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# Genotypic and Phenotypic Variation of the Florida Scrub Lizard (Sceloporus Woodi)

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GENOTYPIC AND PHENOTYPIC VARIATION OF THE FLORIDA SCRUB
LIZARD (*SCELOPORUS WOODI*)

by

DEREK B. TUCKER


(Under the Direction of Lance D. McBrayer & John Scott Harrison)

ABSTRACT

In my 1st chapter I investigate the phenotypic variation of the Florida scrub lizard by examining sprinting and jumping ability. These are key performance measures that have been widely studied in vertebrates. The vast majority of these studies, however, use methodologies that lack ecological context by failing to consider the complex habitats many animals live in. Here, I filmed running lizards to address how behavioral and performance strategies change as lizards approach obstacles of varying height. Obstacle size had a significant influence on both behavior (e.g. obstacle crossing strategy, intermittent locomotion) and performance (e.g. sprint speed, jump distance). Researchers should thus consider the complexity of a species' habitat in designing studies of locomotion. In the 2nd chapter I examine the genotypic variation of *S. woodi* in the Ocala National Forest. The loss of natural habitat due to fragmentation is a major threat to the conservation of species. The Florida scrub lizard (*Sceloporus woodi*) is restricted to open, sunny, scrub habitat, historically maintained through frequent wildfires. The ONF is fragmented from clearcut logging, fire suppression, and by major roadways. I examined five microsatellite loci to estimate genetic differentiation across the forest and near a major roadway (Florida State Route 40). The results suggest that there is a considerable amount of isolation among *S. woodi* populations in the ONF. Decades of

fire suppression have resulted in overgrown forest that hinders lizard dispersal and

separates populations by expanses of unsuitable habitat.  Though SR-40 may act as a

barrier for wildlife, my findings do not denote any added genetic differentiation caused

by the road.


INDEX WORDS: Bipedal locomotion, Florida scrub lizard, Genetic differentiation, Genetic patchiness, Habitat fragmentation, Intermittent locomotion, Jumping, Microsatellite, Roads, *Sceloporus woodi*, Sprinting

GENOTYPIC AND PHENOTYPIC VARIATION OF THE FLORIDA SCRUB
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by

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DEDICATION

I would like to dedicate this thesis to my wife Rachael Tucker for all her support and assistance during the completion of this project and degree. I apologize for the 64 bug bites you sustained while helping catch lizards in the Ocala National Forest.

ACKNOWLEDGMENTS

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CHAPTER 1

Overcoming obstacles: the effect of obstacle size on the behavioral repertoire and

locomotor performance of running lizards

**ABSTRACT**

Sprinting and jumping ability are key performance measures that have been widely

studied in vertebrates. The vast majority of these studies, however, use methodologies

that lack ecological context by failing to consider the complex habitats many animals live

in. In complex environments, animals must avoid or overcome obstacles in order to

effectively escape predators or capture prey. Here, I filmed running lizards to address

how behavioral and performance strategies change as lizards approach obstacles of

varying height. Obstacle size had a significant influence on both behavior (e.g. obstacle

crossing strategy, intermittent locomotion) and performance (e.g. sprint speed, jump

distance). Jumping frequency and jump distance increased with obstacle size. Jumping,

as opposed to climbing onto a large obstacle, is likely beneficial because it reduces time

and distance to reach a target position. Jump angle, jump velocity, and approach velocity

accounted for 58% of the variation in jump distance on the large obstacle and only 33%

on the small obstacle. Although the variables placed in the multiple regression models

have been shown in previous studies of static jumping to significantly influence jump

distance, they did not account for a large amount of variation on my small obstacle. I

demonstrate that obstacle size has a significant impact on both lizard behavior and

performance. Researchers should thus consider the complexity of a species' habitat in

designing studies of locomotion.

**INTRODUCTION**

Sprint performance has been well documented in vertebrates due to its ecological

relevance for gathering food and avoiding predators (Arnold, 1983; Huey & Stevenson,

1979).  However, most of these studies have been conducted on flat, uniform trackways

(Goodman, 2009; Husak, Fox & Van Den Bussche, 2008).  In nature, terrestrial

vertebrates navigate through complex habitats that contain highly variable terrain (e.g.

rocky outcrops, woody debris, shrubs with many branches, etc.).  In complex

environments, animals must avoid or overcome obstacles and/or move intermittently in

order to effectively escape predators or capture prey (Kohlsdorf & Biewener, 2006).  The

ability for small vertebrates such as lizards to overcome obstacles by jumping or other

means is likely under selection due to its involvement in foraging, territory defense, and

predator escape (Irschick & Losos, 1999; Pounds, 1988).  Unfortunately knowledge of

how, and when, animals modulate their behavior and performance to negotiate obstacles

is lacking.

Animals possess a range of behaviors (i.e. a behavioral repertoire) to negotiate

obstacles and move about their environment (Garber & Pruetz, 1995; Pace & Gibb,

2011).  This repertoire could consist of but is not limited to walking, sprinting, pausing,

hopping, jumping, flying, quadrupedal, or bipedal locomotion, depending on the

organism and the environment.  Most terrestrial vertebrates are quadrupedal and thus

walk and run with their body parallel to the substrate (Reilly & Delancey, 1997), making

even relatively small obstacles visually obtrusive.  In particular, lizards have been shown

to climb, run bipedally, or jump over small obstacles (Kohlsdorf & Biewener, 2006).

Little is known regarding the frequency of each of these behaviors and how they might

change as animals approach obstacles of varying height, especially large obstacles that reduce their visual field.

A possible strategy that may enhance the visual field over or around obstacles is bipedal locomotion (Kohlsdorf & Biewener, 2006). It has been hypothesized that bipedal locomotion has arisen at least six times within vertebrates (Snyder, 1962). In each case, there is either an advantage over quadrupedal locomotion, or the front limbs are co-opted for some other function (e.g. flight in birds, tool use in humans, etc.; Bennett, 1985; Howell, 1944). Since lizards only use forelimbs for locomotion, it is not clearly understood why bipedalism has evolved in multiple lizard clades. Early research proposed that bipedal locomotion allowed lizards to sprint faster or conserve energy by not using forelimbs (Snyder, 1949; Snyder, 1952; Snyder, 1954; Snyder, 1962), although subsequent studies have provided conflicting evidence (Irschick & Jayne, 1998; Irschick & Jayne, 1999; Roberts, Kram, Weyand & Taylor, 1998). Recent studies indicate that bipedal locomotion in lizards may be a result of high velocity and acceleration (Aerts, Van Damme, D'Aout & Van Hooydonck, 2003; Clemente, Withers, Thompson & Lloyd, 2008).

