Summer 2011

The Ontogeny of Escape Responses and Locomotor Performance in Sceloporus Woodi

Reed B. Stiller

Recommended Citation

Stiller, Reed B., "The Ontogeny of Escape Responses and Locomotor Performance in Sceloporus Woodi" (2011). *Electronic Theses and Dissertations*. 753.
https://digitalcommons.georgiasouthern.edu/etd/753

THE ONTOGENY OF ESCAPE RESPONSES AND LOCOMOTOR PERFORMANCE IN *SCELOPORUS WOODI*

by

REED B. STILLER

(Under the direction of Lance D. McBrayer)

ABSTRACT

Predator prey interactions have the potential to shape patterns of natural selection. For prey, avoiding detection by predators is of primary importance; however prey species risk detection by movement. Other than crypsis, prey species also use secondary defenses when detected by a predator. The most common secondary defense is flight. Flight initiation distance describes the distance between a prey item and a predator where the benefits of fleeing outweigh the benefits of remaining stationary. There are many factors that influence flight initiation distance including ontogenetic stage, ability to escape, and the degree of crypsis. Of these, the ontogenetic effects on escape velocity and flight initiation distance are likely to be substantial.

Juvenile and hatchling animals typically have a lower absolute velocity than adults. If escape velocity is a key variable in survival, then juveniles may be forced to tolerate shorter flight initiation distances than adults. As a result, they may switch anti-predator tactics or be susceptible to higher predation risk than adults. Hence, flight initiation distance of juveniles may be optimized such that their decreased locomotor abilities and use of immobility for concealment changes at a particular body size.

I examined this hypothesis in *Sceloporus woodi*, a small terrestrial lizard. Field measurements of escape velocity were recorded on an ontogenetic series of lizards using high speed video. Maximal running velocity was also quantified on a laboratory raceway to examine if the velocities used by lizards in the field are reflective of maximal velocities as measured in the lab, or if other variables, such as muscle size and limb size, are correlated with flight initiation distance and running performance.

I found that hind limb morphology scales isometrically with body size. Maximum velocity in the lab increased with size, adults being fastest and hatchlings being slowest ($F_{2, 97}$ = 12.6088, P = <0.0001). Escape velocity in the field did not vary between adults, juveniles, and hatchlings ($F_{2, 24}$ = 2.39, P = 0.114). Flight initiation distance increased as body size increased ($F_{2, 39}$ = 3.32, P = 0.047). Larger animals did not allow close approach of a human predator presumably escaping early and to avoid the need to use high sprint velocities to escape. Smaller lizards, due to slower sprint velocities, must use behavior to compensate for decreased sprint velocity. Small lizards remained immobile longer, allowing close approach of the predator, likely relying on crypsis to remain concealed. By remaining immobile longer, smaller lizards did not attract unnecessary attention of the predator and likely increase the probability of being required to use sprinting to escape predation. Isometric scaling coupled with the findings for sprint and escape velocity allow all classes to perform similarly thus optimizing hatchling and juvenile survival.

INDEX WORDS: Sceloporus woodi, Ontogeny, Locomotor performance, Allometry, Flight initiation distance, Escape behavior

THE ONTOGENY OF ESCAPE RESPONSES AND LOCOMOTOR PERFORMANCE IN *SCELOPORUS WOODI*

by

REED STILLER

B.S., Ball State University, 2008

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

STATESBORO, GEORGIA

2011

THE ONTOGENY OF ESCAPE RESPONSES AND LOCOMOTOR PERFORMANCE IN *SCELOPORUS WOODI*

by

REED STILLER

Major Professor:	Lance D. McBrayer
Committee:	C. Ray Chandler
	David C. Rostal

Electronic Version Approved:
July 2011

ACKNOWLEDGEMENTS

I would like to thank Dr. Lance McBrayer for his direction and support throughout my time at Georgia Southern University. I would also like to thank Dr. Ray Chandler and Dr. David Rostal, my committee members, for taking time out of their schedules to give me advice and guidance as well. I would like to thank Derek Tucker, Clint Collins, Daniel May, and Chase Patrick for field assistance and for advice on my research. My wife, Amber Stiller, was of great help in the field and her patience and support throughout my studies was greatly appreciated. I would finally like to thank my family for their support.

This equipment used in this research was funded by the Phase I Catalyst Grant awarded to Dr. Lance McBrayer. All live animal care and use was done in accordance with Georgia Southern University animal care protocol (IACUC I10006). Animal collection was permitted under Florida Fish and Wildlife Conservation Commission (LSSC-10-00057).

TABLE OF CONTENTS

PAGE

CHAPTER

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Predator prey interactions have the potential to shape patterns of natural selection. For prey, avoiding detection by predators is of primary importance; however prey species risk detection by movement. Other than crypsis, prey species also use secondary defenses when detected by a predator. The most common secondary defense is flight. Flight initiation distance describes the distance between a prey item and a predator where the benefits of fleeing outweigh the benefits of remaining stationary. There are many factors that influence flight initiation distance including ontogenetic stage, ability to escape, and the degree of crypsis. Of these, the ontogenetic effects on escape velocity and flight initiation distance are likely to be substantial.

Juvenile and hatchling animals typically have a lower absolute velocity than adults. If escape velocity is a key variable in survival, then juveniles may be forced to tolerate shorter flight initiation distances than adults. As a result, they may switch anti-predator tactics or be susceptible to higher predation risk than adults. Hence, flight initiation distance of juveniles may be optimized such that their decreased locomotor abilities and use of immobility for concealment changes at a particular body size.

I examined this hypothesis in *Sceloporus woodi*, a small terrestrial lizard. Field measurements of escape velocity were recorded on an ontogenetic series of lizards using high speed video. Maximal running velocity was also quantified on a laboratory raceway to examine if the velocities used by lizards in the field are reflective of maximal velocities as measured in the lab, or if other variables, such as muscle size and limb size, are correlated with flight initiation distance and running performance.

I found that hind limb morphology scales isometrically with body size. Maximum velocity in the lab increased with size, adults being fastest and hatchlings being slowest ($F_{2, 97}$ = 12.6088, P = <0.0001). Escape velocity in the field did not vary between adults, juveniles, and

hatchlings ($F_{2, 24} = 2.39$, $P = 0.114$). Flight initiation distance increased as body size increased ($F_{2, 39} = 3.32$, $P = 0.047$). Larger animals did not allow close approach of a human predator presumably escaping early and to avoid the need to use high sprint velocities to escape. Smaller lizards, due to slower sprint velocities, must use behavior to compensate for decreased sprint velocity. Small lizards remained immobile longer, allowing close approach of the predator, likely relying on crypsis to remain concealed. By remaining immobile longer, smaller lizards did not attract unnecessary attention of the predator and likely increase the probability of being required to use sprinting to escape predation. Isometric scaling coupled with the findings for sprint and escape velocity allow all classes to perform similarly thus optimizing hatchling and juvenile survival.

CHAPTER 1

INTRODUCTION

As organisms grow they experience an array of physical and ecological changes (Calder, 1984; Cediel et al., 2008). Juveniles and hatchlings, like adults, must avoid predators, acquire nutrients, and perform other necessary tasks to survive, but due to their smaller size and limited experience they also have unique challenges (Ricklefs, 1979; Martin and Lopez, 1995). Juveniles and hatchlings undergo tissue growth, such as muscle development, and limb elongation, both of which might alter locomotor performance (Carrier, 1996; Herrel and Gibb, 2006). The combination of these processes often results in high mortality in juveniles and hatchlings (Ashley et al., 1991; Warner and Andrews, 2002; Husak, 2006a). Juveniles and hatchlings use unique behaviors to remove themselves from direct competition with adults and increased predation pressure (Caro and Bateson, 1986). These behaviors include varying activity times, altering the length of activity, altering responses to predators, or utilizing refuges or foraging opportunities that adults do not or cannot use (Aragon et al., 2004). Juveniles and hatchlings may also inhabit different microhabitats than adults. For example hatchling brown trout *(Salmo trutta*) preferentially select shallower habitats than adults. Larger individuals require more space in which to feed and increased territory size decreases predation risk for larger fish (Ayllon et al., 2010).

Morphological characteristics of juveniles not only affect behavior but also may function in removing juveniles and hatchlings from competition with adults (Irschick et al., 2000). Juvenile and hatchling Australian brush turkeys (*Alectura lathami*) rely on wing assisted incline running to avoid a predator while adults use size and running speed to avoid predation. Younger, smaller turkeys are able to use powerful flight muscles to run up inclines while larger turkeys have higher mass and proportionally weaker flight muscles (Dial and Jackson, 2011).

Another common strategy is to adopt unique growth trajectories that allow smaller individuals to function at levels similar to their adult counterparts. Morphological or physiological traits may develop at similar (isometric) or different (positively or negatively allometric) rates as overall body size (Ricklefs, 1968; Pounds et al., 1983; Ashley et al., 1991; Promislow et al., 1992; Shine and Charnov, 1992; Young, 2005; Thompson and Kier, 2006; Young and Fernandez, 2009). Positive allometry results from a given trait (e.g. hind limbs) developing at a faster rate than overall body size. Negative allometry describes traits that develop slower than body size. Juveniles and hatchlings are often hypothesized to show negative allometry because this is thought to optimize an animal’s fitness at a young age. For example, the hind limbs are proportionally longest, relative to their body size, in juveniles and hatchlings. Thus smaller individuals may obtain higher running velocities for their size and thereby increase their probability of survival.

Among vertebrates, hind limb morphology correlates with sprint velocity (Huey and Hertz, 1982; Bonine and Garland, 1999). Animals with longer hind limbs often exhibit higher sprint velocities and, presumably, an increased ability to avoid predators or find prey (Losos, 1990). Organisms exhibiting isometry will have performance abilities that are proportional to their size. Those organisms exhibiting positive hind limb allometry as hatchlings or juveniles would have proportionally longer legs compared to body size at sexual maturity. Organisms that require parental care at hatching typically exhibit positive allometry because hatchlings, which are not capturing their own prey or moving extensively through the habitat, allocate energy to the growth of other systems. It has also been hypothesized that this developmental strategy is associated with large territory size and the need to travel long distances in organisms that have no parental care at hatching (Dodson, 1975). Those organisms exhibiting negative allometry would experience slower growth of the hind limbs (Irschick, 2000). Proportional to body size the legs of an individual showing negative allometry will be the longest at hatching, possibly enabling them to reach higher relative velocities than adults. The “improved” locomotor ability of hatchlings due to this pattern of growth may allow them to evade predators or find food more efficiently (Garland, 1985; Carrier, 1994). These developmental strategies also allow juvenile and hatchling organisms to differentially develop muscular or skeletal components to obtain higher sprint velocity, or acceleration, than if they had isometric growth trajectories. Allometric patterns of development and increased sprint performance in juveniles and hatchlings may decrease negative effects of smaller size on juveniles’ ability to compete and survive within an environment and has implications on predator avoidance strategies (Marsh, 1988; Carrier, 1994).

