher speeds can be achieved by more frequent strides, exhibited in bipedal birds and humans, or by taking longer strides as seen in many quadrupeds (Clemente *et*

al., 2013; Roberts *et al*., 1998; Gatesy and Biewener, 1991). For example, ground-dwelling species change stride length to increase speed while climbing species modify stride frequency (Zaaf *et al*., 2001; Clemente *et al*., 2013). During escape locomotion of *Callisaurus draconoides*, the average bipedal stride is 1.18 times the length of quadrupedal strides (Irschick and Jayne, 1999a). Here, longer bipedal strides likely allow for stepping over an obstacle, rather than stumbling over it or stepping on it. Doing so should retain greater sprint speed. I show that bipedal running results in fewer total strides than quadrupedal running, signifying that *S. woodi* modulates stride length during bipedal running and may also increase speed (Figure 1.3, Table 1.1). Modulating stride frequency would result in shorter, more numerous, strides in the same distance. Shorter strides may increase stability, and *S. woodi* could switch to a quadrupedal gait if contact is made with the obstacle. Unfortunately stride length could not be quantified in the present study due to blind spots in the mirrored view along the racetrack. Only one individual was observed sustaining bipedalism over 1 meter, thus additional analysis on the degree of stability between postures is needed.

On uneven terrain, pheasants use visual route planning in anticipation of negotiating an obstacle, thereby minimizing the likelihood of a misplaced footfall resulting in stumbling (Birn-Jeffery and Daley, 2012). In similar context, a lizard may choose to run bipedally to avoid obstacle contact, and thus escape a predator with greater efficiency. However, tradeoffs are likely. Humans modify stride length to maximize obstacle clearance, but a high-stepping gait is energetically demanding (Sparrow *et al*., 1996). Similarly, bipedal lizards must anticipate optimal hind-foot placement to avoid obstacle interference. Olberding *et al.* (2012) suggested that choosing to step on or over an obstacle was by chance. In contrast, my results suggest that lizards may choose to use a bipedal posture to avoid contacting the first obstacle (Figure 1.2).

Stepping over the obstacle allowed *S. woodi* to pass the obstacle without deceleration and experience a faster velocity compared to stepping over with quadrupedal running (Figure 1.1, Table 1.1). Further analyses of footfall patterns, stride length, and stride frequency leading up to an obstacle would provide useful insight for obstacle anticipation in bipedal lizards.

Bipedal running kinematics

Elevation of the trunk and head serves to improve visual perception and increase the animal's COM potential energy, thus contributing to the work necessary for clearing the obstacle (Kohlsdorf and Biewener, 2006). Two studies show that a bipedal posture is associated with holding the tail horizontally, and suggest that this may increase the stability of the body COM (Irschick and Jayne, 1999b; Self *et al*., unpublished). However, other studies suggest elevating the tail above the COM is needed during sustained bipedal running and that both tail elevation and bipedal running are related to rapid initial acceleration (Van Wassenbergh and Aerts, 2013; Aerts *et al*., 2003; Clemente, 2014). When approaching an obstacle, lizards had an average bipedal body angle of 15.035 ± 2.9 degrees (Figure 1.5, Table 1.2), similar to the body angle of 15° observed in Van Wassenbergh and Aerts (2013) and of 25° observed in bipedal running cockroaches (Alexander, 2004). Basilisk lizards maintain an upright posture (45°) at high velocity by dragging the tail behind through the water (Hsieh, 2003). In contrast, *S. woodi* has a much lower body angle, and a much shorter tail, than bipedal running basilisks. *Sceloporus woodi* can achieve maximum acceleration very rapidly (within 0.5m), yet has not been observed to frequently pitch upward at the start of a run (McElroy and McBrayer, 2010). Therefore, it seems unlikely that bipedalism, and tail elevation, are solely a consequence of rapid initial acceleration as has been suggested.

In anticipation of crossing an obstacle, *S. woodi* must hold the tail horizontal or slightly below horizontal to maintain an upright bipedal posture, since elevating the tail would decrease its effectiveness as a counterbalance by anteriorly shifting the tail's COM (Irschick and Jayne, 1999b). For all but one trial (Table 1.2), bipedal lizards also raised their hip height, a mechanism utilized by birds in anticipation of uneven terrain (Birn-Jeffery and Daley, 2012). Together with an increase in body angle and raising the hips, *S. woodi* depresses the tail to maintain a bipedal posture, and pitch the body COM forward and over the obstacle as it crosses it.

Performance and behavior with multiple obstacles

In complex habitats, an increase in the size of obstacles has been shown to decrease sprint speed in *Sceloporus malachiticus* (Kohlsdorf and Biewener, 2006) and *Sceloporus woodi* (Tucker and McBrayer, 2012) compared to level running. *Sceloporus woodi* had the highest velocity crossing a single obstacle followed by an 11% loss in velocity between the one obstacle and two obstacle trials (Figure 1.1, Table 1.1). Many lizard and rodent species have lower escape speeds in dense vegetation compared to open areas (Vasquez *et al*., 2002; Schooley *et al*., 1996; Goodman, 2009; Vanhooydonck and Van Damme, 2003), yet those utilizing bipedal running may be able to exploit more habitat types via increasing visual perception and/or reaching their maximum speed more quickly (Rieder *et al*., 2010; Djawdan and Garland, 1988; Rocha-Barbosa *et al*., 2008; Kohlsdorf and Biewener, 2006). Since two and three obstacles create the same negative performance effect on stride characteristics and velocity, bipedalism may only be beneficial when negotiating a single obstacle (Figure 1.1, Table 1.1), or distantly spaced obstacles (which remains untested). Data from the multiple obstacle trials clearly shows that bipedalism is more efficient on a single obstacle. Here, the majority of lizards switched to a

quadrupedal posture to cross the 2nd and 3rd obstacle. Beyond a single obstacle, quadrupedal running and intermittent locomotion appear to be more beneficial.

The negative impact of running over obstacles results in the use of bipedal running or intermittent locomotion to counteract the decrease in forward velocity caused by the obstacle. In this study, lizards paused significantly less with bipedal running than individuals that only ran with a quadrupedal posture (Figure 1.4). If pausing and bipedalism provide advantages for negotiating obstacles (Kohlsdorf and Biewener, 2006), then it would not be necessary for a lizard to employ each behavior in the same escape run. A disadvantage of pausing during high-speed locomotion is the rapid initial acceleration needed after a pause (Higham *et al*., 2001). Since bipedalism is likely not solely a consequence of rapid acceleration in *S. woodi*, then it is unlikely that this posture would subsequently follow a pause. Pausing in a habitat cluttered with obstacles may be strategically and energetically favorable (Vasquez *et al*., 2002; Higham *et al*., 2001), plus allow the animal to assess upcoming terrain. Bipedal running in more open habitats may allow for enhanced visual range while still in motion (Olberding *et al*., 2012), and therefore may be a more efficient strategy than pausing when encountering obstacles.

Conclusion

This study has identified mechanisms by which small terrestrial vertebrates alter their behavior in response to habitat characteristics that impede sprint locomotion. Terrestrial vertebrates are faced with tradeoffs where one behavioral strategy is offset by the efficiency of another. I show that lizard sprint velocity declines as obstacle number increases, and surprisingly that intermittent locomotion is unchanged (Figure 1.1, Table 1.1). Multiple obstacles illicit behavioral and kinematic shifts in locomotor posture (to quadrupedalism), and stride frequency. For a single obstacle, bipedalism enables maintenance of high forward velocity, taking fewer,

longer strides, and a decrease in intermittent locomotion (Figure 1.1-1.4, Table 1.1). Use of a

bipedal posture also increases the likelihood that an animal may step over an obstacle to

minimize disruption of the body COM and likelihood of stumbling (Figure 1.2, Table 1.1).

Future research should examine the effects of altering body angle (elevated), hip height, and

lowered tail in both quadrupedal and bipedal postures. Furthermore the effect of obstacle

spacing, size, and orientation on locomotor performance has yet to be adequately understood for

either posture.

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TABLES AND FIGURES

Table 1.1: Raw data of locomotor performance and behavior in *S. woodi*. Data are presented as either frequency, or mean ± S.E.M., for performance and behavior among obstacle trials. Total sample size is indicated (N), as well as the sample size for each trial type (n). Behavior was quantified as stepping on or over the obstacle. Posture (bipedal or quadrupedal) was quantified in the stride prior to the obstacle. Posture at 0.4m was quantified as the posture at this position in no obstacle trials and obstacle trials. Dashes indicate variables that could not be quantified for the specified condition. Posture velocity was excluded from the "with" column since it was not necessary to analyze all trials together. Total strides and bipedal strides were counted in the 1 meter run. Total strides were quantified as the total number of strides completed when the specified posture was used at any point in the run. Shared letters indicate p-values are ≤ 0.05.