A host of animals use jumping as a means to overcome obstacles. Jumping performance has been widely studied in an array of vertebrates including primates (Demes, 1995; Peters & Preuschoft), squirrels (Essner Jr, 2002; Essner Jr, 2007; Scheibe & Essner Jr), cats (Harris & Steudel, 2002), frogs (Emerson, 1978; Gomes, Rezende, Grizante & Navas, 2009; Lutz & Rome, 1994; Lutz & Rome, 1996; Marsh & Johnalder, 1994; Wilson, 2001; Wilson, Franklin & James, 2000), and lizards (Kohlsdorf & Navas, 2007; Toro, Herrel & Irschick, 2004). In these studies, subjects are induced to jump from

a motionless state. High-speed cameras or force platforms are utilized to quantify important jump variables (e.g. takeoff angle, velocity, acceleration, force, power, and distance) as the animal leaps off of a takeoff platform. In nature, animals also jump or hurdle obstacles as they encounter them during a run. The capacity to overcome obstacles while running has been far less studied. Kohlsdorf & Biewener (2006) showed that lizards altered limb kinematics (e.g. angle, motion) and behavioral strategies while crossing obstacles of varying heights, but did not measure sprinting and jumping ability. To my knowledge, no studies have been conducted that measure sprint and/or jump performance as animals approach obstacles in which they must climb over, or jump on, in order to move past.

In addition to obstacle-crossing strategies, intermittent locomotion is an important component of an animal's behavioral repertoire that is frequently used during locomotion through complex habitats. It seems to confer an advantage in prey detection and predator avoidance (Vasquez, Ebensperger & Bozinovic, 2002). However, intermittent locomotion is thought to also potentially increase energy expenditure due to repeated bouts of acceleration/deceleration, while at the same aiding in fatigue recovery (Kramer & McLaughlin, 2001). Since obstacles are common in many complex habitats, it is likely that the presence and size of obstacles may influence an animal's decision to move intermittently. Understanding the frequencies at which animals alter behavior based on various obstacle sizes can provide insight into how habitat composition influences behavioral decisions. In turn, these behavioral strategies can increase understanding of the conditions under which animals alter their sprinting and/or jumping performance due to obstacles.

In this study, I investigate the effect of obstacle size on behavior and locomotor performance.  I incorporate both sprinting and jumping performance of lizards as they run towards obstacles of varying heights.  Although sprinting and jumping ability have been extensively studied, scant information exists on the relationship between them, or relative to negotiating obstacles for lizards or any other taxa.  I will test the following hypotheses: 1) If obstacle height increases, then obstacle-crossing strategies will favor jumping and intermittent locomotion will increase. 2) If obstacle height increases, then lizards should increase jump distance but decrease sprint performance. 3) If running jumps are different from stationary jumps, then jump angle and velocity should not accurately predict jump distance in running lizards.  To address these hypotheses, lizards were placed in a custom built arena and induced to sprint toward obstacles of different heights.  High-speed video was used to record trials for behavior and performance quantification.

**MATERIAL AND METHODS**

STUDY ANIMALS

The Florida scrub lizard (*Sceloporus woodi* Stejneger 1918) was chosen as the study species because this species uses flat, sandy areas in which they commonly sprint to flee from predators.  Their habitat preferences range from relatively open sand pine scrub where they are highly terrestrial, to longleaf pine where they are semi-arboreal.  In both habitats, lizards are frequently observed jumping onto, and over, obstacles such as downed wood or course woody debris, during feeding and when escaping predators (Williams, 2010).

Fifty adult, male lizards (50.6 ± 0.55 mm; range = 45 – 57 mm snout-vent length) were captured via noose from six sites in the Ocala National Forest, FL from April – June

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2009.  Lizards were taken to Georgia Southern University and housed in 10 gallon glass

aquaria with a loose sandy substrate. Heat lamps created a gradient of temperatures from

32 - 41 ˚C and UV lighting provided a 12:12 light-dark cycle.  Lizards were fed vitamin-

dusted crickets three times weekly and sprayed with water daily.

OBSTACLE PERFORMANCE TRIALS

Performance trials began on the day after arriving at the facility.  A linear jump arena (90

cm length, 20 cm width, 61 cm height) was constructed from acrylic to test behavior and

performance.  To mimic natural conditions, I used a packed sandy substrate.  Some

minimal slippage was apparent in a few trials, but lizards were able to sprint and jump

with ease.  Logs with diameters of 5.70 cm and 9.55 cm were cut to the width of the

arena to serve as obstacles.  A third obstacle (diameter = 15.92 cm) was also used

initially, but in trials, 17 out of 20 lizards attempted to hide under or run around it, thus it

was discarded.  Prior to trials, lizards were warmed to their field active body temperature

(35 ˚C) for a minimum of 30 minutes.  Upon removal from the incubator, warmed lizards

were placed in the jump arena 38 cm from the obstacle and chased toward the obstacle by

tail tapping or hand waving once lizards had initiated locomotion (Fig. 1).  This distance

was chosen because other studies have shown that lizards can reach near maximum

velocity (Huey & Hertz, 1984), and acceleration (McElroy & McBrayer, 2010) within 30

– 40 cm.

Trials were filmed at 300 frames s$^{-1}$ using two Casio EXILIM EX-F1 cameras.

One camera was placed above the jump chamber (dorsal view) while the other was

placed in lateral view.  Lizards were run 5 – 10 times on each obstacle size over a five

day period with a minimum of two hours rest between trials.  Individuals were not tested

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more than twice on each sized obstacle per day. All trials were classified as either 'successful' or 'unsuccessful'. 'Unsuccessful' trials (e.g. lizard attempted to hide under the obstacle) were only used in analysis of intermittent locomotion. 'Successful' trials were those in which the lizard ended the trial at any location on or beyond the obstacle. Upon review of the video (see below), successful trials were further separated into 3 obstacle-crossing strategies: climbing, jumping, or bipedal locomotion. Jumping required that all limbs were airborne during the transition between the substrate and the obstacle, and that the airborne phase exceeded the individual's snout-vent-length. Bipedal locomotion required that the lizard take a minimum of 3 steps in which the front limbs were not touching the substrate prior to reaching the obstacle. The number of pauses (i.e. intermittent locomotion) while the lizard approached the obstacle was also recorded.

VIDEO ANALYSIS

Each successful trial was trimmed using Adobe Premier Elements software. Trials were trimmed to the frame prior to any lizard movement until the frame that the lizard remained motionless on the obstacle or had moved beyond it and out of camera view. The dorsal, lateral trimmed videos were imported into DLTdataviewer3 software (Hedrick, 2008). A landmark painted on the lizard's snout was used to manually digitize the positional data from each frame and thus generate three dimensional coordinate data from the video. A quintic spline function (GCVSPL software; Woltring, 1986) was used to smooth to the output coordinate data and calculate the instantaneous velocities for each frame. Because minimal movement occurred in the y and z planes during the lizard's approach, average velocity, peak velocity, and peak acceleration were calculated using x

values only.  Smoothing was not required to calculate jump distance because I was only interested in the distance between takeoff and the obstacle.

Jump distance was quantified as the distance between the lizard's snout and the face of the obstacle at toe-off during takeoff (Fig. 2A). Average sprint velocity was calculated as the mean of all smoothed instantaneous velocities during the approach to the obstacle.  Peak sprint velocity and acceleration were calculated as the maximum instantaneous values reached during the approach obtained from smoothed data coordinates.  Jump velocity was calculated by averaging instantaneous velocities over the 8 frames (26.66 ms) prior to toe-off.  This time frame was chosen because for all trials, 8 frames were most representative of the entire takeoff phase (Bels, Theys, Bennett & Legrand, 1992; Toro et al., 2004).  To calculate jump angle, three markers were digitized in each camera view to represent the three vertices of a right triangle (Fig. 2B; Lutz & Rome, 1996).  Steps were numbered sequentially as one hindfoot contacted the substrate until the opposite hindfoot made contact. Because some, although minimal, slippage was apparent on the video, force and power calculations were not made as any slippage would bias those estimates.