Predator avoidance strategies affect the survival and fitness of juveniles, and consist of primary and secondary avoidance tactics. Primary avoidance tactics involve defense against detection by predators, such as crypsis, and are employed regardless of the presence of the predator. Secondary predator avoidance tactics are employed after the failure of primary tactics like crypsis, and are typically employed only in the close presence of a predator. The most common means of secondary predator evasion is flight, or rapid locomotion away from a predator (Edmunds, 1974).

Flight decisions are influenced by an extensive cost-benefit analysis (Ydenberg and Dill, 1986). Costs include loss of foraging opportunities, loss of reproductive opportunities, loss of territory to a rival, and energy expenditure (Downes, 2001; Cooper and Frederick, 2007; Cooper, 2009ab; Lagos et al., 2009). Factors that affect the weight given to these costs include individual physical condition, predator approach velocity, distance to refugia, degree of crypsis, locomotor ability, and experience (Blamires, 1999; Cooper, 2003; Capizzi et al., 2007; Cooper and

Frederick, 2007) . Flight is initiated when a perceived predation risk reaches a level at which the benefits of remaining in the area no longer outweigh the cost of running from the predator (Cooper and Frederick, 2007). This distance, from predator to prey, is termed flight initiation distance (FID) (Ydenberg and Dill, 1986).

Regardless of age or development, all individuals engage in a cost-benefit analysis when encountering a predator. Less experienced individuals (e.g. juveniles and hatchlings) may have different behavioral responses than more experience ones (adults). Juveniles and hatchlings may increase FID if they are unable to reach the high maximal sprint velocities of adults. Increasing flight initiation distance would allow a higher probability of escape for slower individuals. Conversely, juveniles and hatchlings may decrease flight initiation distance and remain immobile. Remaining immobile would decrease the probability of a cryptic individual being detected (Cooper et al., 2008; Ioannou and Krause, 2009; Martin et al., 2009). In contrast adults might also have high flight initiation distance to decrease the need for a high burst of speed to escape a nearby predator (Blumstein, 2010), or if the cost of locomotion is low, then adults could afford short flight initiation distance, and rely on high sprint velocity. This strategy would maximize benefits of staying motionless (cryptic), while still ensuring escape (Cooper, 2009a).

Sprint performance, morphological development, and predator escape behavior can be used to assess which locomotor traits might enhance survival. Studies on sprint performance, morphology, and escape behavior are common, but few integrate all of these parameters. The integration of these parameters will allow for a better understanding of the development of anti-predator behavior and escape performance. Integrating these parameters will also elucidate possible compensatory mechanisms for development that increase the probability of survival of juveniles and hatchlings and help define possible selection regimes imposed on juveniles and hatchlings.

The species of interest in this study is *Sceloporus woodi.* This species exhibits positive allometry in femur and shank length and body size (Pounds et al., 1983). Hence, adults should exhibit the longer hind limbs proportional to their body size than hatchlings or juveniles. Also, adults should exhibit significantly higher sprint velocities than juveniles and hatchlings due to their relatively longer hind limbs. If this species exhibits positive allometry, then juveniles and hatchlings would be at a disadvantage (compared to adults) in a predator encounter and be required to exhibit compensatory mechanisms (e.g. crypsis) to ensure survival.

This study will address the following questions: 1) Does *S. woodi* exhibit allometry in hind limb development through ontogeny? If *S. woodi* exhibits positive hind limb allometry, then relative to body size, the legs should be proportionally longest in adults. 2) Do lizards exhibit different running velocities through ontogeny? If hatchlings and juveniles exhibit positive allometry, then, relative to body size, the legs will develop faster through growth. Such a pattern implies that adults would have the highest sprint velocities. If hatchlings and juveniles exhibit negative allometry, then relative to body size, hatchlings would have the longest legs proportional to their body size. This development pattern implies that hatchlings would exhibit high sprint velocity. 3) Do adults, juveniles, or hatchlings exhibit the longest flight initiation distances? Presumably juveniles and hatchlings employ the greatest degree of crypsis, and thus they are predicted to have the shortest flight initiation distance. 4) Do adults, juveniles, and hatchlings exhibit different escape velocities? If these lizards use sprint velocity to escape a predatory even, then escape velocity should increase as body size increases. If other means of predator evasion are used, then escape velocity should reflect the tactics used. (Figure 1)

CHAPTER 2

METHODS

This study took place from July to October 2010 in Ocala National Forest in central Florida. *Sceloporus woodi* is a short-lived lizard native to the pine scrub habitat of central Florida (McCoy et al., 2004). This species reaches a maximum of 144 mm in total body length (Collins, 1998). *Sceloporus woodi* is a sit and wait predator. These lizards are abundant in recently harvested timber sites with open sand and little ground cover, and in longleaf-wiregrass stands found throughout the forest. *Sceloporus woodi* is sexually dimorphic, and only males were used in this study because females vary in reproductive state which subsequently may affect locomotor performance (Sinervo et al., 1991; Lee et al., 1996; Cromarty et al., 1998; Iraeta et al., 2010). Juveniles and hatchlings are cryptically colored (Jackson and Telford, 1974)(Figure 2). Identification of adult males and juveniles was obtained by inspection for enlarged post anal scales, blue body patches, and dimorphic dorsal coloration.

Lizards with snout-vent length less than 25 mm were classified as hatchlings, greater than 25 mm but less than 40 mm were classified as juveniles, and those greater than 40 mm were classified as adults (Jackson and Telford, 1974). Morphological measurements were taken including snout-vent length (SVL), longest toe length (Toe), foot length (MTL), and upper (FL) and lower (TFL) leg length (Thompson and Withers, 1997; Losos and Miles, 2002).

Flight Initiation Distance and Escape Behavior

Surveys took place on days with little cloud cover (air temperature 27-35 °C) when lizards were most active. I surveyed each site for lizards by walking slowly through the habitat. When a motionless lizard was located a field technician, acting as a predator, approached the lizard. I filmed the resulting escape on a Casio Exilim high speed digital camera at 300 frames per second (Van Damme et al., 1998). Filming was restricted to lizards found in open sand as dense vegetation has varying effects on escape tactics. For video calibration and distance measurements a poster board marked in five centimeter increments was placed near the original location of the lizard after the escape event. Flight initiation distance was quantified by measuring the distance between a researcher acting as a predator, and the lizard when it initiated flight (Frid and Dill, 2002). The location of the researcher when the lizard first engaged in escape was marked with a wire flag. The original location of the lizard was marked with a second wire flag and the distance between the two flags was measured using a tape measure. The exact path the lizard traveled after initiating flight was also measured using multiple wire flags as reference points. The distance between the original location of the lizard and the closest refuge (e.g. a bush or log the lizard did escape to) was measured and defined as distance to refuge (DTR). If the lizard could be, it was captured and taken to the lab. If a male lizard was spotted but not able to be filmed it was captured, sexed, and taken to the lab for inclusion in trials to quantify maximum velocity. GPS coordinates were taken for each captured lizard to ensure that all lizards could be released at their capture site.

Each escape video was cropped using Adobe Premier Elements software. The cropped videos were then uploaded into DLT dataviewer3 software and was used to digitize the location of the lizard in each frame and subsequently determine the distance moved and velocity (Hedrick, 2008). Because data was collected on field active lizards, and a landmark could not be placed or painted on the lizard, the tip of the snout of the lizard was used as the landmark and was used to manually digitize the position of the lizard as it progressed through an escape event. The reference grid of known dimensions placed in the frame at the time of the recording was also digitized. Because the actual distances were known on the reference grid, the pixel distance from the digitized files could be converted to centimeters by dividing the measured distance by the pixel distance. As the recordings took place at 300 frames per second the distance information was converted to velocity in centimeters per second and then converted to meters per second. The same method was used to verify the data by finding the distance traveled from the digitized recordings and comparing it to the field measured distance traveled. Average escape velocity was also calculated by averaging the calculated velocities over the entire run.

Maximum Sprint Velocity

Lizards brought back to the lab were housed in the animal facility at Georgia Southern University in ten gallon aquaria (N = 99). Each aquarium had a sand substrate, unlimited water supply, and a hide. Lizards were fed crickets three to four times weekly. The temperature in the aquarium was graded from 30-40 °C, and a twelve hour light cycle was used to mimic natural conditions. Maximal sprint velocity, as defined by average velocity on the 2-m track, was obtained because lizards may not perform maximally in the field (Irschick et al., 2005) but may in the lab. For raceway sprint trials, the lizard was placed in a custom-built racetrack with photocells installed at 0.25 m increments. The time it took the lizard to travel from one photocell to the next was captured and stored via a custom built LabView Virtual Instrument. This software calculated 0.25 m incremental velocities from each photocell. These data were used to define maximum velocity along the full 2 m. Lizards were run on the track four times each and upon completion, returned to the capture site within 3 weeks of capture. The average of all four trials was calculated and used as maximum speed in statistical analyses.

Hind Limb Dissections

Twelve adults, ten juveniles, and six hatchlings, were euthanized with an overdose of sodium pentobarbital. These specimens were fixed in 10% formalin and preserved in 70%

ethanol. The length and diameter of the following muscles were recorded: puboischiotibialis (PIT), ambiens (AMB.), gastrocnemius (GAST.), iliotibialis (ILTIB), flexor tibialis internus (FTIL), iliofibularis (ILFIB), flexor tibialis externus (FTE) to the nearest 0.1 mm using dial calipers, dissected free, and weighed (Snyder, 1954). After removal each muscle was placed in a vial of 70% ethanol and allowed to soak for 5 min. The muscle was then removed from the vial, blotted dry, and weighed to the nearest 0.0001 g on an Ohaus Adventurer Pro AV64 electronic balance.