Variable	N	0 obstacles (n=15)	With obstacle (n=53)	1 obstacle (n=20)	2 obstacles (n=14)	3 obstacles (n=19)
Behavior (on/over)	53	-	17,36	6,14	3,11	8,11
Crossing posture (B,Q)	53	-	19,34	10,10	4,10	5,14
Posture at 0.4m (B,Q)	68	6,9$_A$	22,31$_A$	10,10	5,9	7,12
Velocity (m/s)	68	2.7±0.09	2.7±0.05	2.9±0.09$_B$	2.5±0.07$_B$	2.6±0.08$_B$
Bipedal velocity	46	2.4±0.06	-	2.6±0.07$_C$	2.2±0.04$_D$	2.3±0.07$_E$
Quadrupedal velocity	22	2.3±0.16	-	2.2±0.08$_C$	2.1±0.15$_D$	2.2±0.09$_E$
Bipedal over velocity	16	-	2.5±0.06$_F$	-	-	-
Quad. over velocity	20	-	2.3±0.06$_F$	-	-	-
Pauses	141	0.42±0.1	0.5±0.07	0.54±0.15	0.63±0.1	0.31±0.09
Total strides	68	6.9±0.27	7.04±0.16	6.7±0.22	6.9±0.29	7.6±0.27
Bipedal strides	68	1.6±0.4	1.5±0.2	2.1±0.45	1.5±0.27	1.0±0.26
Total strides w/ Bipedal	46	6.6±0.34 (n=10)$_G$	6.8±0.21 (n=36)$_G$	6.5±0.27	6.6±0.31	7.6±0.48
Total strides w/ Quad.	22	7.6±0.24 (n=5)$_H$	7.5±0.16 (n=17)$_H$	7.0±0.27	7.7±0.31	7.6±0.48

Table 1.2: Raw kinematic data for bipedal and quadrupedal running in *S. woodi*. Data are presented as either frequency, or mean ± S.E.M., for posture kinematics among obstacle trials. Total sample size is indicated (N), as well as the sample size for each trial type (n). All variables are measured before reaching the obstacle at 0.4m. Body angle and tail angle (total and by posture) are quantified as positive or negative degrees. Hip height (total and by posture) is measured in centimeters. Tail elevation (by posture) is quantified as the frequency of positive, or negative, elevation. Bipedal tail is the frequency of elevated (E) or lowered (L). One individual was excluded from tail elevation due to a missing tail. Shared letters indicate p-values are ≤ 0.05.

Variable	N	0 obstacles (n=15)	With obstacle (n=53)	1 obstacle (n=20)	2 obstacles (n=14)	3 obstacles (n=19)
Body angle at 0.4m	68	11.5±2.6	10.2±1.4	12.5±2.2	12.1±2.7	6.4±2.3
Bipedal body angle	68	$18.4\pm2.4_A$	$17.7\pm1.8_B$	$16.2\pm2.1_C$	$21.3\pm2.4_D$	$17.3\pm4.1_E$
Quadrupedal body angle	68	$6.8\pm2.0_A$	$4.9\pm1.6_B$	$8.7\pm2.1_C$	$7.0\pm1.8_D$	$0.08\pm3.1_E$
Hip height (cm)	68	2.3±0.14	2.3±0.07	2.3±0.12	2.3±0.15	2.4±0.13
Bipedal hip height	68	$2.6\pm0.19_F$	2.6±0.13	$2.7\pm0.13_G$	2.6±0.27	$2.7\pm0.18_H$
Quadrupedal hip height	68	$2.1\pm0.15_F$	2.1±0.1	$1.9\pm0.13_G$	2.2±0.2	$2.2\pm0.14_H$
Tail angle at 0.4m	67	-0.32	-0.20	-0.34	-0.17	-0.09
Tail elevated (B,Q)	67	2,2	2,10	1,1	0,4	1,5
Tail lowered (B,Q)	67	4,7	20,20	9,9	5,4	6,7
Bipedal tail (E,L)	67	$2,4_I$	$2,20_I$	1,9	0,5	1,6