STATISTICAL ANALYSES

This study has two major parts.  The first focuses on how obstacle size influences the behavioral repertoire.  To address this, I quantify differences in obstacle-crossing strategy (climb, jump, bipedal) and intermittent locomotion between obstacles.  All successful trials, including multiple runs from each lizard, were used to define the behavioral repertoire.  Hence, I used contingency analysis to test for the effect of obstacle size on the frequency of behavioral strategies.  Contingency analysis was also used to compare the

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frequency of intermittent locomotion between obstacles (both successful and unsuccessful trials). In the second part of the study I focus on the influence of obstacle size on locomotor performance (e.g. sprint and jump ability). To quantify locomotor performance, only trials in which the lizard did not pause or run into the sides of the arena during the approach were analyzed for jump and sprint ability. If lizards had multiple trials that fit these criteria, only the trial with the longest jump distance was retained. Students T-tests were used to analyze step frequency, jump distance, jump velocity, jump angle, average velocity, and peak velocity between obstacles. A Mann-Whitney U-test was used to test peak acceleration. Average sprint velocity, jump velocity, and jump angle were placed in a multiple regression analysis to predict jump distance (square root transformed). No lizards with broken tails were used in any analyses. Analyses were conducted using JMP8 software and values presented below are mean $\pm$ 1 SE.

## RESULTS

BEHAVIORIAL REPERTOIRE

Lizards successfully negotiated the small obstacle in 88% of trials compared to only 52% for the large obstacle ($\chi^2 = 92.09$, $P < 0.001$, $N = 610$). The obstacle-crossing strategy used differed significantly by obstacle size ($\chi^2 = 17.79$, $P = 0.001$, $N = 419$). Lizards jumped more often onto the large obstacle, climbed more often onto the small obstacle, and used bipedal locomotion more often on the small obstacle (Fig. 3). The difference was due to the high proportion of jumps onto the large obstacle. Hence, all jumping trials were removed to test the effect of obstacle size on climbing versus bipedal frequency.

There was no significant effect ($\chi^2 = 0.001$, $P = 0.9787$, $N = 170$). Intermittent

locomotion increased with obstacle size ($\chi^2 = 33.93$, $P < 0.0001$, $N = 611$; Table 1).

SPRINT AND JUMP PERFORMANCE

Sprint performance was greater for the small obstacle (Fig. 4). Sprint velocities were

slower for the large obstacle ($\bar{x} = 0.95 \pm 0.05$ m s$^{-1}$) than for the small obstacle ($\bar{x} = 1.11$

$\pm 0.04$ m s$^{-1}$; $t = 2.683$, $P = 0.011$, $N = 34$). Peak sprint velocities averaged $1.45 \pm 0.06$ m

s$^{-1}$ for the large obstacle and $1.59 \pm 0.05$ m s$^{-1}$ for the small obstacle ($t = 1.696$, $P =$

0.099, $N = 34$). Peak accelerations were greater for the large obstacle ($\bar{x} = 54.5 \pm 6.34$ m

s$^{-2}$) than the small obstacle ($\bar{x} = 77.0 \pm 5.64$ m s$^{-2}$; $U = 215$, $P = 0.013$, $N = 34$). Lizards

jumped significantly further onto the large obstacle ($\bar{x} = 7.44 \pm 0.65$ cm) than the small

obstacle ($\bar{x} = 4.25 \pm 0.58$ cm; $t = -3.420$, $P = 0.002$, $N = 34$; Fig. 4). Jump velocity did

not significantly differ between obstacles ($t = 1.165$, $P = 0.252$, $N = 34$). Jump angle

increased for the large obstacle ($\bar{x} = 49.9 \pm 2.9°$) compared to the small obstacle ($\bar{x} =$

$37.4 \pm 2.6°$; $t = -3.229$, $P = 0.003$, $N = 34$).

The multiple regression analysis indicated that jump angle, jump velocity, and

approach velocity, differed in importance between obstacles. The model explained

58.3% of the variation in jump distance onto the large obstacle (Table 2). Lower jump

angle had the greatest effect on increased jump distance, with jump velocity and average

sprint velocity having similar effects. For the small obstacle, however, the model only

explained 32.6% of the variation in jump distance. Average velocity was most

predictive, followed by jump velocity, and jump angle.

For jumping trials, obstacle size had no effect on the number of steps taken to

reach the obstacle ($7.40 \pm 0.31$ = large obstacle, $7.68 \pm 0.36$ = small obstacle; $t = 0.583$, $P$

= 0.564, $N$ = 34).  The step at which peak sprint velocity was reached was also not

significantly different between the large and small obstacle ($t$ = 1.175, $P$ = 0.249, $N$ = 34;

large: $\overline{x}$ = 5.13 ± 0.42, small $\overline{x}$ = 5.95 ± 0.52).  However, a comparison between total

number of steps until toe-off and the step at peak velocity demonstrates that peak velocity

is reached roughly 2 steps prior to takeoff ($t$ = 2.764, $P$ = 0.009, $N$ = 38, small obstacle; $t$

= 4.338, $P$ = 0.0002, $N$ = 30, large obstacle).

## DISCUSSION

Although sprint and jump performance have been widely investigated, this study is the

first to examine how obstacles of varying sizes influence the behavior and locomotor

performance of running lizards.  To my knowledge, Kohlsdorf & Biewener (2006)

published the first and only study to investigate how lizards modify behavior when

crossing obstacles of varying height.  I add insight to their study by examining the effect

of obstacle size on locomotor performance and by quantifying intermittent locomotion.

By using relatively large obstacles, the potential benefits of using bipedal locomotion to

negotiate obstacles could also be examined.   Here, I show that obstacle size has

substantial impacts on *S. woodi* behavior and performance, and that bipedal locomotion is

important for rapidly overcoming smaller obstacles.

BEHAVIORAL REPERTOIRE

Like earlier work, lizards used three principal obstacle-crossing strategies to negotiate

obstacles: climb, jump, or bipedal locomotion (Kohlsdorf & Biewener, 2006).  My results

also show that obstacle-crossing behavioral strategy is dependent upon obstacle height

and that jumping frequency increases with obstacle size.  I hypothesize that increased

jump frequency on larger obstacles is beneficial because it reduces the amount of time to

reach the target position (Higham, Davenport & Jayne, 2001). If lizards jump at a 45°

angle and initiate takeoff at a distance equal to the obstacle's height, then to climb over a

10 cm obstacle a lizard would travel a total distance of 20 cm to complete this task (10

cm horizontally, 10 cm vertically). If the lizard instead jumps in a straight line from a

distance of 10 cm, it will only travel 14.1 cm to reach the top of the obstacle, reducing the

distance traveled by nearly 6 cm. The distance (and/or time) saved by jumping instead of

climbing increases linearly with obstacle size (as long as it can jump to a height equal to

the linear distance away from the obstacle). Even on small obstacles, it is plausible that

jumping engenders a similar result because jump frequency (51%) is much greater than

climbing frequency (20%; Fig. 3). Climbing an obstacle (principally a large obstacle),

has an additional disadvantage because it requires a high degree of deceleration to

transition from horizontal to vertical running. Although there is evidence of deceleration

associated with jumping (see below), it likely does not have as substantial of an impact

on the time required to cross the obstacle. Reducing the distance to the obstacle, and in

turn the amount of time to the obstacle, has the benefit of a more rapid predator escape.