Statistical Analyses

Relationships between body size and velocity, flight initiation distance, distance to refuge, and escape velocity were quantified using a linear regression. Differences in these same parameters and size class were assessed using ANOVA with post hoc tests. Relationships between velocity and body size were as assessed using a linear regression. Velocity differences between size classes were assessed using an ANOVA and post hoc tests. Muscle measurements were log transformed and regressed on the log transformed snout to vent length to quantify allometric relationships.

CHAPTER 3

RESULTS

Morphology

Reduced Major Axis (RMA) regression estimated slopes, lower and upper 95% confidence intervals, y-intercepts, and R^2 values (Table 2). The expected slope for isometry is 1(length x length). All muscle lengths were found to scale with isometry. All muscle masses were found to scale with isometry (mass x length, slope = 3) except the iliofibularis muscle which scaled with negative allometry (Table 4). All muscle cross sectional areas were found to scale with isometry (area x length, slope = 2) (Table 5). All anatomical measurements scaled with isometry (Table 3). The toe length deviated significantly from isometry and was found to scale with negative allometry. All other morphological measurements scaled with isometry.

Maximum Velocity in the Lab

In the lab, adults ran faster than juveniles and juveniles ran faster than hatchlings ($F_{2, 97} = 12.6$, $p = <0.0001$, Figure 3). Maximum velocity did not increase as leg length increased when the effects of body size were removed ($F_{1, 96} = 0.006$, $p = 0.939$).

Escape Response in the Field

Habitat type, long leaf pine or scrub, did not affect flight initiation distance or distance to refuge. Adult lizards exhibited significantly longer flight initiation distances than juveniles and hatchlings, but hatchlings and juveniles did not differ from one another ($F_{2, 39} = 3.32$, $p = 0.047$ Figure 4). Distance to refuge increased with body size, though this relationship was weak ($R^2 = 0.131$, $F_{1, 39} = 5.87$, $p = 0.020$, Figure 5). Flight initiation distance increased as distance to refuge increased ($R^2 = 0.344$, $F_{1, 39} = 20.40$, $p < 0.001$, Figure 6). Mean escape velocity did not differ between age groups ($F_{2, 24} = 2.39$, $p = 0.114$, Figure 8). Escape velocity increased as flight initiation distance increased ($R^2 = 0.338$, $F_{1, 25} = 5.63$, $p = 0.037$, Figure 7). Lizards that exhibited slower maximal velocities in the lab used a higher proportion of their maximum velocity during escape ($R^2 = 0.349$, $F_{1, 17} = 9.08$, $p = 0.008$, Figure 9).

The removal of the effect of body size resulted in few relationships between variables (FID, distance to refuge, escape velocity, and maximum velocity). There was a relationship between distance to refuge and flight initiation distance ($R^2_{1,39} = 0.272$, $F = 14.5$, $p = 0.0005$). As distance to refuge increases flight initiation distance increases.

CHAPTER 4

DISCUSSION

This study found that total hind limb length largely scales with isometry. This finding has implications on sprint performance. Maximum velocity on the laboratory raceway increased with size, which is also consistent with isometric expectations. This means juveniles and hatchlings likely use different escape behaviors to ensure successful escape and survival. Escape velocity in the field did not vary between adults, juveniles, and hatchlings, yet flight initiation distance increased as body size increased. Maximum sprint velocity in the lab (adults faster than juveniles and juveniles faster than hatchlings) shows that animals can allow closer approach of a predator if they choose to flee at higher sprint velocities.

Overall, limb elements and muscle variables scale isometrically. Throughout development *S. woodi* experiences an increase in absolute sprint velocity and an isometric increase in hind limb length. Isometry in development in ectotherms is unusual as most are precocial and are required to be active shortly after birth (Christian and Garland, 1996; Glasheen and McMahon, 1996; Dohm et al., 1998; McGuire, 2003; Herrel and O'Reilly, 2006; Shea et al., 2009; Kilbourne and Makovicky, 2010). However, isometric development does not confer much advantage to any particular size class especially in a short - lived species where rapid development is essential. Given its short life span, this may be true for *S. woodi*. Retaining a consistent growth rate throughout development allows juveniles and hatchlings an improved chance of survival, as they perform proportionally as well as adults. Two of eleven variables, the iliofibularis muscle mass and toe length, scale with negative allometry. Though their departure from isometry is slight, these two variables could have implications on performance (Van Damme et al., 1998; Aerts et al., 2000; McBrayer and Wylie, 2009). As long distal elements of the limb have been found to affect sprint velocity, the development pattern of the longest toe would suggest that smaller individuals would have the longest toes proportional to body size thus increasing smaller individuals' sprinting ability (Garland and Losos, 1994). However, this finding does not coincide with performance data. My findings contrast Pounds (1983) which suggest that *S. woodi* exhibits positive hind limb allometry. Pounds used three different methods to estimate scaling patterns: only non linear regression resulted in a statistically significant departure from isometry. The reduced major axis regression results of Pounds coincide with those found in the present study i.e. isometric scaling of hind limbs to body size. Pounds used museum specimens that had been preserved for a number of years, which may have an effect on the morphology of the specimens used (Vervust et al., 2009).

Hind limb morphology, in particular hind limb length, has been shown to correlate with running velocity, longer limbs resulting in higher running velocities (Miles, 1994; Bonine and Garland, 1999). The isometric development of the hind limb in *S. woodi* explains why smaller animals exhibit slower absolute running velocities. The slower running velocities of juveniles and hatchlings likely explain why these size classes rely on crypsis as the primary means of predator avoidance. Juvenile and hatchling males exhibit different dorsal coloration than adult males and this coloration has been described as cryptic (Jackson, 1973). The color pattern of juveniles and hatchlings may allow smaller individuals to escape detection more than adults that are not as cryptically colored (Figure 9). If so, then hatchlings and juveniles are likely compensating for their lower sprint velocity by relying on this primary means of predator avoidance to escape a threat.

Not surprisingly, the maximum velocity trials in the lab revealed that adults run faster than juveniles, and juveniles run faster than hatchlings. After adjusting for their differences in body size, there was no difference in running velocity between hatchlings, juveniles, and adults. This too is consistent with observed isometric growth rates. Because this species is short-lived (12-18 months), rapid growth must occur as individuals must quickly reach reproductive size. Isometric growth rates allow the most efficient means of fast growth. Isometric growth dictates that adults, juveniles, and hatchlings perform at proportionally the same level during their development, thus no size class is disadvantaged more than another through ontogeny. Because growth rates do not vary with size, smaller individuals do not have to compensate for increased strain on muscles and bones that would be a result of differing allometric growth rates (Main and Biewener, 2007).

Maximum velocity increased with body size as measured in the lab, yet escape velocity during FID trials in the field was not affected by body size. Maximal sprinting capabilities are not always used in the natural environment and thus may not predict escape response effectively in the field (Irschick et al., 2005; Husak, 2006b). Hatchlings and juveniles are absolutely slower than adults and therefore use higher proportions of their maximum velocity in predator escape (Figure 8). Conversely adults can afford to use a lower proportion of their max yet still escape successfully because they flee at greater distances (Figure 3). Maximal sprint performance is energetically costly and using slower escape velocities ensure that energy may be allocated to other processes (Taylor et al., 1970; Nagy, 2000). Just because adults can reach higher velocities, they are not required to use high velocities to escape if they flee early. Thus adults may run proportionally slower than juveniles and hatchlings during escape. This strategy has implications on flight initiation distance.

Flight initiation distance was positively correlated with body size (Figure 3). Adults exhibited longer flight initiation distances than juveniles and hatchlings. Escape velocity did not vary with size (Figure 7). Hatchlings and juveniles, being absolutely slower (Figure 2), may depend on crypsis to decrease the probability of detection and therefore avoid the costs of running from a predator (Cooper et al., 2008). Using crypsis requires immobility which shortens flight initiation distance (Stuart-Fox et al., 2003; Ioannou and Krause, 2009). The affect of the use of crypsis as a primary predator avoidance tactic has been observed in other species. The Texas horned lizard (*Phrynosoma cornutum*) can be almost stepped on before initiating flight and this species flight initiation distance reflects this use of crypsis (Cooper and Sherbrooke, 2010). The common lizard (*Zootoca vivipara*) is a cryptically colored ground lizard that exhibits shorter flight initiation distances than the conspicuous, fast moving Horvath's rock lizard (*Iberolacerta horvathi*). These lizards are similar in size but, due to the use of crypsis, have different escape responses (Capizzi et al., 2007). In contrast, adults flee early to avoid the high velocities necessary to escape a predator and ensure successful escape (Blumstein, 2010). In *S. woodi*, escape velocity did not differ between adults, juveniles, and hatchlings. However the proportion of maximum velocity did vary (Figure 8). Lizards with slower maximum velocities used a higher proportion of their maximum velocity than did those with higher maximum velocities. Because adults are faster, they can afford to flee early at a slower velocity, yet still have the ability to increase their velocity, thereby saving energy, yet retaining the ability to flee again at high velocity if needed.

Distance to refuge also increased as flight initiation distance increased suggesting that animals further way from refuge did not allow close approach of a predator. Lizards found farther from refuge would be required to travel a greater distance to reach the relative safety of the refuge. By fleeing early individuals increase their probability of successfully reaching refuge even at slower velocities (Dill and Houtman, 1989; Cooper, 2003; Stankowich and Blumstein, 2005; Cooper, 2010).

The small size and short life span of *S. woodi* dictates fast growth and development (Kozlowski, 1996). Isometric growth rates ensure that smaller individuals allocate energy resources as efficiently as possible throughout development to optimize growth while still ensuring the animals ability to survive in the habitat and escape predation. In order to reproduce, and have fitness, an individual must first survive adolescence. The isometric development of hind limb length coupled with behavioral shifts in predator evasion improves the ability of juvenile and hatchling *S. woodi* to survive. Further studies of the ontogeny of escape performance in other species of lizards with different life histories or body proportions are needed as well as additional studies linking performance in the field, performance in the lab, and morphology across species. Further study would allow better understanding of the relationships between behavior, morphology, and performance and may help explain unique growth trajectories and their influences on life history.

REFERENCES

Aerts, P., Van Damme, R., Vanhooydonck, B., Zaaf, A., Herrel, A. 2000. Lizard locomotion: How morphology meets ecology. Netherlands Journal of Zoology 50, 261-277.