Figure 1.1: Mean velocity (m/sec) ± S.E.M. by obstacle group and obstacle crossing behavior for total velocity (postures combined), bipedal, and quadrupedal posture. Mean velocity was greatest with one obstacle. Bipedal running was faster than quadrupedal with one obstacle. Crossing over the obstacle with a bipedal posture was faster than crossing over the obstacle with a quadrupedal posture. * indicate p-values are ≤ 0.05.
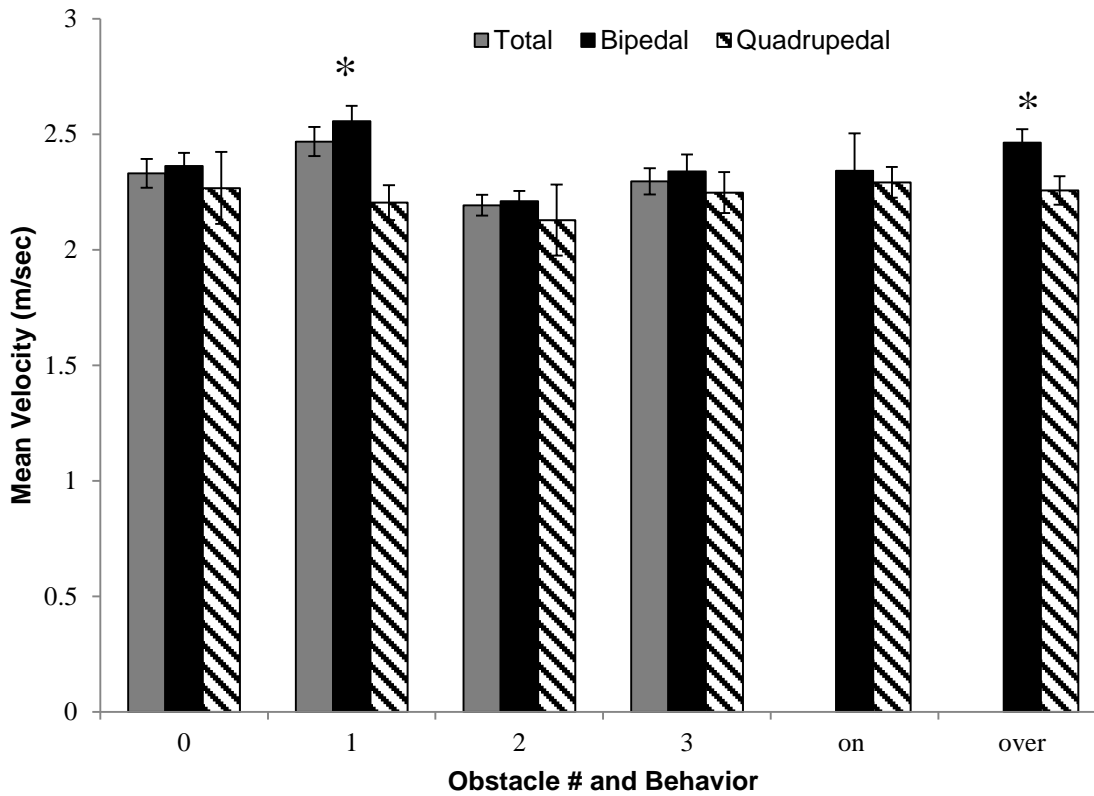
Figure 1.2: Frequency of obstacle crossing behavior and posture without an obstacle, with obstacle (1-3), and within each obstacle trial type (1-3). Bipedal posture was used significantly more with obstacles than without, and the frequency of quadrupedal posture when touching the obstacle was greater than bipedal. * indicate p-values are ≤ 0.05.
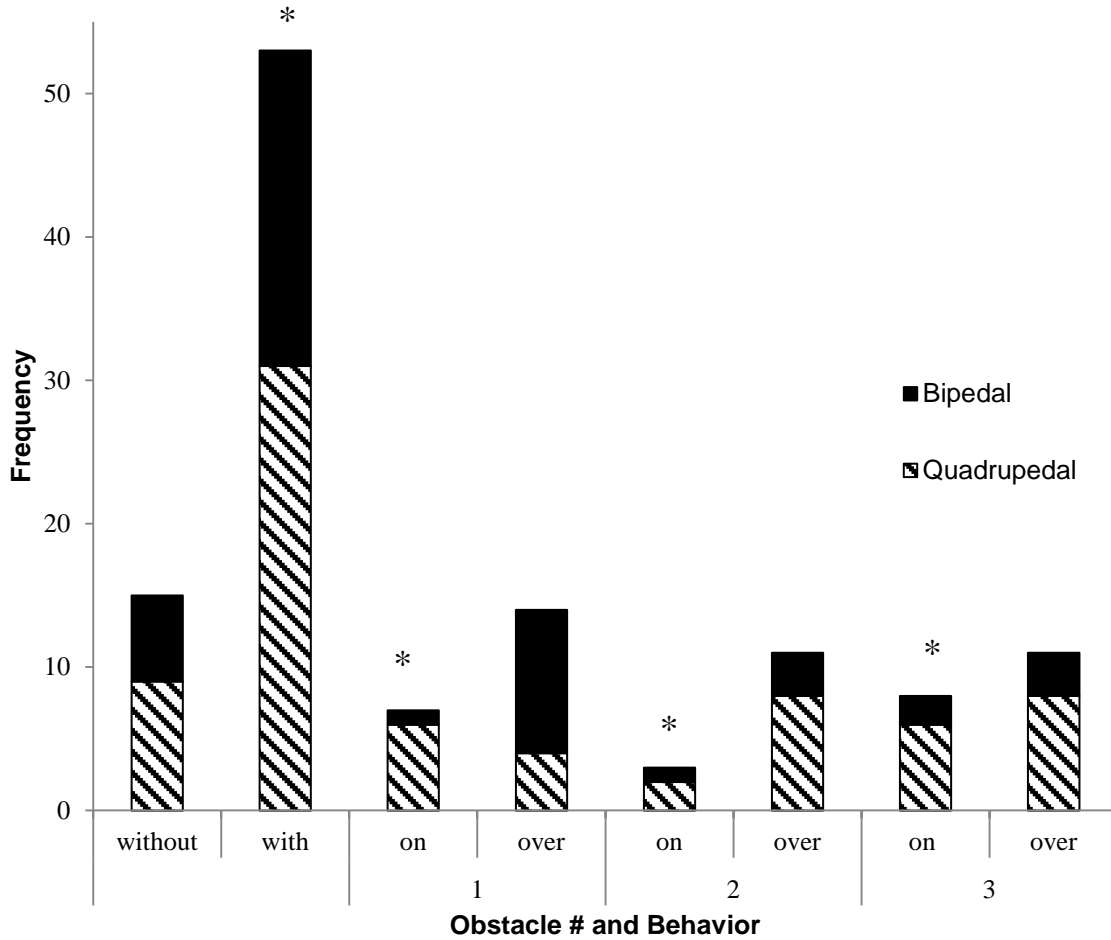
Figure 1.3: The mean frequency (± 1.0 S.E.M.) of total strides completed when bipedalism was used, and total strides completed when only a quadrupedal posture was used over a 1-meter racetrack. Fewer total strides were taken when a bipedal posture was used (trials 1-3 combined). * indicate p-values are ≤ 0.05.
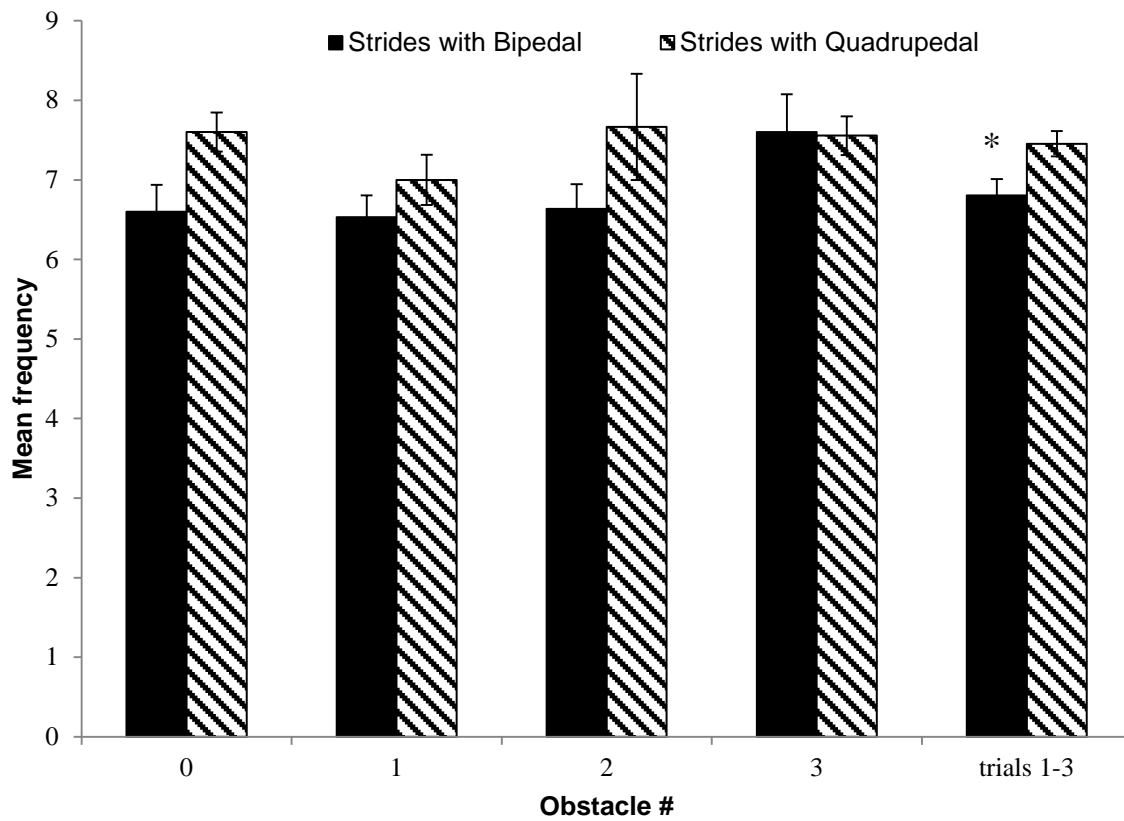
Figure 1.4: Mean frequency (± 1.0 S.E.M.) of total pauses, pausing with bipedal running, and pausing with quadrupedal running by obstacle group. Lizards paused significantly less when a bipedal posture was used compared to a quadrupedal posture. * indicate p-values are ≤ 0.05.
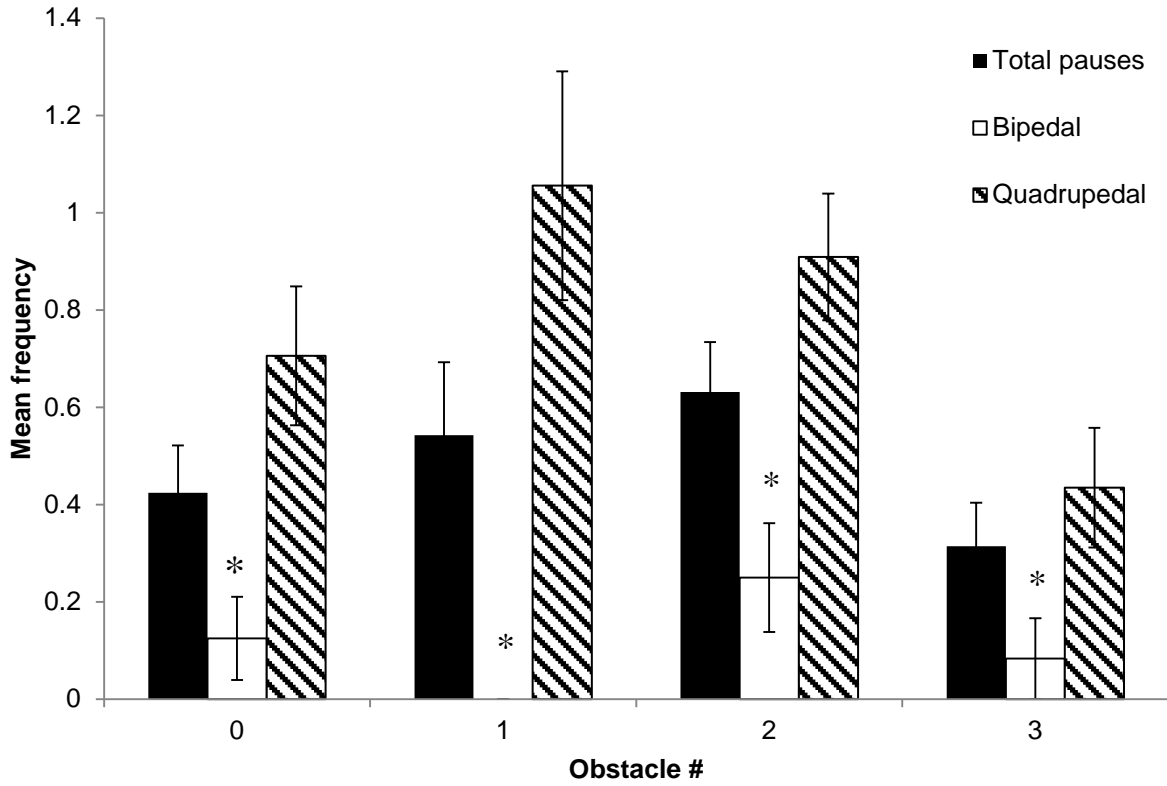
CHAPTER 2
VARIATION IN SCRUB LIZARD (SCELOPORUS WOODI) POPULATIONS BETWEEN TWO HABITAT TYPES IN OCALA NATIONAL FOREST, FL

ABSTRACT

One of the largest remaining populations of Florida scrub lizards exists throughout managed stands in the Ocala National Forest. However, recent data suggest this species is rare in many scrub stands. The differing microhabitat of sand pine scrub and longleaf pine (henceforth SPS, LLP) habitat may generate within stand variation in lizard occupancy, encounter rate, and behavior. Understanding lizard behavior (i.e., risk tolerance vs. risk aversion) at the microhabitat scale should provide insight into the likelihood of population persistence and survivorship. To compare risk behavior, I analyzed flight distance, distance to refuge, and refuge type between LLP and SPS populations. Detection distance, encounter rate, and population density were also used to compare LLP and SPS populations. Finally, I compared morphology and body temperature to link any variations to different microhabitat use between habitats. Lizards in LLP had greater flight distance, indicating higher risk aversion compared to SPS populations. Males in LLP had lower body temperature than in SPS, indicating potential effects on thermoregulatory behavior between habitats. Males were found further from a refuge, and had greater flight distance than females in both habitats. As a result, males may be more sensitive to predation risk during the breeding season. Detectability of adult lizards varied similarly within both habitat types; males were encountered more often than females, and detected at a great distance. Though detection distance was greater in LLP, encounter rate and population density for all lizard observations did not vary among habitats. The present study revealed subtle variations in risk assessment behavior and microhabitat use between SPS and LLP populations, which has implications for monitoring scrub lizard health and survival between two distinct habitat types in the ONF.