To verify these predictions, future work could focus on quantifying whether obstacle-

crossing strategies do indeed differ in velocity and time to cross obstacles of varying

height.

Bipedal locomotion was used more frequently than climbing on both obstacles

indicating it is a fairly important behavioral strategy for *S. woodi*. Recent work suggests

that bipedal locomotion in lizards may be a result of excessive speed and torque

(Clemente et al., 2008). Additional hypotheses are that bipedal locomotion is beneficial

for improving an animals' environmental perception and raising its center of mass in

preparation for encountering an obstacle (Kohlsdorf & Biewener, 2006). However, as obstacle height surpasses body length, bipedal locomotion would no longer increase environmental perception as the obstacle would obstruct the animal's visual field. In the present study, lizard height (SVL + femur + tibia/fibia + metatarsus) ranged from 6.87 – 9.02 cm ($\overline{x}$ = 7.83 ± 0.77 cm). This range suggests that it would be possible for all lizards in the study to see over the small obstacle (5.70 cm) while running bipedal, but none of them would be able to see over the large obstacle (9.55 cm). This may explain why *S. woodi* uses bipedal locomotion more on the small obstacle (30.6%) than the large obstacle (16.8%). I suggest that lizards utilize facultative bipedalism even at low speeds to increase environmental perception or prepare for obstacle negotiation. Further experiments are underway to examine this hypothesis.

While many potential benefits of intermittent locomotion (e.g. fatigue recovery, reduced energy consumption, etc.) have been proposed (Avery, Mueller, Smith & Bond, 1987; Higham et al., 2001; Kramer & McLaughlin, 2001), an additional hypothesis is that moving intermittently contributes to increased time to search out additional travel routes. As shown here, lizards are less likely to cross obstacles of increasing size. The results of this study combined with an increase in intermittent locomotion on larger obstacles, support the idea that *S. woodi* likely pauses on the approach to large obstacles to seek out alternative travel routes.

SPRINT AND JUMP PERFORMANCE

While little is known regarding the similarities and/or differences between stationary and running jumps, variables that have been shown to be predictive of jump performance are jump angle, velocity, acceleration, force, and power (Emerson, 1978; Toro et al., 2004;

Toro, Herrel & Irschick, 2006; Wilson, 2001) . Certain variables (e.g. jump acceleration)

become increasingly difficult to quantify during running jumps due to the lack of a

comparative starting point to stationary jumps. I focused on takeoff angle and velocity

(two common and important predictors of jump distance; Emerson, 1985; Marsh &

Johnalder, 1994) in the multiple regression analysis to predict jump distance. Further,

average approach velocity was added preceding the jump because this initial velocity

likely contributes to jump distance.

In my study, it is evident that for a large obstacle the principle predictor of jump

distance is jump angle (see Table 2). Ballistic motion predicts that if force and

acceleration are constant during takeoff, the optimal takeoff angle for achieving

maximum distance is 45˚ (Emerson, 1985). Hence a tradeoff exists. Greater takeoff

angles lead to greater jump height and flight duration, whereas lower takeoff angles lead

to lower jump height and shorter flight duration. *Anolis* lizards jump at less than 45˚,

presumably to reduce flight time and height (Toro et al., 2004). It is interesting that *S.*

*woodi* jumped at 49.9˚ onto a large obstacle, slightly higher than optimal. However in

this study, lizards were gaining elevation following their jump; i.e. increasing the jump

angle is required when the landing position (obstacle) is at a higher elevation than the

takeoff location. The majority of studies investigating jumping ability have studied

animals as they jump from a platform to an object at the same or lower height (Burrows,

2006; James & Wilson, 2008; Toro et al., 2004). When jumping to a lower or higher

position, which would be common in complex habitats, the height of the obstacle has a

significant effect on the angle and distance from which the subject should commence

takeoff (Toro et al., 2006).  Results on the large obstacle support studies of static jumping which show that jump angle is important for traveling long distances.

Do running animals decelerate to maximize jump performance onto an obstacle? Results indicate that lizards do not continually accelerate and reach peak velocity at takeoff.  Lizards in this study reached peak velocity roughly 2 steps prior to jumping and then reduced their velocity before jumping.  While the character of this deceleration is not clearly understood, it is plausible that lizards must reduce their velocity to get their limbs into position to jump onto an obstacle.  Higham, Davenport, & Jayne (2001) manipulated perch angle to test if turning had an effect on sprinting ability in *Anolis* lizards.  They found that with increased turn angle running speed decreased, stride length decreased, intermittent locomotion increased, and jumping frequency increased.  Another interesting discovery was that lizards commonly decelerated and even paused prior to jumping, presumably in preparation to jump.  These findings support my results that lizards decelerate in preparation to jump, likely to maximize jump distance, velocity, and/or accuracy.

Studies of human athletes have shown that joint movements and power patterns do not differ between stationary and running jumps (for both vertical and horizontal jumps; Stefanyshyn & Nigg, 1998).  Overall, the multiple regression analysis failed to explain a large amount of variation in jump distance.  Although it explained 58% percent of jump distance on the large obstacle, jump angle was the only statistically significant variable.  On the small obstacle both jump velocity and approach velocity were significant, but the entire model only explained 33% of the variation in jump distance. This leads me to conclude that variables that have been shown to influence jump distance

for static jumps do not share the same predictive relationship with running jumps in lizards. This is likely due to the complex nature of a running jump or the soft, shifting substrate. These complexities include the sprinting velocity prior to jumping, the lack of a consistent origin of takeoff, and the deceleration associated with jump preparation. When jumping on sand instead of a high traction, solid substrate, lizards might alter their velocity and angle to land at a specific location on the obstacle. I was also unable to measure force and power which have been shown influence jump performance (Marsh & Johnalder, 1994; Wilson et al., 2000).

In conclusion, this study shows that obstacle size has a significant influence on lizard behavior and locomotor performance. Seeing that many vertebrates live in complex habitats with obstacles of varying sizes, researchers should consider an organism's environment and behavioral repertoire when constructing studies of locomotor performance. My study draws attention to the relevance of obstacles in studies of locomotion and provides insight into how obstacle size influences animal behavior and performance.