Aragon, P., Lopez, P., Martin, J. 2004. The ontogeny of spatio-temporal tactics and social relationships of adult male Iberian rock lizards, Lacerta monticola. Ethology 110, 1001-1019.

Ashley, M.A., Reilly, S.M., Lauder, G.V. 1991. Ontogenetic Scaling of Hindlimb Muscles Across Metamorphosis in the Tiger Salamander, *Ambystoma tigrinum*. Copeia, 767-776.

Ayllon, D., Almodovar, A., Nicola, G.G., Elvira, B. 2010. Ontogenetic and spatial variations in brown trout habitat selection. Ecology of Freshwater Fish 19, 420-432.

Blamires, S.J. 1999. Factors influencing the escape response of an arboreal agamid lizard of tropical Australia (Lophognathus temporalis) in an urban environment. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77, 1998-2003.

Blumstein, D.T. 2010. Flush early and avoid the rush: a general rule of antipredator behavior? Behavioral Ecology 21, 440-442.

Bonine, K.E., Garland, T. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. Journal of Zoology 248, 255-265.

Calder, W.A. III.   1984. Size, Function, and Life History. Cambridge, MA, Harvard Press.

Capizzi, D., Luiselli, L., Vignoli, L. 2007. Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition in two lacertids with contrasting habits. Amphibia-Reptilia 28, 403-407.

Caro, T.M., Bateson, P. 1986. Organization and Ontogeny of Alternative Tactics. Animal Behaviour 34, 1483-1499.

Carrier, D.R. 1994. Ontogeny of Jumping Performance in the Black-Tailed Jackrabbit (*Lepus californicus*). Zoology-Analysis of Complex Systems 98, 309-313.

Carrier, D.R. 1996. Ontogenetic limits on locomotor performance. Physiological Zoology 69, 467-488.

Cediel, R.A., Blob, R.W., Schrank, G.D., Plourde, R.C., Schoenfuss, H.L. 2008. Muscle fiber type distribution in climbing Hawaiian gobioid fishes: Ontogeny and correlations with locomotor performance. Zoology 111, 114-122.

Christian, A., Garland, T. 1996. Scaling of limb proportions in monitor lizards (Squamata: Varanidae). Journal of Herpetology 30, 219-230.

Collins, R.C.a.J.T. 1998. A Field Guide to Reptiles and Amphibians of Eastern and Central North America. New York City, Houghton Mifflin Company.

Cooper, W.E. 2003. Risk factors affecting escape behavior by the desert iguana, Dipsosaurus dorsalis: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. Canadian Journal of Zoology-Revue Canadienne De Zoologie 81, 979-984.

Cooper, W.E. 2009a. Flight initiation distance decreases during social activity in lizards (Sceloporus virgatus). Behavioral Ecology and Sociobiology 63, 1765-1771.

Cooper, W.E. 2009b. Fleeing and hiding under simultaneous risks and costs. Behavioral Ecology 20, 665-671.

Cooper, W.E. 2010. Pursuit deterrence varies with predation risks affecting escape behaviour in the lizard Callisaurus draconoides. Animal Behaviour 80, 249-256.

Cooper, W.E . Frederick, W.G., 2007. Optimal flight initiation distance. Journal of Theoretical Biology 244, 59-67.

Cooper, W.E. Sherbrooke, W.C., 2010. Initiation of Escape Behavior by the Texas Horned Lizard (*Phyrnosoma cornutum*). Herpetologica 66, 23-30.

Cooper, W.E. Caldwell, J.P., Vitt, L.J., 2008. Effective crypsis and its maintenance by immobility in Craugastor frogs. Copeia, 527-532.

Cromarty, S.I., Mello, J., Kass-Simon, G. 1998. Comparative analysis of escape behavior in male, and gravid and non-gravid, female lobsters. Biological Bulletin 194, 63-71.

Dial, K.P., Jackson, B.E. 2011. When hatchlings outperform adults: locomotor development in Australian brush turkeys (Alectura lathami, Galliformes). Proceedings of the Royal Society B-Biological Sciences 278, 1610-1616.

Dill, L.M., Houtman, R. 1989. The Influence of Distance to Refuge on Flight Initiation Distance in the Gray Squirrel (*Sciurus carolinensis*). Canadian Journal of Zoology-Revue Canadienne De Zoologie 67, 233-235.

Dodson, P. 1975. Relative Growth in 2 Sympatric Species of Sceloporus. American Midland Naturalist 94, 421-450.

Dohm, M.R., Garland, T., Cole, C.J., Townsend, C.R. 1998. Physiological variation and allometry in western whiptail lizards (Cnemidophorus tigris) from a transect across a persistent hybrid zone. Copeia, 1-13.

Downes, S. 2001. Trading heat and food for safety: Costs of predator avoidance in a lizard. Ecology 82, 2870-2881.

Edmunds, M. 1974. Defence in Animals. A Survey of anti-predator defences. New York, Longman Group Limited.

Frid, A., Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6, 16.

Garland, T. 1985. Ontogenetic and Individual Variation in Size, Shape, and Sped in the Australian Agamid Lizard *Amphibolurus nuchalis*. Journal of Zoology 207, 425-439.

Garland, T., Losos, J.B. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: P.C. Wainwright, S.M. Reilly (Eds.), Ecological Morphology: Integrative Organismal Biology, pp. 240-302. Chicago: University of Chicago Press.

Glasheen, J.W., McMahon, T.A. 1996. Size-dependence of water-running ability in basilisk lizards (Basiliscus basiliscus). Journal of Experimental Biology 199, 2611-2618.

Hedrick, T.L. 2008. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. Bioinspiration & Biomimetics 3, 6.

Herrel, A., O'Reilly, J.C. 2006. Ontogenetic scaling of bite force in lizards and turtles. Physiological and Biochemical Zoology 79, 31-42.

Herrel, A., Gibb, A.C. 2006. Ontogeny of performance in vertebrates. Physiological and Biochemical Zoology 79, 1-6.

Huey, R.B., Hertz, P.E. 1982. Effects of Body Size and Slope on Sprint Speed of a Lizard (*Stellio agama stellio*). Journal of Experimental Biology 97, 401-409.

Husak, J.F. 2006a. Does speed help you survive? A test with Collared Lizards of different ages. Functional Ecology 20, 174-179.

Husak, J.F. 2006b. Does survival depend on how fast you can run or how fast you do run? Functional Ecology 20, 1080-1086.

Ioannou, C.C., Krause, J. 2009. Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. Biology Letters 5, 191-193.

Iraeta, P., Salvador, A., Monasterio, C., Diaz, J.A. 2010. Effects of gravidity on the locomotor performance and escape behaviour of two lizard populations: the importance of habitat structure. Behaviour 147, 133-150.

Irschick, D.J. 2000. Effects of behaviour and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. Functional Ecology 14, 438-444.

Irschick, D.J., Macrini, T.E., Koruba, S., Forman, J. 2000. Ontogenetic differences in morphology, habitat use, behavior, and sprinting capacity in two west Indian Anolis lizards. Journal of Herpetology 34, 444-451.

Irschick, D.J., Herrel, A.V., Vanhooydonck, B., Huyghe, K., Van Damme, R. 2005. Locomotor compensation creates a mismatch between laboratory and field estimates of escape speed in lizards: A cautionary tale for performance-to-fitness studies. Evolution 59, 1579-1587.

Jackson, J.F. 1973. Distribution and Population Phenetics of Florida Scrub Lizard, *Sceloporus woodi*. Copeia, 746-761.

Jackson, J.F., Telford, S.R. 1974. Reproductive Ecology of Florida Scrub Lizard, *Sceloporus woodi*. Copeia, 689-694.

Kilbourne, B.M., Makovicky, P.J. 2010. Limb bone allometry during postnatal ontogeny in non-avian dinosaurs. Journal of Anatomy 217, 135-152.

Kozlowski, J. 1996. Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. Proceedings of the Royal Society of London Series B-Biological Sciences 263, 559-566.

Lagos, P.A., Meier, A., Tolhuysen, L.O., Castro, R.A., Bozinovic, F., Ebensperger, L.A. 2009. Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. Canadian Journal of Zoology-Revue Canadienne De Zoologie 87, 1016-1023.

Lee, S.J., Witter, M.S., Cuthill, I.C., Goldsmith, A.R. 1996. Reduction in escape performance as a cost of reproduction in gravid starlings, Sturnus vulgaris. Proceedings of the Royal Society of London Series B-Biological Sciences 263, 619-623.

Losos, J.B. 1990. The Evolution of Forma and Function - Morphology and Locomotor Performance in West-Indian Anolis Lizards. Evolution 44, 1189-1203.

Losos, J.B., Miles, D.B. 2002. Testing the hypothesis that a clade has adaptively radiated: Iguanid lizard clades as a case study. American Naturalist 160, 147-157.

Main, R.P., Biewener, A.A. 2007. Skeletal strain patterns and growth in the emu hindlimb during ontogeny. Journal of Experimental Biology 210, 2676-2690.

Marsh, R.L. 1988. Ontogenesis of Contractile Properties of Skeletal, Muscle, and Sprint Performance in the Lizard *Dipsosaurus dorsalis*. Journal of Experimental Biology 137, 119-139.

Martin, J., Lopez, P. 1995. Escape Behavior of Juvenile *Psammodromus algirus* lizards - Constraint of or Compensation for Limitations in Body Size. Behaviour 132, 181-192.

Martin, J., Jose Luque-Larena, J., Lopez, P. 2009. When to run from an ambush predator: balancing crypsis benefits with costs of fleeing in lizards. Animal Behaviour 78, 1011-1018.

McBrayer, L.D., Wylie, J.E. 2009. Concordance between locomotor morphology and foraging mode in lacertid lizards. Zoology 112, 370-378.

McCoy, E.D., Hartmann, P.P., Mushinsky, H.R. 2004. Population biology of the rare Florida scrub lizard in fragmented habitat. Herpetologica 60, 54-61.

McGuire, J.A. 2003. Allometric prediction of locomotor performance: An example from southeast Asian flying lizards. American Naturalist 161, 337-349.

Miles, D.B. 1994. Population Differentiation in Locomotor Performance and the Potential Response of a Terrestrial Organism to Global Environmental Change. American Zoologist 34, 422-436.

Nagy, K.A. 2000. Energy costs of growth in neonate reptiles. Herpetological Monographs, 378-387.