INTRODUCTION

The relative abundance of a species may indicate the health of a population in a given

habitat (Thomas, 1994; Hokit and Branch, 2003). In fragmented habitats, small terrestrial

vertebrates may decline in abundance due to both human induced habitat destruction and natural

disturbances (Hokit and Branch, 2003; Heath *et al*., 2012). In turn, population density and habitat

characteristics may influence how individuals utilize the habitat for foraging, mating, and

avoiding predation risk. Risk behavior is quantified by the proximity individuals are found from

refuges (distance to refuge, or DTR), and the linear distance of the escape path during flight from

a predator (flight distance, or FD) (Blumstein, 2006; Carter *et al*., 2010; Cooper and Wilson,

2007; Stiller and McBrayer, 2013). These measures are inherently related because flight distance

depends on an individual's proximity to a potential refuge (Cooper and Wilson, 2007). For

instance, when lizards remain visible in the open, they employ longer flight distances (Cooper

and Wilson, 2007; Cooper and Avalos, 2010). Therefore, an animal which is easily detected in

the open (i.e., detection distance) may exhibit different behavior (i.e., longer flight distance or

different refuge preference) than a cryptic individual which remains closer to a potential refuge

(i.e., tree, shrub). The detectability of lizards correlates to the amount of microhabitat structure

(Smith et al., 2012), and therefore may indicate certain risk behavior. Individuals that are easily

detected in the open, far from a refuge, are assumed to be at higher predation risk (Stankowich,

2008) and may show risk aversion, or avoidance, to a potential threat. Conversely, risk-tolerant

individuals occupying open habitats often have shorter flight distances (Carter *et al*., 2010;

Stankowich and Coss, 2006). Animals may show variation in risk behavior (tolerance vs.

aversion) in response to foraging availability, population density, gender, mating behavior, or

differing habitats with various refuges (Blumstein, 2006; Cooper and Avalos, 2010; Cooper and Wilson, 2007; Stankowich, 2008; Guay *et al*., 2013).

The Florida scrub lizard (*Sceloporus woodi*) is a diurnally active, ground-dwelling lizard that occupies flat, open sandy areas to sprint away from predators (Hokit *et al*., 1999; Tucker and McBrayer, 2012). This rare, potentially threatened, species is found in both SPS and LLP habitats in central Florida (Jackson, 1973; McCoy *et al*., 2004). Thus it provides a unique opportunity to study lizard behavior in two distinct habitat types within the same metapopulation. Patches of dry, sandy SPS habitat are characterized by regenerating (0-7 years) sand pine (*Pinus clausa*) and a variety of understory oaks (*Quercus spp.*), crookedwood (*Lyonia ferruginea*), and palmetto (*Serenoa spp.*) shrubs (Greenberg *et al*., 1994). Isolated sand hills of LLP (i.e., islands) are characterized by a dominant longleaf pine (*Pinus palustris*) canopy and an understory comprised of scattered turkey oak and wiregrass (*Aristida beyrichiana*) ground cover (Campbell and Christman, 1982; Hokit *et al*., 1999). Scrub lizards prefer shaded, yet open, sand substrates interspersed with litter and scattered vegetation, commonly found in turkey oak scrub or in LLP stands where prescribed fire is frequently used (Campbell and Christman, 1982; Tiebout and Anderson, 2001). However these traits are not found in sand pine timber stands (Tiebout and Anderson, 2001). Lizards typically abandon SPS stands approaching 7-9 years post-logging as the canopy becomes closed in, which may promote predation on *S. woodi* (Tiebout and Anderson, 1997; Hokit and Branch, 2003). Furthermore, lizards have low dispersal ability in the current landscape due to a combination of dense vegetation and an inability to move further than 200m to an adjacent, mature stand (Hokit *et al*., 1999).

While the ecological dynamics of scrub lizards inhabiting SPS are well documented (Branch *et al*., 2003; Clark *et al*., 1999; Hokit and Branch, 2003; McCoy *et al*., 2004; Tiebout

and Anderson, 2001), few studies have compared LLP and SPS populations. These habitats differ markedly in lizard microhabitat preferences, i.e., scrub lizards favor leaf litter and trees in LLP, while leaf litter and open sand are preferred in SPS (Kaunert, unpublished; Williams, unpublished). Lizards are more abundant in LLP, while SPS stands with 7+ years of growth, and lots of CWD, are noticeably absent of *S. woodi* (Tiebout and Anderson, 1997; Kaunert, unpublished; McBrayer *pers. comm.*). Clear-cutting and prescribed burning management practices are important to healthy scrub and longleaf pine habitat (Greenberg and Thomas, 1995; Outcalt and Greenberg, 1998; Weekley *et al.*, 2011), but may force scrub lizards into highly fragmented populations (Tucker *et al.*, 2014).

Scrub lizards have fewer foraging options in LLP compared to SPS (Williams and McBrayer, 2011). Limited foraging opportunity in LLP may encourage lizards to stray further from a refuge. Lizards in densely vegetated habitats (i.e., SPS) likely have shorter FD due to the proximity of numerous refuges, while lizards in open habitats (i.e., LLP) may have longer FD due to increased aversion to predation risk (Blamires, 1999; Stankowich and Coss, 2006; Blumstein, 2003). Searchers in ONF stands should find it easier to detect individual lizards in open areas where they are more likely to be found away from a suitable refuge, which may lead to higher encounter rates.

Population surveys depend on accurate representation of the spatial distribution and density of the target species (Gurarie and Ovaskainen, 2013). Populations may be monitored using a variety of methods (trapping, line-transect sampling, capture-mark-recapture) and encounter rates (the ratio of individual observations to sampling time; Anton *et al.*, 2013; Gurarie and Ovaskainen, 2013). Encounter rates may be indicative of the health of a particular habitat, if bio-indicator species in an area determine that the habitat is suitable for providing necessary

resources (Burger, 2006). In suitable habitats, species may find it easier to efficiently utilize available resources (i.e., refuges, foraging options) and perform key behaviors that enhance survival, fitness, and ultimately enhance population density (Huey, 1991). For instance, variation among habitats in body temperature may indicate more optimal microhabitat conditions, and/or thermoregulatory opportunity (Huey, 1991), while variation in body size may reflect greater foraging quality and/or longer lifespan (Goodman *et al*., 2008; Stiller and McBrayer, 2013). In this study I will compare body size and temperature among SPS and LLP stands, as well as the detectability of lizards, and population density. Furthermore, I will overlay salient behavioral metrics to examine risk aversion between the two habitat types, as these measures likely reflect responses to predation intensity and/or may influence detectability.

Questions and Predictions

The following questions will be addressed: 1) how does risk tolerance versus risk aversion differ in SPS compared to LLP? I will compare flight distance, distance to refuge and refuge use between habitats and sexes. I predict that scrub lizards will have a shorter flight distance, and shorter distance to refuge, in SPS than in LLP. Furthermore, I predict that lizards in SPS will utilize different refuge types. I will also examine inter-sexual variation across LLP and SPS stands. I predict that males will exhibit greater flight distance and distance to refuge than females in both habitat types. 2) Are lizards more easily detected in SPS or LLP, and does detectability differ between adult males and females? I will compare detection distance and encounter rate between habitats and sexes, and population density between LLP and SPS. I predict that detection distance will be greater in LLP, and that males will be detected at a greater distance within both habitats. I predict that population density and encounter rates will be higher in LLP compared to SPS, and that males will be encountered at a higher rate than females. 3)

Finally, is there variation in lizard morphology and body temperature between habitats? I predict that LLP populations will have a lower body temperature, but a greater snout-to-vent length (SVL), hind-limb length (HLL), and body mass than SPS populations.