**Table 1.1** The degree of intermittent locomotion (number of times a lizard paused) was counted for each trial and found to be significantly different between obstacles ($\chi^2 =$ 33.93, $P < 0.0001$, $N = 611$). The table displays the number of trials for which lizards paused 0 – 7 times.

| Obstacle Size | Number of Pauses on Approach to Obstacle | | | | | | | | Trials |
|---|---|---|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| Small | 101 | 113 | 49 | 18 | 5 | 0 | 1 | 1 | 288 |
| Large | 60 | 122 | 86 | 37 | 10 | 3 | 5 | 0 | 323 |

**Table 1.2** Results of a multiple regression of locomotor variables as predictors of jump distance. The adjusted $R^2$ values were 0.583 (large obstacle) and 0.326 (small obstacle).

| Variable | N | β | t | P |
|---|---|---|---|---|
| Large Obstacle: | | | | |
| Angle | 15 | -0.767 | -3.94 | 0.001 * |
| Jump Velocity | 15 | 0.141 | 0.65 | 0.531 |
| Approach Velocity | 15 | -0.101 | -0.51 | 0.618 |
| Small Obstacle: | | | | |
| Angle | 19 | -0.090 | -0.46 | 0.650 |
| Jump Velocity | 19 | -0.579 | -1.96 | 0.069 |
| Approach Velocity | 19 | 0.961 | 3.24 | 0.006 * |

\* = significance ($P \leq 0.05$)

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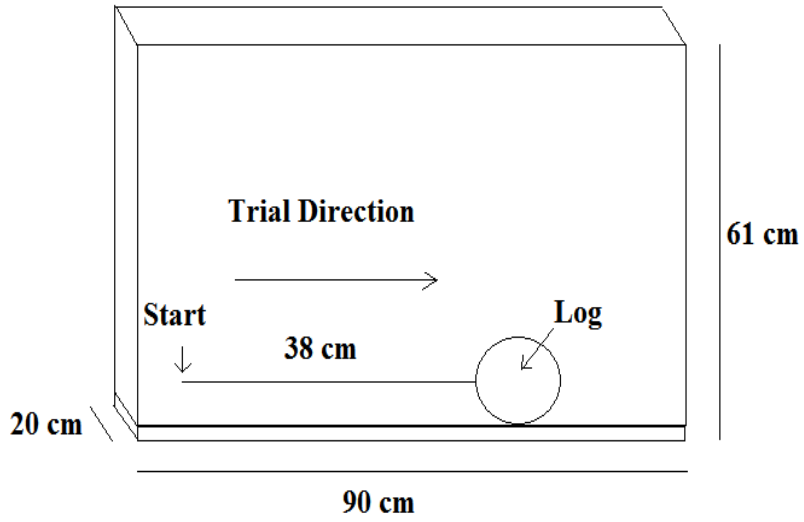
**Figure 1.1** Illustration of the test arena for performance trials (not drawn to scale). Full trial description is contained in Methods.

A



B
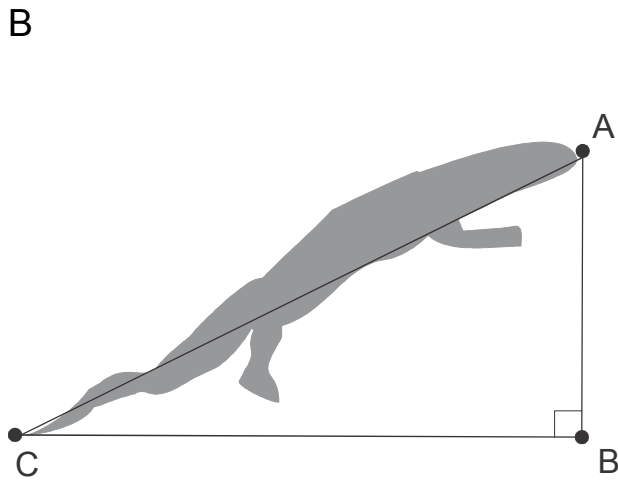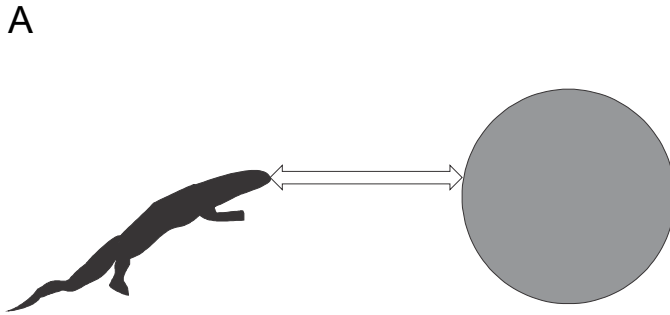


**Figure 1.2** A, jump distance was measured as the distance between the lizard's snout and the face of the obstacle at toe-off during takeoff.  B, a point was digitized on the lizard's snout (A), another was digitized at the substrate directly below the lizards snout (B), and a third at the substrate behind the lizard directly in line with the angle of the body (C). Jump angle was calculated by dividing the arcsine of the line segment *AB* by segment *AC*.