Pounds, J.A., Jackson, J.F., Shively, S.H. 1983. Allometric Growth of the Hind Limbs of some Terrestrial Iguanid Lizards. American Midland Naturalist 110, 201-207.

Promislow, D., Clobert, J., Barbault, R. 1992. Life-History Allometry in Mammals and Squamate Reptiles - Taxon Level Effects. Oikos 65, 285-294.

Ricklefs, R.E. 1968. Patterns of Growth in Birds. Ibis 110, 419-&.

Ricklefs, R.E. 1979. Adaptation, Constraint, and Compromise in Avian Postnatal - Development. Biological Reviews of the Cambridge Philosophical Society 54, 269-290.

Shea, G., Jourdan, H., Sadlier, R., Bauer, A. 2009. Natural history of the New Caledonian whiptailed skink Tropidoscincus variabilis (Bavay, 1869) (Squamata: Scincidae). Amphibia-Reptilia 30, 207-220.

Shine, R., Charnov, E.L. 1992. Patterns of Survival, Growth, and Maturation in Snakes and Lizards. American Naturalist 139, 1257-1269.

Sinervo, B., Hedges, R., Adolph, S.C. 1991. Decreased Sprint Speed as a Cost of Reproduction in the Lizard *Sceloporus occidnetalis* - Variation Among Populations. Journal of Experimental Biology 155, 323-336.

Snyder, R.C. 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. American Journal of Anatomy 95, 1-45.

Stankowich, T., Blumstein, D.T. 2005. Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society B-Biological Sciences 272, 2627-2634.

Stuart-Fox, D.M., Moussalli, A., Marshall, N.J., Owens, I.P.F. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. Animal Behaviour 66, 541-550.

Taylor, C.R., Schmidtn.K, Raab, J.L. 1970. Scaling of the Energetic Cost of Running to Body Size in Mammals. American Journal of Physiology 219, 1104-&.

Thompson, G.G., Withers, P.C. 1997. Comparative morphology of western Australian varanid lizards (Squamata: Varanidae). Journal of Morphology 233, 127-152.

Thompson, J.T., Kier, W.M. 2006. Ontogeny of mantle musculature and implications for jet locomotion in oval squid Sepioteuthis lessoniana. Journal of Experimental Biology 209, 433-443.

Van Damme, R., Aerts, P., Vanhooydonck, B. 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. Biological Journal of the Linnean Society 63, 409-427.

Vervust, B., Van Dongen, S., Van Damme, R. 2009. The effect of preservation on lizard morphometrics - an experimental study. Amphibia-Reptilia 30, 321-329.

Warner, D.A., Andrews, R.M. 2002. Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. Biological Journal of the Linnean Society 76, 105-124.

Ydenberg, R.C., Dill, L.M. 1986. The Economics of Fleeing from Predators. Advances in the Study of Behavior 16, 229-249.

Young, J.W. 2005. Ontogeny of muscle mechanical advantage in capuchin monkeys (Cebus albifrons and Cebus apella). Journal of Zoology 267, 351-362.

Young, J.W., Fernandez, D. 2009. Ontogenetic allometry of limb bone strength in capuchin monkeys (Cebus albifrons and Cebus apella): implications for locomotor development and life history. American Journal of Physical Anthropology, 278-278.

Table 1: Means table of muscle measurements by size class. Mean includes standard deviation. Adult N = 12, Juvenile N = 10, Hatchling N = 6.

Muscle	Mean Length (mm)	Mean Mass (g)	Mean Area (mm^2)
Puboischiotibialis			
Adults	11.13 ± 0.856	0.008 ± 0.003	2.075 ± 0.654
Juveniles	7.880 ± 1.121	0.003 ± 0.001	1.35 ± 0.837
Hatchlings	5.533 ± 0.631	0.002 ± 0.002	0.850 ± 0.606
Ambiens			
Adults	10.03 ± 1.616	0.006 ± 0.002	1.333 ± 0.695
Juveniles	7.430 ± 1.237	0.003 ± 0.002	0.970 ± 0.663
Hatchlings	5.283 ± 0.618	0.001 ± 0.001	0.600 ± 0.657
Gastrocnemius			
Adults	9.167 ± 1.102	0.009 ± 0.005	1.167 ± 0.509
Juveniles	7.200 ± 1.409	0.003 ± 0.002	0.680 ± 0.336
Hatchlings	4.983 ± 0.655	0.002 ± 0.001	0.517 ± 0.293
Iliotibialis			
Adults	9.458 ± 0.894	0.011 ± 0.003	1.975 ± 0.954
Juveniles	6.800 ± 1.026	0.003 ± 0.002	1.290 ± 0.947
Hatchlings	5.083 ± 0.454	0.002 ± 0.001	0.967 ± 0.472
Flexor tibialis internus			
Adults	7.933 ± 0.795	0.006 ± 0.004	0.958 ± 0.848
Juveniles	5.940 ± 1.130	0.002 ± 0.001	0.430 ± 0.298
Hatchlings	4.550 ± 0.373	0.001 ± 0.0004	0.317 ± 0.194
Iliofibularis			
Adults	8.375 ± 1.091	0.004 ± 0.001	0.858 ± 0.776
Juveniles	5.940 ± 1.006	0.002 ± 0.002	0.520 ± 0.489
Hatchlings	4.367 ± 0.333	0.001 ± 0.001	0.317 ± 0.117
Flexor tibialis externus			
Adults	8.108 ± 0.909	0.007 ± 0.003	1.008 ± 0.869
Juveniles	5.390 ± 0.953	0.003 ± 0.002	0.690 ± 0.792
Hatchlings	4.183 ± 0.960	0.002 ± 0.001	0.500 ± 0.200

Table 2: Ontogenetic scaling of muscle length with snout to vent length. Slopes represent the allometric growth relationship of each muscle length to snout to vent length. Lower CI and Upper CI indicate the 95% confidence interval for the given slope. All variables scale with isometry. Abbreviations, puboischiotibialis (PIT), ambiens (AMB.), gastrocnemius (GAST.), iliotibialis (ILTIB), flexor tibialis internus (FTIL), iliofibularis (ILFIB), flexor tibialis externus (FTE)

Muscle	Slope	Lower CI	Upper CI	Intercept	R^2
PIT	1.014	0.93	1.09	-0.66	0.95
AMB	1.007	0.89	1.15	-0.69	0.78
GAST	0.94	0.77	1.12	-0.62	0.77
ILTIB	0.92	0.83	1.04	-0.57	0.90
FTIL	0.88	0.76	1.02	-0.58	0.85
ILTIB	1.004	0.86	1.19	-0.77	0.82
FTE	1.1	0.87	1.37	-0.95	0.77

Table 3: Ontogenetic scaling of external anatomical measurements with snout to vent length. Slopes represent the allometric growth relationship of each anatomical measurement to snout to vent length. Lower CI and Upper CI indicate the 95% confidence interval for the given slope. Toe length scales with negative allometry (slope = < 1)(*). All other variables scale with isometry. Abbreviations, Femur length (FL), Tibio-fibialis length (TFL), and Metatarsal length (MTL).

Anatomical Measurement	Slope	Lower CI	Upper CI	Intercept	R^2
FL	0.910	0.817	1.061	-0.521	0.91
TFL	0.976	0.881	1.148	-0.711	0.89
MTL	0.858	0.753	0.997	-0.666	0.85
Toe	0.689*	0.577	0.817	-0.079	0.77

Table 4: Ontogenetic scaling of muscle mass with snout to vent length. Slopes represent the allometric growth relationship of each muscle mass to body size. Lower CI and Upper CI indicate the 95% confidence interval for the given slope. The iliofibularis muscle exhibits negative allometry. All other variables scale with isometry (slope = 3). Refer to Table 1 for explanation of abbreviations.

Muscle	Slope	Lower CI	Upper CI	Intercept	R^2
PIT	4.13	2.84	5.28	-9.01	0.60
AMB	3.46	2.67	4.31	-8.00	0.67
GAST	3.14	2.40	4.09	-7.36	0.58
ILTIB	3.44	3.02	4.00	-7.79	0.86
FTIL	3.17	2.53	4.05	-7.62	0.56
ILFIB	2.46*	2.10	2.99	-6.50	0.62
FTE	2.88	2.23	3.86	-7.01	0.46

Table 5: Ontogenetic scaling of muscle cross sectional area. Slopes represent the allometric growth relationship of each muscle area to body size. Lower CI and Upper CI indicate the 95% confidence interval for the given slope. All slopes were not significantly different from 2 which indicates isometry. Refer to Table 1 for explanation of abbreviations.

Muscle	Slope	Lower CI	Upper CI	Intercept	R^2
PIT	2.62	1.66	3.61	-4.01	0.36
AMB	2.83	1.79	3.85	-4.53	0.23
GAST	2.14	1.54	2.81	-3.50	0.35
ILTIB	2.01	1.50	2.77	-3.04	0.24
FTIL	2.88	1.94	4.06	-4.87	0.18
ILFIB	2.50	1.67	3.54	-4.26	0.22
FTE	2.38	1.41	3.31	-3.96	0.07