METHODS

Scrub lizards were observed in the Ocala National Forest throughout the breeding season (May to August 2013). The ONF covers over 180,000 hectares in Marion County, Florida, and contains the largest remaining continuous area of SPS habitat (Greenberg *et al*., 1994). Only regenerating SPS stands that were clear-cut and roller-chopped within the last 3 to 4 years were sampled. These management criteria create habitat that is analogous to LLP stands, which was important for comparable populations of lizards between stand types. The LLP islands sampled are on a 2 year burn cycle to reduce buildup of understory vegetation (Kaunert, unpublished). A total of 5 SPS (N = 178 lizards observed) and 3 LLP (N = 243 lizards observed) stands were sampled; five, rather than three, SPS stands were sampled because SPS stands contained less searchable area than LLP stands (Kaunert, unpublished; Williams, unpublished). Stands were haphazardly searched daily between 0800 and 1900 hours. In SPS, open sand patches were searched, as were areas beneath vegetation where scrub lizards are typically found foraging and thermoregulating. The interior of regenerating SPS stands does not contain mature trees hence this refuge type was unavailable in SPS. In LLP which contains mature turkey oak and longleaf pine trees, lizards were sampled on both the ground and trees up to 1.5 m high; lizards are known to commonly perch below 1.5m on mature trees in LLP. Perimeter roads and stand interiors were sampled in equal proportion at each site. Encounter rates (lizards observed per minute) were calculated for each sampled stand. Total area sampled within each stand was calculated by measuring walking rate (0.72 meter/second) and forward visual range (9.8 m^2) while searching.

Based on total search time, sampled area was greater in LLP (1,751,636 m^2) compared to SPS (1,561,868 m^2). This area estimate was used to calculate population density of all lizard observations (all age/sex classes).

Male scrub lizards were captured via slip noose made from monofilament fishing line threaded through the tip of a fishing pole. Adults were sexed by determining the presence of post-anal scales. Body temperature was measured via cloaca thermometer within 30 seconds of capture. I measured snout-to-vent length, hind-limb length and body mass for each male (Appendices; Figure 3C). Only adult males were measured for morphology and body temperature. Females and juveniles were not captured, but were visually identified in the field by observing the presence of dorsal chevrons and the absence of large, bright blue throat patches.

All observations of adults and juveniles were included for analysis between habitats, however only adult males and females were used for comparison between sexes. For all lizards, detection distance, distance to nearest refuge, and flight distance was measured immediately after sighting or capture. Data were collected in the following manner. Upon initial detection of a lizard, I marked the placement of my feet on the ground, and then began approaching the target lizard. If the lizard fled, a marker was thrown in the spot where the animal was originally seen. Detection distance was measured between the animal's initial sighting location and the searcher's original standing location. Distance to nearest refuge was quantified as the straight line distance between the animal's original location and the closest potential refuge (i.e. tree, shrub). Flight distance was measured as the complete, linear distance of the flight path between the marker where the lizard was originally seen and the spot where the lizard ultimately stopped, sought refuge or was captured. All statistical tests were performed using JMP Pro[©] v10.0 software; alpha was the standard p ≤ 0.05. One-way ANOVAs, Welch's ANOVA, Chi Square

Likelihood, nonparametric Mann-Whitney U and Kruskal-Wallis tests were used for analysis between habitats and adult sexes (Appendices; Table 2E).

RESULTS

Risk aversion between habitats

Flight distance was significantly greater in LLP than SPS ($\chi^2_{1,389} = 19.6$, $p < 0.0001$) (Table 2.1). Given that most lizards in LLP fled from the ground to a tree (36%) or fled only on a tree (35%), it was necessary to further examine those encounters where flight occurred solely on the ground (10% in LLP) to compare the same behavior between the two. Still, flight distance on the ground was significantly greater in LLP than SPS ($\chi^2_{1,190} = 10.0$, $p = 0.0016$). Thus, lizards in LLP show greater risk aversion in their response to predation. Interestingly, there was not a significant difference in distance to refuge between sites ($\chi^2_{1,361} = 2.4$, $p = 0.125$), although the type of refuge used varied within each habitat (Table 2.2; in LLP $\chi^2_{7,217} = 371.8$, $p < 0.0001$; in SPS $\chi^2_{7,153} = 263.5$, $p < 0.0001$). In LLP lizards utilized turkey oaks (65%) as refuges, while lizards principally used myrtle oaks (60%) in SPS (Table 2.2).

Risk aversion between sexes within each habitat type

Male and female behavior patterns were the same across both habitat types. Adult males had the greatest distance to refuge ($\chi^2_{1,146} = 23.1$, $p < 0.0001$) and flight distance in SPS ($\chi^2_{1,151} = 72.4$, $p < 0.0001$) (Table 2.1). Adult males also had the greatest distance to refuge ($\chi^2_{1,175} = 15.9$, $p < 0.0001$) and flight distance in LLP ($\chi^2_{1,194} = 19.9$, $p < 0.0001$) (Table 2.1).

Detectability between habitats and sexes

Detection distance was significantly greater in LLP than SPS ($\chi^2_{1,368} = 23.1$, $p < 0.0001$) (Table 2.1). In SPS, detection distance was significantly greater for adult males compared to females ($\chi^2_{1,149} = 89.4$, $p < 0.0001$) (Table 2.1). In LLP, detection distance was also significantly

greater for adult males compared to females ($\chi^2_{1,178} = 181.5$, p < 0.0001) (Table 2.1). Lizard

encounter rate was not significantly different between LLP and SPS ($F_{1,55} = 1.24$; p = 0.27)

(Table 2.1; Figure 2.1). Within SPS (N = 178), males were encountered at a higher rate

compared to females ($F_{1,54} = 6.5$; p = 0.014). In SPS, 56% of lizards encountered were males,

30% females and 14% juveniles. In LLP (N = 243), males were also encountered at a higher rate

($U_{1,56} = 205.5$; $N_1 = 28$; $N_2 = 28$; p = 0.0022). In LLP, 55% of lizards encountered were males,

36% females, and 9% juveniles. Though a previous study found that LLP harbored a greater

density of scrub lizards per hectare than SPS (Kaunert, unpublished), here mean lizard density

per square meter was not significantly different (LLP = 0.00014 lizards/m^2; SPS = 0.00011

lizards/m^2; Table 2.1; $F_{1,55} = 3.24$; p = 0.078).

Morphology and body temperature of males between habitats

Morphology did not differ between LLP and SPS populations. There were no differences

in SVL ($\chi^2_{1,225} = 0.003$, p = 0.96), HLL ($F_{1,225} = 0.47$; p = 0.50) or body mass ($\chi^2_{7,225} = 6.2$, p =

0.52) between male lizards in LLP and SPS. Mean body temperature of male lizards was

significantly higher in SPS than in LLP (35.7°C in SPS; 34.8°C in LLP; $\chi^2_{1,156} = 13.1$, p =

0.0003).

DISCUSSION

I investigated scrub lizard populations in LLP and SPS habitats to show differences in the

degree of detectability and associated risk behaviors. Adult lizards were detected from a greater

distance and had greater flight distance in LLP than in SPS. Distance to refuge was not different

between LLP and SPS, indicating that both habitats contain numerous refuges with similar

distributions. Patterns of risk aversion behavior between males and females were similar across

habitat types. Males had greater distance from a refuge and flight distance compared to females.

Adult males were encountered at a higher rate and detected from a greater distance than adult females within both habitat types. Population density estimates were similar between SPS and LLP, and males did not vary in morphology. Interestingly, males in LLP had a lower body temperature, which may reflect variation in the microclimate of each habitat type.

Risk aversion between LLP and SPS

Refuges have a similar distribution within each habitat (Table 2.2). Scrub lizards in LLP are typically captured on trees, most frequently turkey oaks (65%; Table 2.2), but are also commonly encountered on open ground (23%; Kaunert, unpublished). Lizards in LLP had a greater flight distance than SPS lizards, regardless of whether lizards fled on the ground or up a tree. In a similar study by Cooper and Wilson (2007), *Sceloporus virgatus* on trees exhibited a shorter distance to refuge and shorter flight distance, than lizards on logs, rocks, open ground or grasses. Sand pine scrub has few mature trees (except for the bordering sand pine forest which does not harbor lizards, and was not sampled; Tiebout and Anderson, 1997; 2001). Scrub lizards move twice as far in open habitat compared to areas with dense vegetation (Hokit *et al*., 1999), thus the available open habitat in LLP may allow similar movement compared to the more densely vegetated SPS. In Columbian black-tailed deer (*Odocoileus hemionus columbianus*), individuals have shorter flight distances due to their greater proximity to protective cover in their native habitat (Stankowich and Coss, 2006). Deer fled shorter distances in areas with scrub and grasses compared to areas with only grass, which suggests that dense cover keeps an animal hidden from an approaching threat (Stankowich and Coss, 2006). This means an individual will remain motionless while a predator approaches, or move a relatively short distance as needed (Stiller and McBrayer, 2013). Though distance to refuge was similar between habitats, the dense vegetation cover of SPS (Hokit and Branch, 2003) likely conceals lizards from predators.