## Small Obstacle
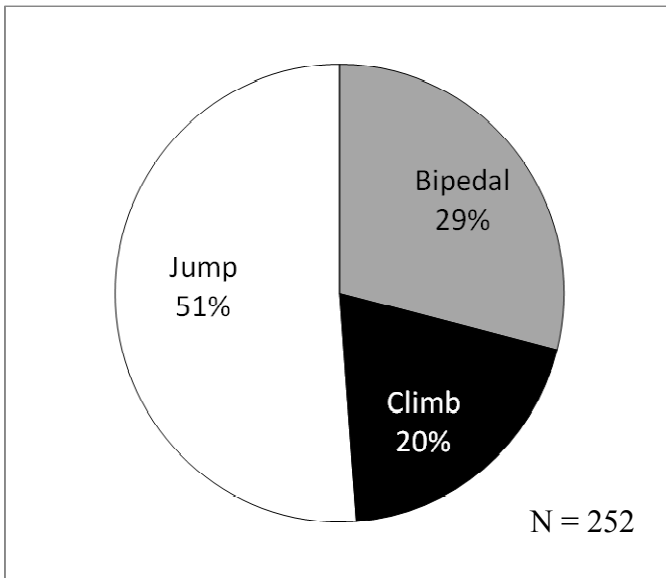


## Large Obstacle
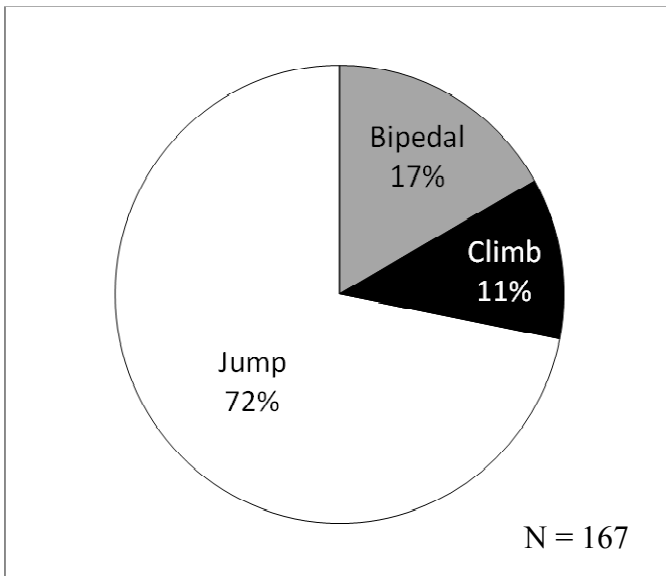


**Figure 1.3** Frequencies of obstacle crossing strategies in *S. woodi*. Behavior was influenced by obstacle size ($\chi^2 = 17.79$, $P = 0.001$, $N = 419$) principally due to the increase in jumping frequency on the large obstacle.
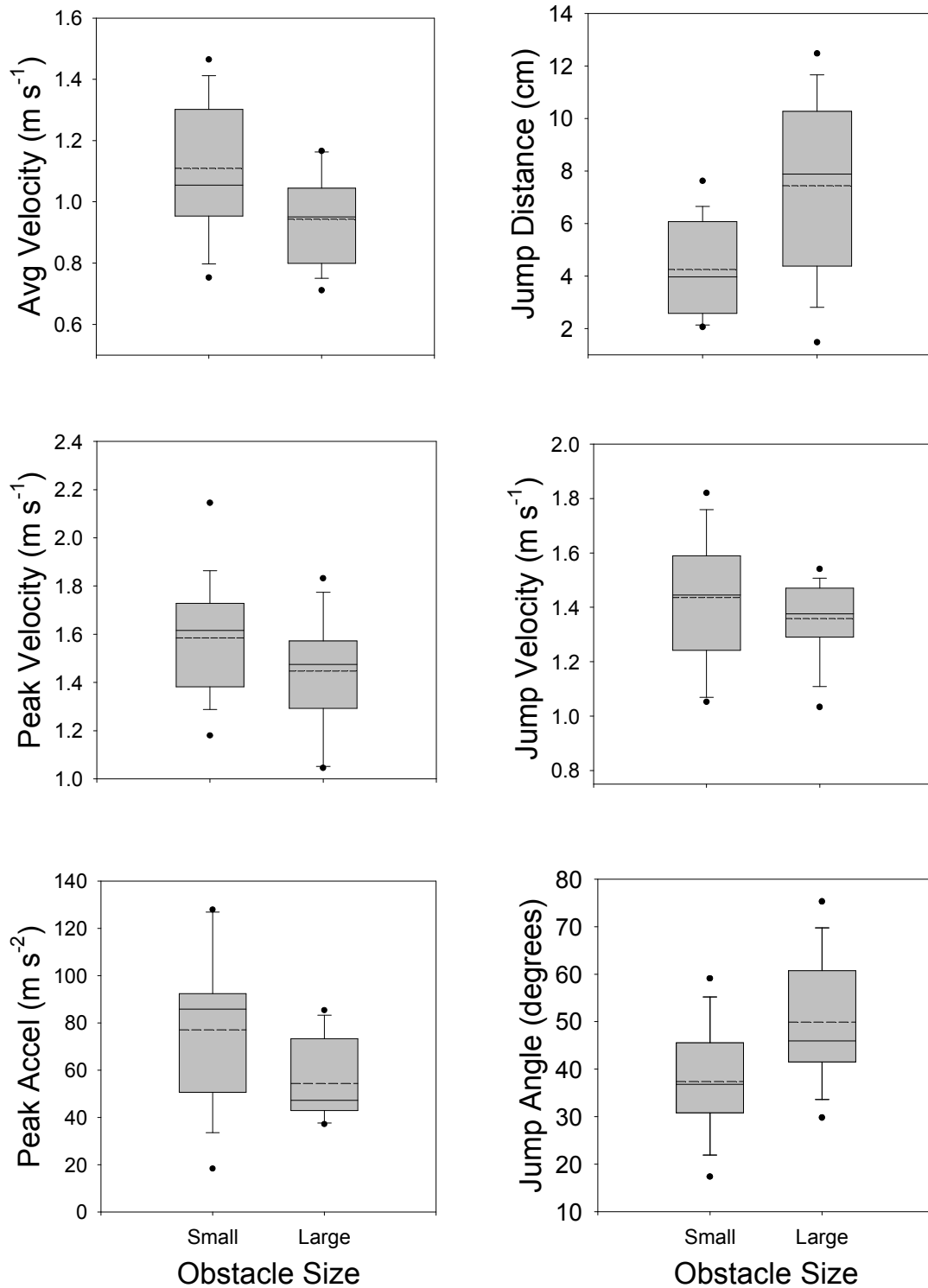
**Figure 1.4** Box plots comparing sprint and jump performance on large and small obstacles. All performance variables measured were significantly different ($P \leq 0.05$) between obstacles except for peak velocity and jump velocity. Although not significantly

different, these two variables followed the pattern of higher velocity on the small obstacle.  The box margins indicate the 25th and 75<sup>th</sup> percentiles. The median (solid) and mean (dashed) are represented with each.  Whiskers indicate the 90th and 10th percentiles.  In addition, outliers are indicated individually by dots.

# CHAPTER 2
## Chaotic genetic patchiness in a terrestrial landscape
## ABSTRACT

The loss of natural habitat due to fragmentation is a major threat to the conservation of species. The Florida scrub lizard (*Sceloporus woodi*) is restricted to open, sunny, scrub habitat, historically maintained through frequent wildfires. The largest remaining population of *S. woodi* is found in the Ocala National Forest, FL. The ONF is fragmented from clearcut logging, fire suppression, and by major roadways. I examined five microsatellite loci to estimate genetic differentiation across the forest and near a major roadway (Florida State Route 40). Pairwise combinations of seven populations revealed that 71% of *Fst* values were significantly different. I tested for a pattern of isolation by distance and discovered that there was no significant relationship between geographic and genetic distance. To investigate the barrier effects of SR-40, I used AMOVA to group populations into two clusters based on whether they were situated north or south of the road. My group classifications only explained 0.02% of the genetic variation across the forest. The results suggest that there is a considerable amount of isolation among *S. woodi* populations in the ONF. Decades of fire suppression has resulted in overgrown forest that hinders lizard dispersal and separates populations by expanses of unsuitable habitat. Though SR-40 may act as a barrier for wildlife, my findings do not denote any added genetic differentiation caused by the road. The highly dynamic nature of the ONF has resulted in random patterns of genetic differentiation and chaotic genetic patchiness.

**INTRODUCTION**

The loss of natural habitat due to fragmentation is one of the major threats to the long-term conservation of species (Hanski, 1998; Keller, Nentwig & Largiader, 2004; Wilcox & Murphy, 1985). Habitat fragmentation can render many small, isolated populations. If the distance between isolated populations is too far, or substantial barriers to dispersal exist, then gene flow will decrease or cease. Reduced gene flow and small population size can reduce genetic variability and heterozygosity through inbreeding and genetic drift (Amos & Balmford, 2001; Corlatti, Hacklander & Frey-Roos, 2009; Frankham, 2005; Hedrick, 2005). Drift and inbreeding can result in even smaller populations (Gilpin & Soule, 1986). A loss of genetic diversity and small population sizes reduces evolutionary potential and can eventually lead to extinction events (Hartl, Markowski, Swiatecki, Janiszewski & Willing, 1992; Johnson & Collinge, 2004).