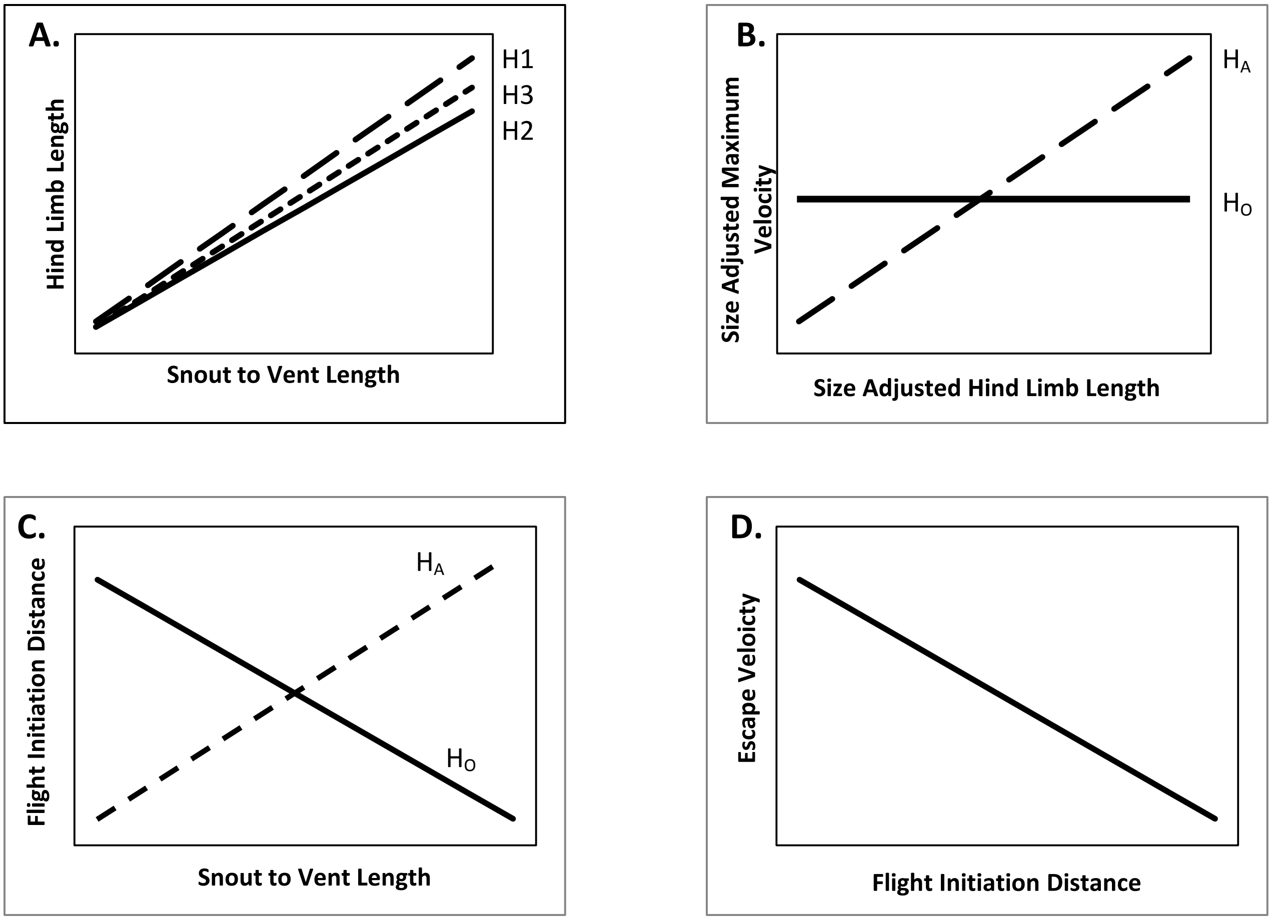

Figure 1: A) (H1) The results of Pounds (1983) suggest that *S.woodi* exhibits positive allometry in hind limb growth. If hind limb length is critical for sprint velocity, then positive hind limb allometry would result in adults sprinting proportionally faster than smaller body sizes. Juveniles and hatchlings would need to alter their behavior to compensate for lower performance abilities. (H2) In order to maximize juvenile performance *S. woodi* may exhibit negative hind limb allometry so that their sprint velocity is proportionally higher at smaller body sizes. (H3) Negative allometry would result in juveniles and hatchlings having improved locomotor abilities, relative to body size. If performance is dictated mainly by size, *S. woodi* will exhibit isometry. B) If *S.woodi* exhibits positive allometry in hind limb development, then removing the effect of body size would result in adults having the highest maximum velocity and hatchlings having the

lowest (H_A). If body size is the main indicator of performance abilities removing the effect of body size would result in proportionally equal performance abilities throughout ontogeny (H_O). C) Flight initiation distance should decrease as snout-vent length increases. If *S.woodi* exhibits positive allometry, then faster lizards should allow closer approach of a predator and still escape (H_O). However if alternative predator evasion techniques are used, flight initiation distance may increase with snout-vent length because smaller individuals will remain immobile longer to maintain crypsis (H_A). D) If adults have longer flight initiation distances than juveniles or hatchlings then, adults flee with slower escape velocities. As a result, escape velocity is predicted to decrease while flight initiation distance increases. Lizards allowing close approach of a predator are predicted to use high escape velocities, while those not allowing close approach of a predator are predicted to use slower escape velocities. See text for details.

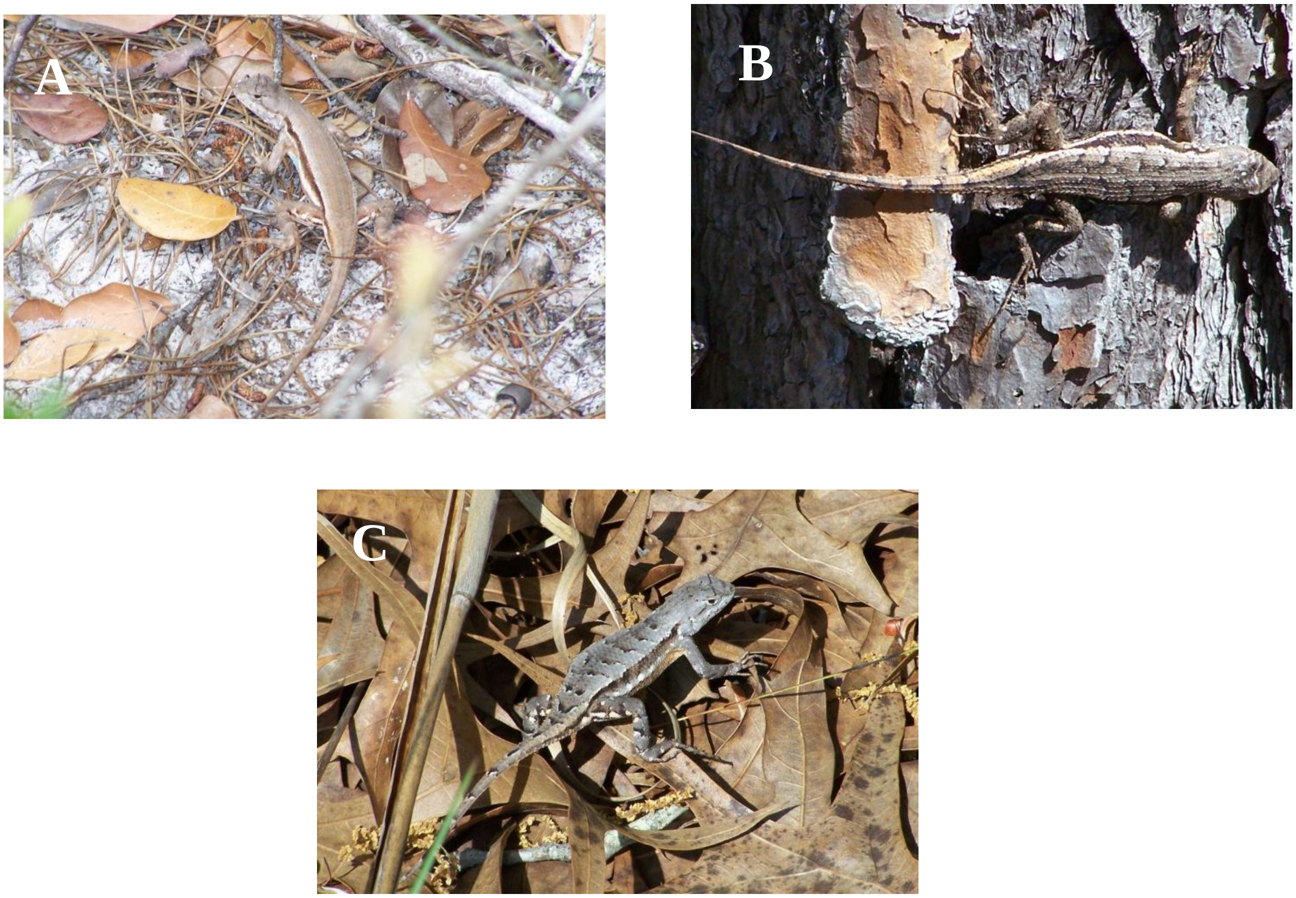

Figure 2: A) Male *S. woodi* exhibit a light brown dorsal surface with no other markings. B) Female *S. woodi* exhibit a light patterning on the dorsal surface decreasing their conspicuousness. C) Juveniles exhibit similar coloring to females and thus may rely on crypsis to escape predation.

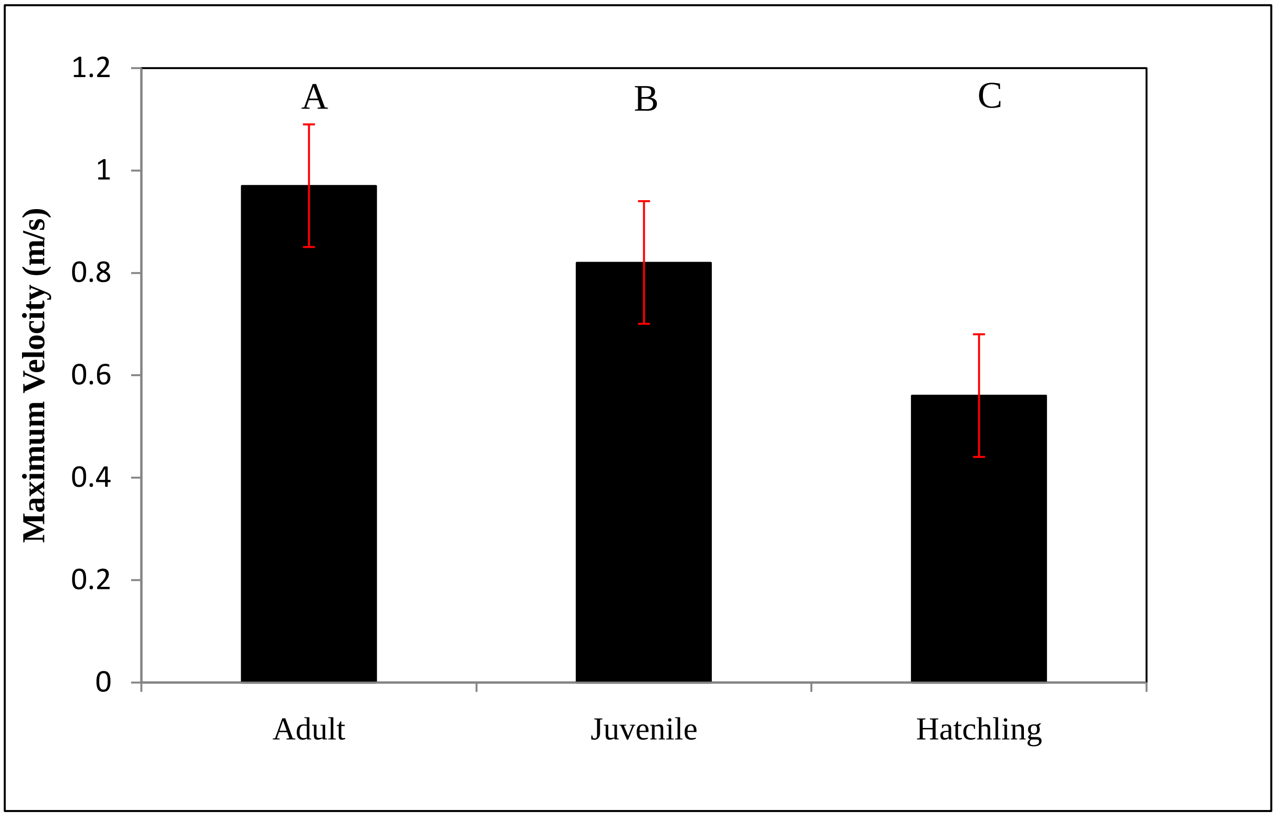

Figure 3: Average maximum velocity by size class collected on the 2 meter raceway. Adults exhibited significantly higher maximum velocities than juveniles and juveniles exhibited significantly higher maximum velocities than hatchlings ($F_{2,97} = 12.6$, $P = <0.0001$). Different letters signify a significant difference between groups.