Risk assessment is strongly influenced by social behavior (Cooper, 2009). This study was conducted during the breeding season and thus social interactions likely influence risk assessment. Males were found further from a refuge than adult females in both habitats (Table 2.1). Males also exhibited greater flight distance, which is correlated with increased distance to refuge (Cooper and Wilson, 2007; Cooper and Avalos, 2010). Male rock agamas (*Agama planiceps*) use risk-taking behaviors that make them obvious to predators, such as prominently basking and moving while signaling mates (Carter *et al*., 2010). In similar fashion, male scrub lizards presumably patrol specific areas during the breeding season, which they likely defend, and use for mating purposes, thereby making them more conspicuous (McCoy *et al*., 2004; Hokit and Branch, 2003). Greater FD was likely observed because male territories often extend out in the open or further from a potential refuge, thereby increasing risk. Female lizards exhibit shorter FD and DTR during the breeding season, potentially to protect their reproductive investment (Plasman *et al*., 2007; Cooper, 2009). Additionally, female lizards may be hesitant to flee since locomotor performance is hindered by gravidity (Capizzi *et al*., 2007). Hesitation may allow searchers to approach closer before the lizard flees. The effect of gravidity was not controlled in the present study, even though field data collection occurred during the peak breeding season (May – August), and it is very likely that female scrub lizards were gravid. Hence, female scrub lizards display different risk aversion behavior than males due to tradeoffs in reproductive effort, foraging options, and life expectancy during this period.

Detectability between habitats and adults

Not surprisingly, the conspicuous behavior exhibited by male scrub lizards led to their higher encounter rate and greater detection distance within both habitats (Table 2.1). A recent

study determined that lizard density was significantly higher in LLP than SPS. Kaunert (unpublished) showed that all LLP perimeter roads and the interior of stands were occupied by lizards, and estimated their density at 49 lizards per hectare. Because similar roads and stands were sampled in this study, one would expect encounter rates to be higher in LLP. Despite higher abundance in the 3 LLP stands than in the 5 SPS stands, encounter rate and density was the same between LLP and SPS stands sampled in this study (Table 2.1; Figure 2.1). This contrasting result may be due to the fact that *S. woodi* has highly variable densities (10-124 individuals/hectare) within SPS (Williams and McBrayer, 2011; Jackson and Telford, 1974; McCoy *et al*., 2004). Furthermore, the current finding of similar population densities in LLP and SPS may be attributed to differing sampling methods. The same 3 LLP sites were sampled as Kaunert (unpublished); however different SPS stands were selected. I chose SPS stands which were most suitable to harbor lizard populations, while Kaunert (unpublished) chose SPS stands based solely on management criteria (number of years post-logging). In doing so, only 3 of the 5 SPS stands that I sampled were also used in Kaunert's (unpublished) analysis, leaving 2 SPS stands between our studies with potential for variation in lizard density. Therefore, LLP is suitable for harboring healthy scrub lizard densities, as are some, but not all, SPS stands. Understanding the factors that enhance *S. woodi* density in SPS habitat (e.g., connectivity between adjacent scrub stands) warrants additional study.

Morphology and body temperature of males between habitats

The environment through which animals must move can influence how natural selection shapes morphology (Goodman *et al*., 2008). Male scrub lizard growth rate is positively correlated with habitat patch size in SPS (Hokit and Branch, 2003); unfortunately growth rate data are not available for lizards in LLP. Since individual LLP islands encompass a greater area

in the ONF than individual scrub stands (Tucker *et al*., 2014), then one would expect males to be

larger in this habitat. Previous work indicates that females, not males, differ in body size and

shape between LLP and SPS (Williams, unpublished), and this study corroborates this finding.

Despite any habitat differences between LLP and SPS, male lizards achieve similar body sizes.

Difference in body temperature may be a direct consequence of the varying microhabitat

in LLP and SPS and how lizards use it (Williams, unpublished). The ground in LLP offers poor

refuge from thermal extremes and predators due to a mosaic of small open sand patches

separated by clumps of dense wiregrass (Williams, unpublished). Thus, longleaf pines and

mature turkey oaks provide important perch sites for thermoregulation and foraging

opportunities in LLP, yet trees are not available in SPS (Tiebout and Anderson, 2001; Williams,

unpublished). Consequently, wind exposure and shade create a cooler microclimate in LLP

(Williams, unpublished), which is likely reflected by lower body temperatures in male *S. woodi*

in that habitat. Scrub lizards must choose microhabitats that are suitable for thermoregulation

(i.e., turkey oaks, open sand), and LLP may harbor more suitable microhabitat for this than is

available in SPS. It remains unclear whether thermoregulatory opportunity may influence growth

rate and/or population density in the ONF.

Conclusion

The purpose of this project was to quantify behavioral, morphological, and physiological

variation between LLP and SPS populations of *S. woodi*. Adult scrub lizards tend to exhibit risk

aversion and are easier to detect in the LLP habitat. Their detectability is possibly due to

microhabitat differences between SPS and LLP, with more open sand available in SPS but more

mature trees in LLP (Tiebout and Anderson, 2001; Kaunert, unpublished). Females move less to

forage during the breeding season (Williams and McBrayer, 2011), presumably to protect their

reproductive investment (Williams and McBrayer, 2011; McCoy *et al*., 2004; Cooper, 2009). Therefore, an observer moving through stands in the ONF is more likely to detect male scrub lizards during the breeding season, and most likely to encounter more males. In LLP, population densities are greater than in SPS. This is likely linked to management (2 year prescribed fire cycle), and its resultant mix of open sand for foraging and social interactions, as well as numerous mature trees for refuge from predators and additional sites for thermoregulation.

As human recreation and disturbance in natural areas increases, so will the disturbance to wildlife (Stankowich, 2008). Scrub lizards have been used as a model for studies regarding habitat fragmentation (Tiebout and Anderson, 2001; Hokit *et al*., 1999; Hokit and Branch, 2003; Clark *et al*., 1999; Heath *et al*., 2012; McCoy *et al*., 2004). Clear-cut logging for wood pulp and roads is the leading cause of fragmentation in the ONF, which reduces genetic variability and increases risk of extinction for *S. woodi* populations (Tucker *et al*., 2014). Habitat fragmentation may also increase predation on scrub lizards (Hokit and Branch, 2003). The present analysis reveals that scrub lizards behave differently in LLP vs. SPS stands. Future research should quantify risk aversion behavior among stands with varying degrees of connectedness. Furthermore, variation in neither growth rate nor survivorship has been studied in LLP yet should be. Understanding the factors which limit colonization, growth, and survival in this species will inform management techniques within the sand pine scrub and longleaf pine habitat in the Ocala National Forest.

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Table 2.1: Risk behavior and detectability between habitats and adult lizards. Data is presented as mean ± S.E.M. Distance to refuge, flight, and detection distance are presented in meters. Encounter rate is measured as lizards per minute, and density is measured as lizards per square meter. Shared letters indicate p-values are ≤ 0.05.

	SPS	LLP	SPS ♂	LLP ♂	SPS ♀	LLP ♀
Detection distance	$2.29\pm0.10_A$	$2.75\pm0.12_A$	$2.62\pm0.12_C$	$3.00\pm0.14_F$	$1.88\pm0.18_C$	$2.42\pm0.25_F$
Distance to refuge	0.81 ± 0.06	0.86 ± 0.09	$0.91\pm0.08_E$	$0.77\pm0.11_H$	$0.75\pm0.11_E$	$1.26\pm0.20_H$
Flight distance	$1.57\pm0.15_B$	$1.83\pm0.13_B$	$1.94\pm0.19_D$	$1.68\pm0.17_G$	$1.30\pm0.27_D$	$2.34\pm0.25_G$
Encounter rate	0.05 ± 0.004	0.06 ± 0.004	$0.03\pm0.003_I$	$0.03\pm0.003_J$	$0.02\pm0.003_I$	$0.02\pm0.003_J$
Density	$1.1\times10^{-4} \pm 8.0\times10^{-5}$	$1.4\times10^{-4} \pm 9.0\times10^{-5}$				

**Table 2.2**: Summary of refuge type where lizards were captured among each habitat stand. Shrubs include rosemary, wiregrass, cactus, and palmetto. Dead wood includes logs and stumps. Turkey oak was most commonly used by LLP lizards, and myrtle oak was used most by SPS lizards.