Habitat fragmentation is often a result of anthropogenic impacts such as residential and commercial development (Bolger, 2002), agriculture (Vitousek, Mooney, Lubchenco & Melillo, 1997), logging (St-Laurent, Dussault, Ferron & Gagnon, 2009), and road construction (Keller & Largiader, 2003). The major cause of fragmentation in the Ocala National Forest (ONF) is clearcut logging for wood pulp. Historically, scrub habitat that occupies most of central Florida (including the ONF) was maintained by frequent, high-intensity wildfires that swept across large areas of the forest (Myers, 1990). Fire suppression, which typically increases with urbanization, has promoted forest maturation and less open scrub habitat (Myers, 1990). As fire suppression persists, prescribed burns and the logging regime grow increasingly important as a replacement for the lost disturbance of frequent wildfires. Forest management of sand-pine scrub has

consisted of cutting stands of 8-25 hectares (Greenberg, Neary & Harris, 1994), leaving patches of various shapes and sizes throughout the forest. Although it is unclear how well it mimics a fire maintained ecosystem, logging can provide the open, disturbed habitat necessary for scrub dependent organisms.

These disturbances often have an influence on the genetic structure of populations. The rate and degree to which subpopulations become genetically differentiated from one another is highly dependent upon the vagility of the organism (Corlatti et al., 2009), their habitat specificity (Holderegger & Di Giulio, 2010), generation time (Loveless & Hamrick, 1984), and the size of the isolated populations (Keller et al., 2004). Patterns in the genetic structure can range from no isolation (i.e. panmixia) to complete isolation among populations. Sometimes these patterns can be explained by models such as isolation by distance (IBD), which is often expected in contiguous habitats (Slatkin, 1993). Isolation by distance indicates that the distance between populations is the main contributor to genetic differentiation. In marine systems, ocean currents often create complex genetic structures that lack clear geographic trends (White, Selkoe, Watson, Siegel, Zacherl & Toonen, 2010). This phenomenon has been termed 'chaotic genetic patchiness' (Arnaud-Haond, Vonau, Rouxel, Bonhomme, Prou, Goyard & Boudry, 2008; Banks, Piggott, Williamson, Bove, Holbrook & Beheregaray, 2007; Doherty, Planes & Mather, 1995; Hedgecock, 1994; Johnson & Black, 1982; Johnson & Black, 2006; Larson & Julian, 1999; Muths, Jollivet, Gentil & Davoult, 2009; Selkoe, Gaines, Caselle & Warner, 2006). This highly dynamic character of marine systems may also exist in some terrestrial landscapes with large amounts of disturbance like the ONF.

The Florida scrub lizard (*Sceloporus woodi*) is endemic to Florida and listed as threatened in the state (Demarco, 1992). It thrives in successional habitats and in most cases is restricted to those habitats with open, sunny patches (Demarco, 1992; Mushinsky, 1985). Greenberg et al. (1994) demonstrated that *S. woodi* population numbers were positively correlated with open scrub features like bare ground, and negatively correlated with factors indicating mature forest such as leaf litter and pine canopy. *Sceloporus woodi* colonizes an area following a recent clearcut or severe fire, but the site only remains suitable habitat for 7-9 years before becoming too overgrown with *Pinus clausa*, *Quercus inopina*, *Aristida stricta*, and other scrub plants. As the site closes in, lizards must disperse along forest roads or unsuitable habitat to colonize a new site, or experience local extinction. The scrub lizard has also been shown to have a limited dispersal capability. Hokit et al. (1999) found that *S. woodi* juveniles rarely disperse over 200 m annually and that if suitable habitat patches are separated by more than 200 m, occupancy rates drop sharply. A sympatric lizard, the six-lined racerunner (*Aspidoscelis sexlineata*), can have home ranges up to 13,000 m$^2$ (Clark, 1976) compared to only 400 – 800 m$^2$ in *S. woodi* (Branch, Hokit & Stith, 1996). Depending on the strength of the barrier (i.e. forest growth), this combination of high habitat specificity and low vagility greatly reduces the probability of migrating to a new site when an existing site becomes unsuitable. Thus, the amount of suitable habitat is an important factor to consider in conservation planning.

Studies of *S. woodi* reveal genetic structuring at the regional (Clark, Bowen & Branch, 1999) and local level (Hokit, Ascunce, Ernst, Branch & Clark, 2010). During the Pliocene and Pleistocene periods, the coast of Florida expanded and contracted multiple

times due to the rising and falling of sea levels (Webb, 1990). Sand ridges that run north and south through the center of the state are remnants of ancient shorelines formed millions of years ago. These sand ridges have become islands of xeric habitats surrounded by more mesic and hydric landscapes. It is thought that these sand ridges form the deep genetic structuring of *S. woodi* observed at the regional scale (Clark et al., 1999). Hokit et al. (2010) took a landscape genetics approach to observe genetic differentiation on a much finer scale, within a sand ridge. However, this study was conducted on scrub habitat that is naturally fragmented and has had little human disturbance over at least the last six decades (Hokit et al., 1999).

The purpose of the present study is to investigate the degree of isolation among populations of *S. woodi* in a highly disturbed and dynamic landscape. Organisms with a limited dispersal ability, high habitat specificity, and short generation time, can experience genetic differentiation among populations quite rapidly due to reduced gene flow and increased genetic drift. I will address the following questions: (1) to what degree are populations of *S. woodi* across the ONF genetically isolated and (2) is Florida SR-40 a barrier to gene flow resulting in significant genetic differentiation across the road? To answer these questions, I analyzed multiple microsatellite loci to investigate genetic similarity among individuals and populations.

**METHODS**

POPULATION SAMPLING AND GENOTYPING

Lizards were captured by noose in various populations throughout the ONF (Fig. 1). The aim of the sampling design was to find populations along a north-south gradient (coinciding with the Mount Dora sand ridge) and along SR-40. Upon capture, a small

tissue sample (e.g. toe, tail tip) was removed, preserved in 70% EtOH for extraction of DNA, and lizards were released at point of capture. Whole genomic DNA was extracted from a total of 138 individuals using a Qiagen DNeasy blood and tissue kit following the protocol for animal tissue. Six polymorphic microsatellite DNA loci (SW614-A1, SW614-A4, SW614-A6, SW614-A7, SW614-B1, SW614-B10) were amplified via polymerase chain reaction using primers previously isolated by Ernst et al. (2004). All PCR reactions began with an initial denaturization step for 5 min at 94 ˚C, followed by 30 cycles of 94 ˚C (30 s), 60 ˚C (30 s), and 72 ˚C (50 s), with a final extension for 20 min at 72 ˚C. Genotyping was performed at Georgia Southern University using an ABI 3500 Genetic Analyzer.

GENETIC DIVERSITY AND DIFFERENTIATION

All statistical analyses were performed using the computer program GENEPOP v4 (Rousset, 2008) unless specified otherwise. The number of alleles, allele frequency, observed heterozygosity, and expected heterozygosity were calculated for all of populations and loci using the Excel Microsat Toolkit (Park, 2001). Genotype distributions were checked for linkage disequilibrium and deviation from Hardy-Weinberg equilibrium using Markov chain analysis with 10,000 dememorization steps, 100 batches, and 5,000 iterations per batch. The program MICROCHECKER was used to test for the presence of null alleles, allelic dropouts, and mis-scoring (van Oosterhout, Hutchinson, Wills & Shipley, 2003). For estimation of genetic differentiation I calculated pairwise $Fst$ values among all combinations of populations using a weighted ANOVA as in Weir & Cockerham (1984). Significance was determined using a Fishers exact G test ($P \leq 0.05$) with and without Bonferroni correction.