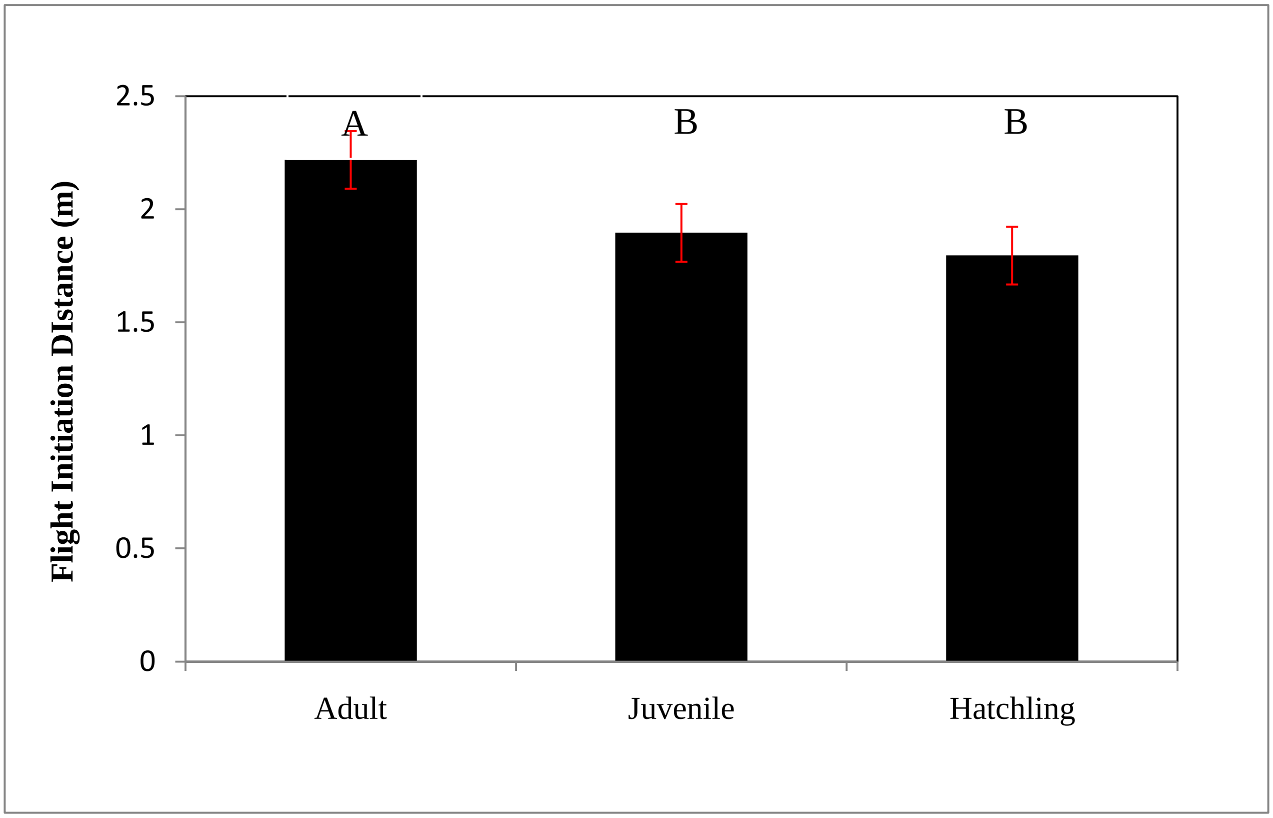

Figure 4: Mean flight initiation distance of adult, juvenile, and hatchling lizards. Adult lizards exhibited significantly longer flight initiation distances than juveniles and hatchlings but hatchlings and juveniles did not differ from one another ($F_{2,39}$=3.32, P = 0.047). Different letters signify significantly different groups, shared letters are not significantly different.

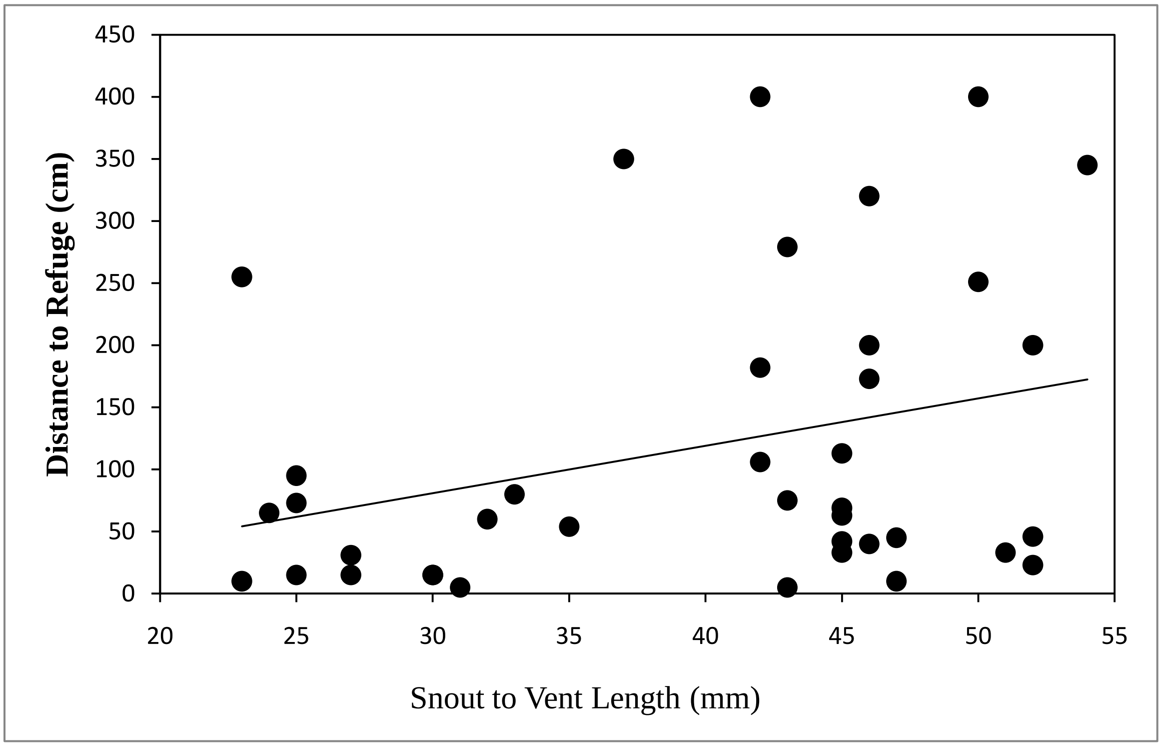

Figure 5: Linear regression of distance to refuge on snout to vent length. Smaller lizards stayed closer to refuges. Distance to refuge increased with body size, but showed a high degree of variability ($R^2_{1,39} = 0.131$, $P = 0.020$).

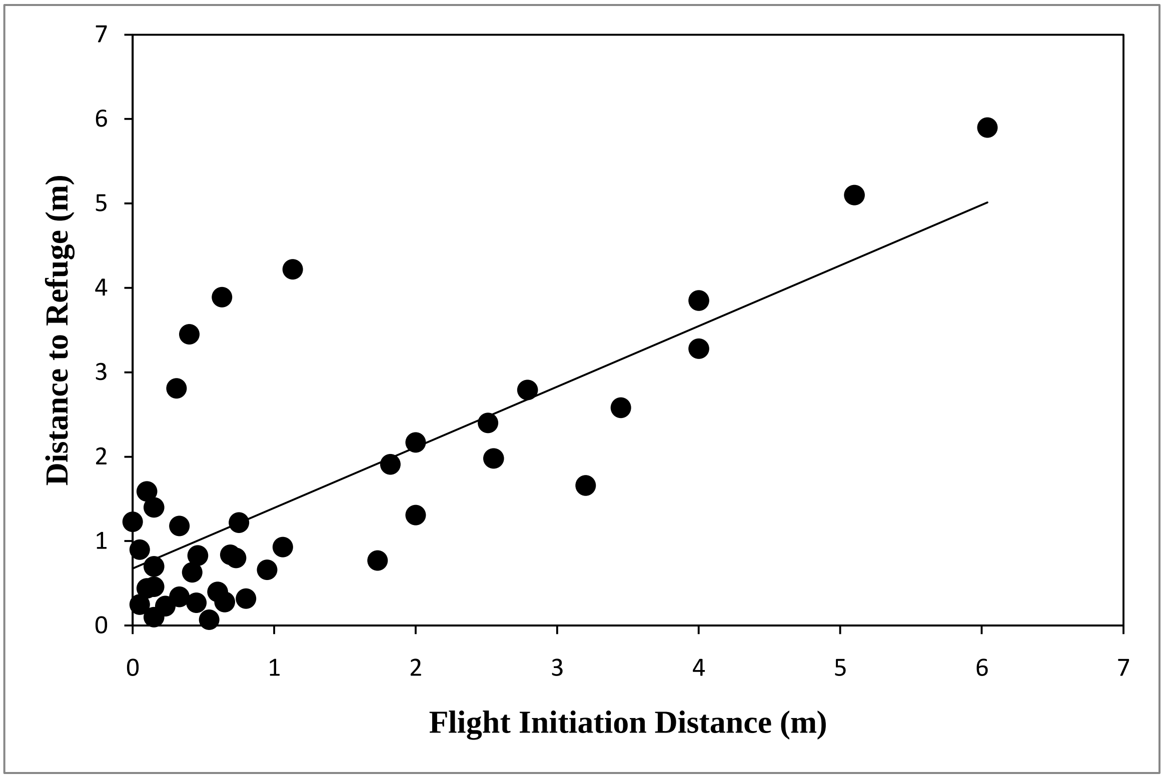

Figure 6: Linear regression of distance to refuge on flight initiation distance. Flight initiation distance increased as distance to refuge increased ($R^2_{1,39} = 0.344$, $P = 0.001$)