Refuge	LLP1	LLP2	LLP3	LLP$_{total}$	SPS1	SPS2	SPS3	SPS4	SPS5	SPS$_{total}$
Turkey oak	53	30	59	142	-	-	2	2	-	4
Longleaf pine	15	1	13	29	-	-	-	-	-	-
Other pines	1	-	12	13	3	3	3	1	-	10
Chapman's oak	-	1	2	3	-	2	4	6	1	13
Myrtle oak	-	1	2	3	11	10	16	49	6	92
Live oak	-	5	-	5	-	-	1	-	-	1
Shrubs	-	2	9	11	4	1	2	23	-	30
Dead wood	3	4	4	11	-	1	-	2	-	3

**Figure 2.1**: Comparison of risk behavior of lizards between scrub and longleaf stands. Data is presented as mean ± 1.0 S.E.M. Flight and detection distance were greater in LLP. * indicate p-values are ≤ 0.05.
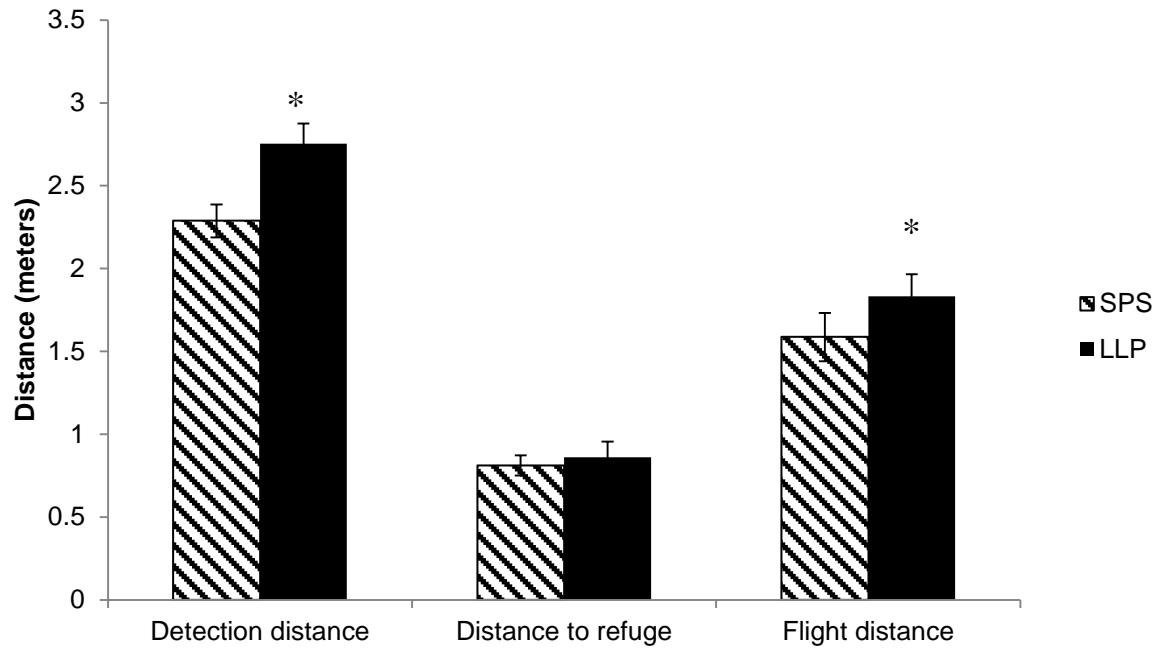
Figure 2.2: Encounter rate of all adult and juvenile lizards among each habitat stand. Data is presented as mean $\pm$ 1.0 S.E.M. Males were encountered at a higher rate in both habitats. Population density between LLP and SPS were the same (SPS $1.1\times10^{-4} \pm 8.0\times10^{-5}$; LLP $1.4\times10^{-4} \pm 9.0\times10^{-5}$; $F_{1,55} = 3.24$; p = 0.078).
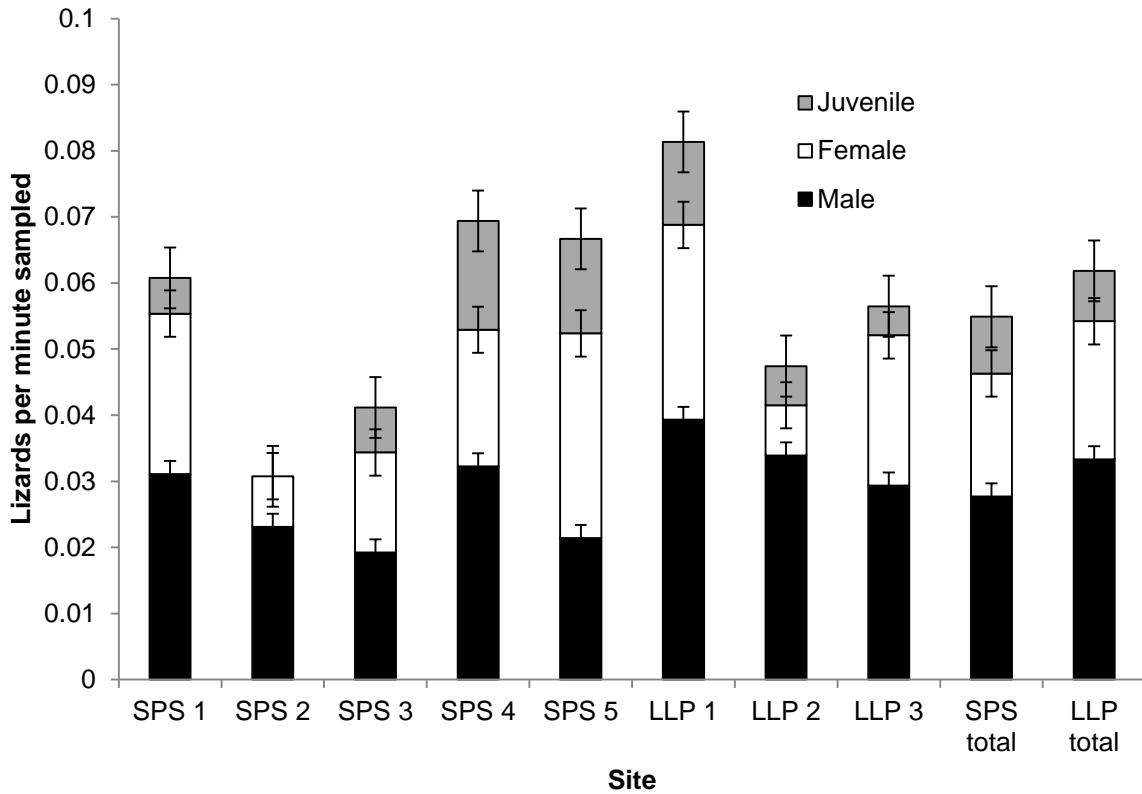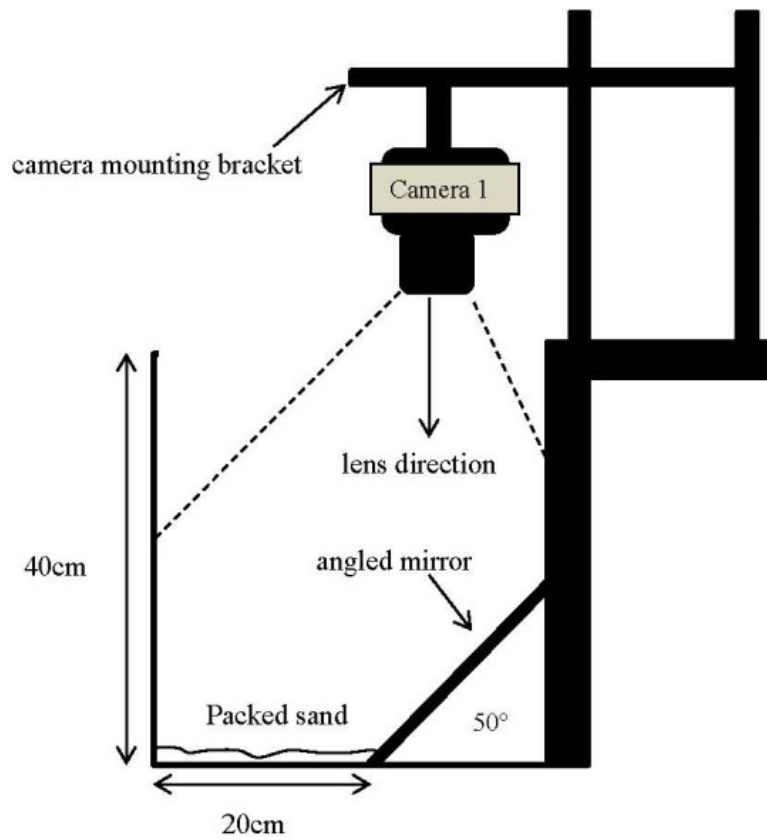
APPENDIX A

Figure 1: Overhead view of the racetrack. Four obstacle trials; 1) No obstacle, 2) one obstacle at 40cm, 3) two obstacles at 40cm and 80cm, and 4) three obstacles at 35cm, 60cm and 85cm. Cameras 1 and 2 are oriented vertically above the track using permanent mounts and angled toward the mirrored sidewall to include both dorsal and lateral views.
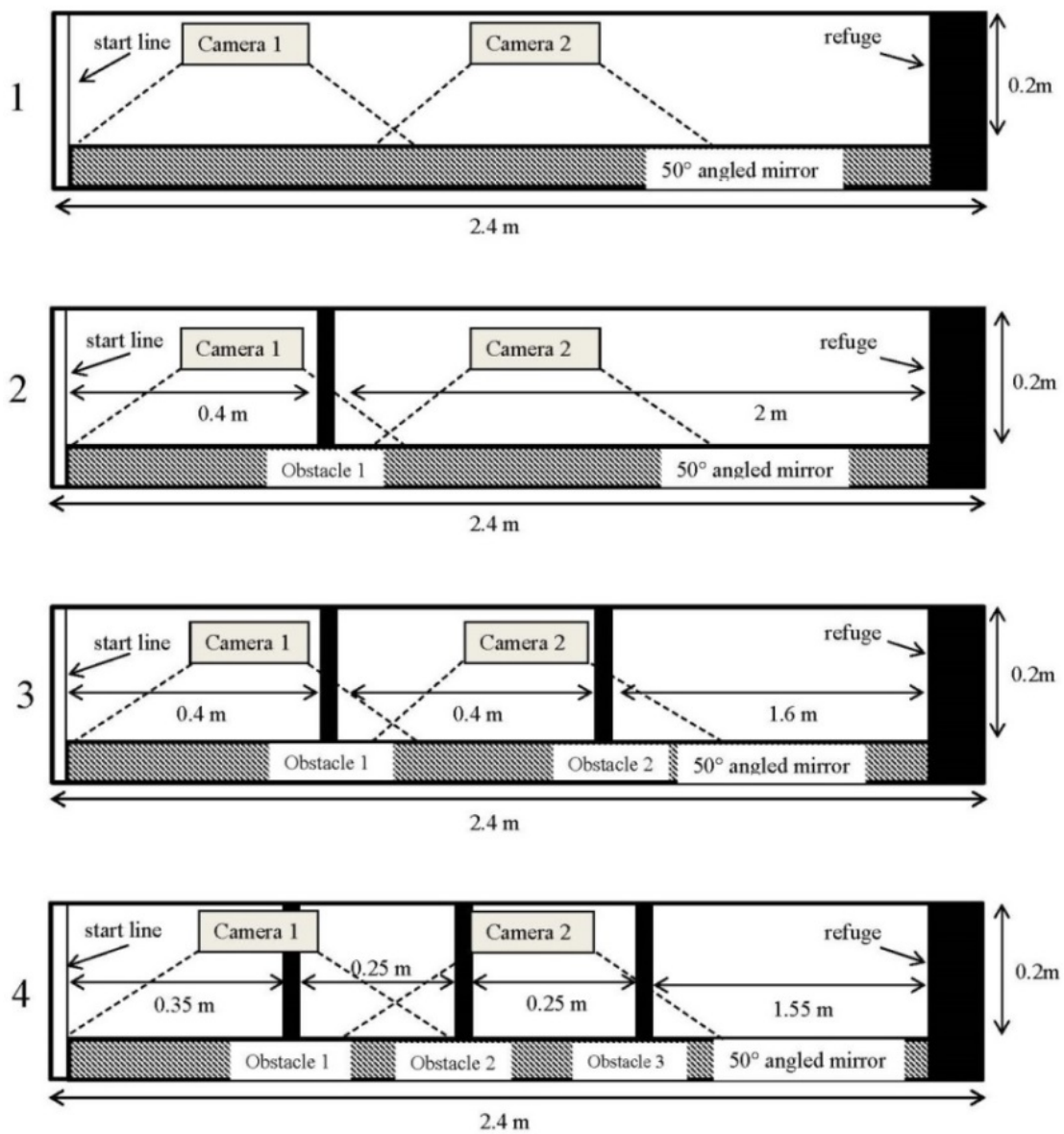
Figure 2: View from the starting position of the racetrack. The 50˚ angled mirror and camera attachment set up is shown along with packed sand substrate. A movable aluminum conduit mounting bracket allowed the cameras to be orientated in any position above the track anywhere along its length.

Figure 3: *Sceloporus woodi* with kinematic landmarks; 1) head mark posterior to the pineal eye for velocity, 2) shoulder mark for body angle, 3) hip height on the ilium, 4) base of the tail, and 5) 40% of the tail length from the base for tail elevation. Body angle was calculated as the difference between point 2 and 3 relative to the horizontal substrate. Hip height was measured as the vertical distance between point 3 and the substrate. Tail elevation was calculated as the difference between point 4 and 5 and the horizontal substrate.
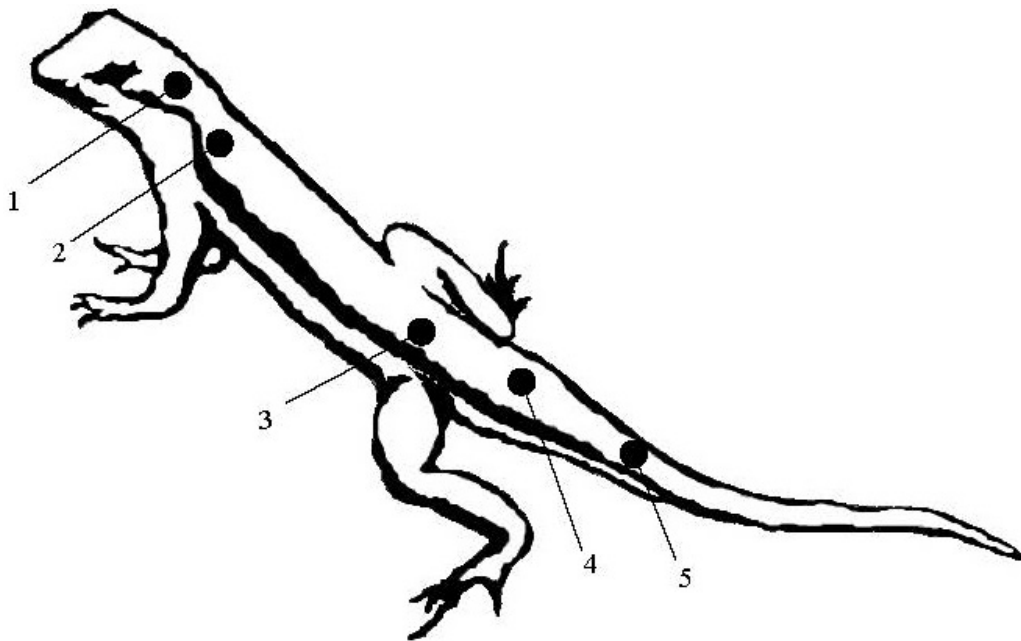
APPENDIX D

Table 1: Experimental design used in chapter 1. Each performance, behavior, and posture kinematics variable is listed with its corresponding question and statistical test.

Category	Variable	Question	Statistical test
Performance	Mean velocity	With vs. without	1-way ANOVA; Tukey-Kramer
		Single vs. multiple	1-way ANOVA; Tukey-Kramer
		B over vs. Q over	Kruskal-Wallis
		B vs. Q trial 0	1-way ANOVA
		B vs. Q trial 1	1-way ANOVA; Tukey-Kramer
		B vs. Q trial 2	1-way ANOVA
		B vs. Q trial 3	1-way ANOVA
		B vs. Q with obstacle	1-way ANOVA; Tukey-Kramer
		Bipedal with vs. w/o obstacle	1-way ANOVA
	Total strides	With vs. without	Mann-Whitney U
		Single vs. multiple	Kruskal-Wallis
		With B vs. w/o B	Kruskal-Wallis
	Bipedal strides	With vs. without	Kruskal-Wallis
		Single vs. multiple	Kruskal-Wallis
Behavior	Pausing	With vs. without	Chi Square
		Single vs. multiple	Chi Square
		With B vs. w/o B	Kruskal-Wallis
	Obstacle crossing	Quadrupedal on vs. over	Chi Square
		Bipedal on vs. over	Chi Square
	Posture before obstacle	B vs. Q trial 1-3	Chi Square
Posture kinematics	Body angle	With vs. without	Kruskal-Wallis
		Single vs. multiple	1-way ANOVA
		B vs. Q Trial 0, trial 3	1-way ANOVA
		B vs. Q Trial 1, trial 2	Kruskal-Wallis
	Hip height	With vs. without	1-way ANOVA
		Single vs. multiple	1-way ANOVA
		B vs. Q trial 0	Welch's ANOVA
		B vs. Q trial 1	1-way ANOVA
		B vs. Q trial 2, trial 3	Kruskal-Wallis
	Tail elevation	With vs. without	Chi Square
		Bipedal above vs. below horizontal	Chi Square

Table 2: Experimental design used in chapter 2. Each variable is listed with the corresponding question and statistical test used.

Category	Variable	Question	Statistical test
Detectability by lizard behavior	Detection distance	LLP vs. SPS	Chi Square
		LLP males vs. females	Chi Square
		SPS males vs. females	Chi Square
	Distance to refuge	LLP vs. SPS	Chi Square
		LLP males vs. females	Chi Square
		SPS males vs. females	Chi Square
	Flight distance	LLP vs. SPS	Chi Square
		LLP vs. SPS (on ground)	Kruskal-Wallis
		LLP males vs. females	Chi Square
		SPS males vs. females	Chi Square
	Refuge type used	Within LLP	Chi Square
		Within SPS	Chi Square
Population estimates	Encounter rate	LLP vs. SPS	1-way ANOVA
		LLP males vs. females	Mann-Whitney U
		SPS males vs. females	1-way ANOVA
	Density	LLP vs. SPS	1-way ANOVA
Morphology and body condition for males	SVL	LLP vs. SPS	Kruskal-Wallis
	HLL	LLP vs. SPS	Welch's ANOVA
	Body mass	LLP vs. SPS	Kruskal-Wallis
	Body temp	LLP vs. SPS	Kruskal-Wallis