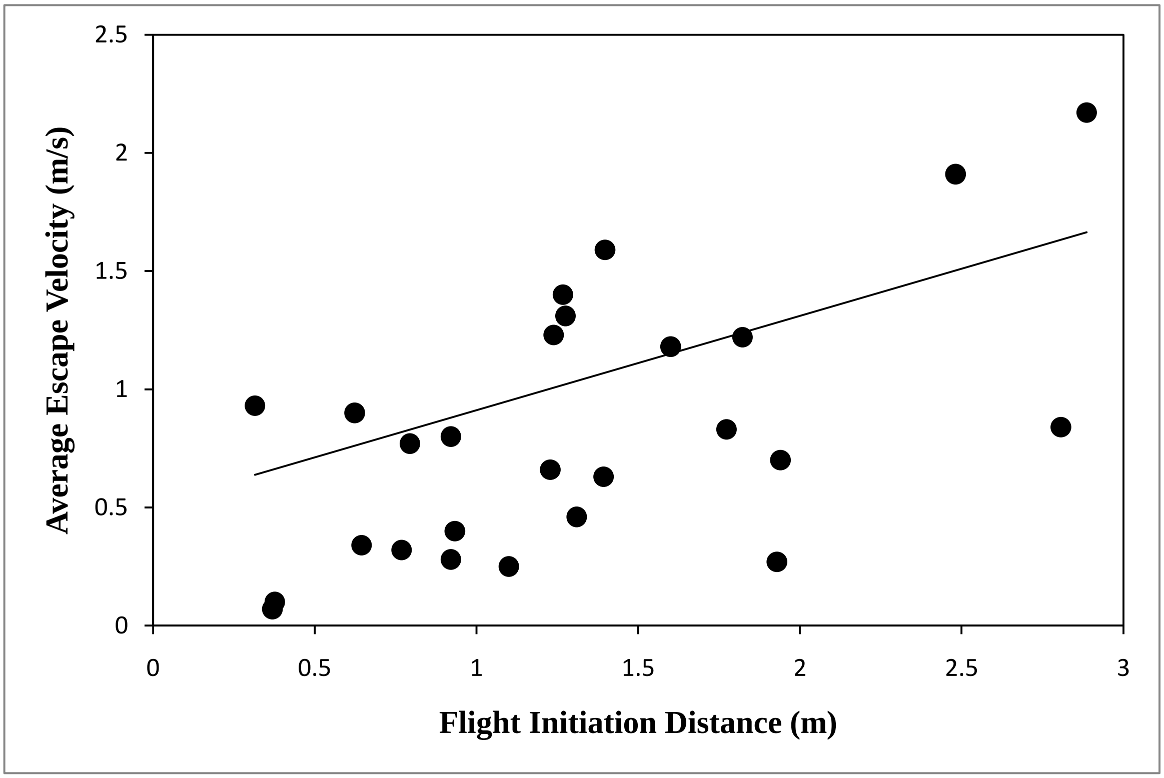

Figure 7: Average escape velocity in the field increased as flight initiation distance increased ($R^2_{1, 25}$ = 0.338, P = 0.037). Lizards farther from a refuge ran from a predator faster than those near a refuge.

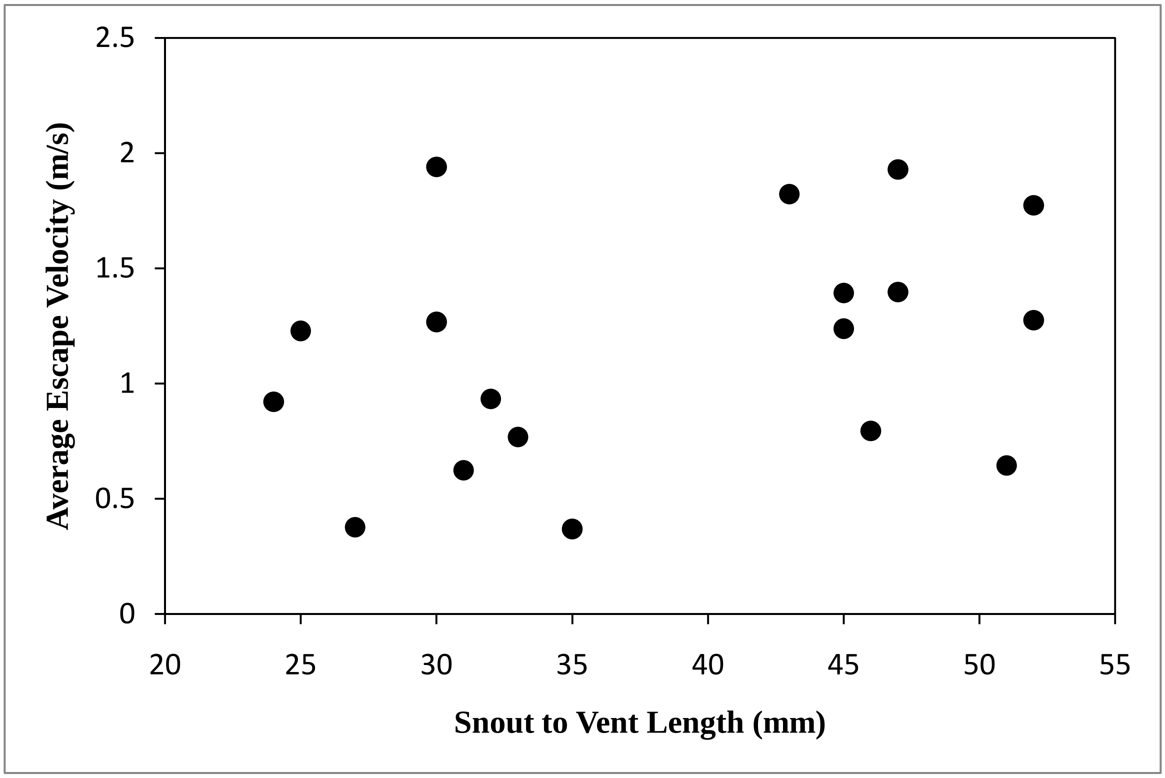

Figure 8: Average escape velocity did not vary with snout to vent length ($F_{2,\ 24} = 2.51$, P = 0.132). *S. woodi* escape a predator encounter with similar escape velocities throughout ontogeny, which may represent a trade off with flight initiation distance.

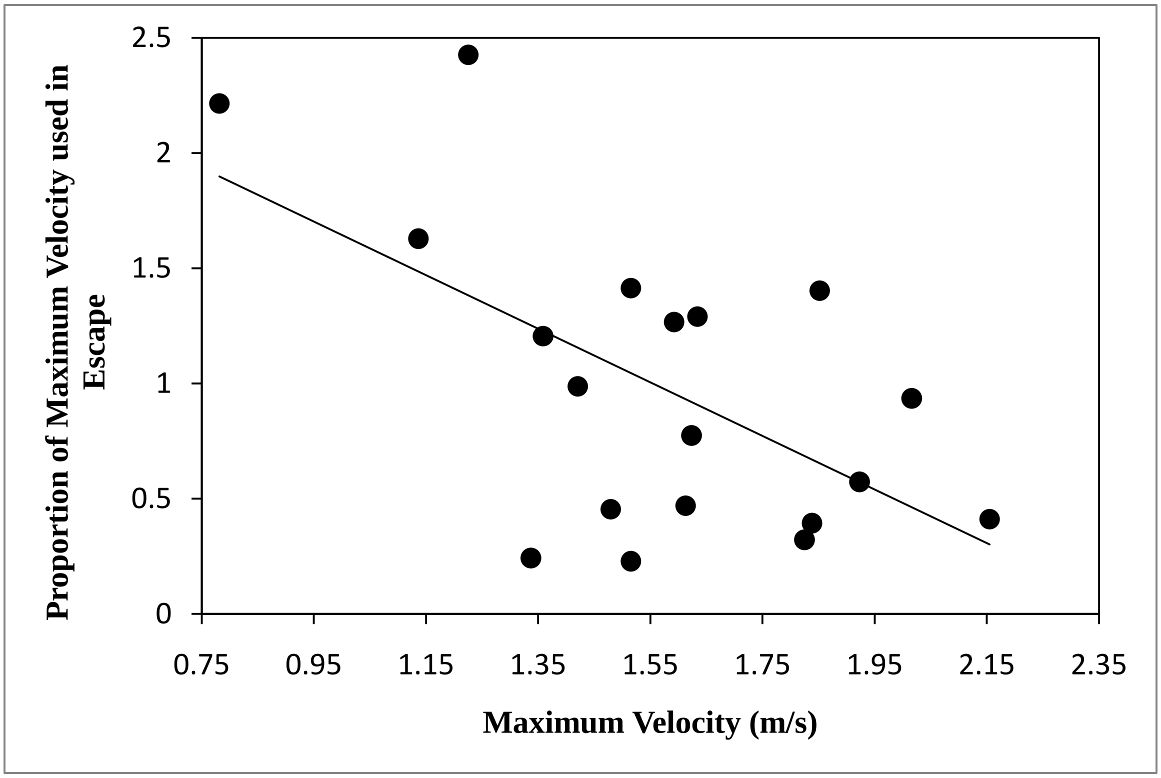

Figure 9: The proportion of maximum velocity used during escape decreased as maximum velocity increased ($R^2_{1, 17} = 0.349$, $P = 0.008$). Those lizards with high maximum velocities used lower velocities during escape.