The subprogram ISOLDE in GENEPOP was used to test for a pattern of isolation

by distance (IBD) using ($Fst$ / (1 − $Fst$)) and the natural logarithm of geographic distance.

Geographic distance was estimated as the shortest straight line distance between

sampling populations using GPS coordinates.  A Mantel test with 1,000 permutations was

used to determine the significance of the Spearman's rank correlation coefficient (Mantel,

1967).  This approach ignores the presence of SR-40 and assumes a large single

population across the ONF.  All pairwise values were subsequently separated into two

groups dependent upon whether or not the pair of populations was separated by SR-40.

Separate regressions were performed to acquire a slope and $R^2$ for each group (all

pairwise combinations, pairwise combinations separated by the road, and pairwise

combinations on the same side of the road).  I used analysis of covariance (ANCOVA) to

compare slopes to determine if there was a difference in patterns of IBD caused by the

road.  Taking this approach, the IBD analysis can help address both study questions (i.e.

overall isolation across forest, barrier effects of road).  As an additional approach to

examine the effect of SR-40 as a barrier to gene flow, I used analysis of molecular

variance (AMOVA) in ARLEQUIN (Excoffier & Lischer, 2010).  All populations were

assigned to one of two groups, 'North' if they were north of SR-40, or 'South' if they

were situated south of SR-40.

**RESULTS**

Locus SW614-A6 amplified for fewer than 20 % of lizards and was thus discarded from

all future analyses.  The other five loci were polymorphic across all populations and the

number of alleles ranged from 7 to 16.  Observed heterozygosities within populations

ranged from 0.684 to 0.770 (Table 1).  The linkage disequilibrium test indicated that 4 of

70 of pairings had significant non-random associations.  Of these associations, three were different combinations of loci and no patterns were seen among populations.  With all loci pooled for each population, there were no significant relationships.  Thus, any significant linkage is likely due to non-random mating or genetic drift (Frankham, 2005).  Two of the seven populations (KI & 40N) had loci that deviated significantly from that expected under Hardy-Weinberg equilibrium.  For KI the loci were SW614-A1 and SW614-A4 and for 40N the loci were SW614-A4 and SW614-B1.  There was no evidence of allelic dropout or mis-scoring.  Locus SW614-A1 in population KI had a homozygote excess indicative of a possible null allele.

Global $Fst$ across all individuals and populations was 0.034.  Geographic distances between populations ranged from 2.01 to 36.0 km, $Fst$ ranged from 0.002 to 0.096, and 71.4% (15 of 21) of pairwise comparisons were significantly different without Bonferroni correction (9 of 21 after correction; Table 2).  While there was significant genetic isolation among populations, the Mantel test revealed there was no pattern of IBD detected ($P = 0.87$).  After grouping pairwise values based on whether or not they were separated by the road, there was still an absence of IBD (Fig. 2).  The ANCOVA verified that there was no significant difference in slope among the three regressions ($F = 0.0115$, $P = 0.98$, $DF = 2$).  Not only did the regressions lack a pattern of IBD, they exhibited a slightly negative relationship between genetic and geographic distance.  I used AMOVA to compare components of variance among groups, among populations within groups, and within populations.  The AMOVA revealed that the 'North' and 'South' group designations explained the least amount (0.02%) of genetic variation in the model (Table 3).

**DISCUSSION**

This study demonstrates a pattern of chaotic genetic patchiness in a terrestrial landscape that is anthropogenically fragmented. Road construction, fire suppression, and logging can act as disturbances that can isolate populations, reducing gene flow and genetic variability (Forman & Alexander, 1998; Frankham, 2005; Myers, 1990). The combination of these disturbances and the habitat specificity and limited vagility of *S. woodi* has consequences for population dynamics and genetic diversity. These results support previous studies of *S. woodi* that indicate landscape structure limits their distribution resulting in isolated populations (Hokit et al., 2010; Hokit & Branch, 2003; Hokit et al., 1999; McCoy, Hartmann & Mushinsky, 2004; Tiebout & Anderson, 1997). Pairwise *Fst* estimates detect a significant degree of genetic isolation throughout the forest. To my knowledge, the only potential barriers to *S. woodi* dispersal are roads, overgrown habitat, and some urbanization. The major cause of the isolation observed across the ONF is overgrown forest that reduces connectivity among suitable habitat patches.

POPULATION DIFFERENTIATION (*Fst*)

Tiebout & Anderson (1997) used *S. woodi* as a model to address the importance of connectivity for species that depend on transient and early successional habitat. Since the ONF houses the largest remaining population of *S. woodi* and is heavily logged, their study focused on the importance of the patch geometry of logging clearcuts for connectivity. Their simulations demonstrate that shape, location, and timing of neighboring clearcuts, play a vital role on whether lizards can successfully migrate to

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suitable habitat when a site becomes overgrown.  The results of this study suggest that *S. woodi* populations across the ONF experience little or no gene flow.

It is interesting that I find both patterns of genetic differentiation and non-differentiation.  Though fifteen of twenty-one pairwise comparisons among populations are genetically different, six are not.  For example, pairwise *Fst* for populations KI and BS is 0.007 ($P \gg 0.05$).  These populations are separated by 36 km of forest and SR-40.  It is nearly impossible that there is any migration or gene flow occurring between these locations without migration among populations closer together.  These populations, and others in this study, are likely genetically similar and different due to random chance.  The term 'chaotic genetic patchiness' has been given to systems (mainly marine) that lack a clear geographic pattern of genetic structure.  Ocean currents, tides, and environmental variables (e.g. habitat quality, temperature, etc.) have been suggested as reasons why this genetic patchiness exists (Johnson & Black, 1982; Selkoe, Watson, White, Ben Horin, Iacchei, Mitarai, Siegel, Gaines & Toonen, 2010).  The ONF is a highly dynamic habitat due to commercial logging.  Suitable habitat is changing constantly due to the location, size, and timing of clearcuts.  This random distribution of genetically similar populations coupled with multiple extinction and colonization events are indicative of metapopulation dynamics.

A metapopulation has been described as a population of unstable populations (Levins, 1969).  It consists of a network of habitat fragments whereby organisms exist as discrete local populations connected by varying levels of migration (Hanski, 1998).  These populations are subject to size fluctuation and extinction caused by environmental variation and demographic stochasticity (Leigh, 1981).  Individual populations

experience local extinctions but the metapopulation as a whole will persist due to emigration and immigration among subpopulations. Although metapopulation dynamics are typically employed to investigate ecological questions, they have profound impacts on genetic structure as well. Gene flow is crucial for maintaining genetic variability within populations and curbing inbreeding and genetic drift in populations that have been isolated via disturbance (Corlatti et al., 2009; Frankham, 2005). It is likely that the ONF is a metapopulation for many scrub organisms. In an ecosystem currently maintained by logging, suitable habitat appears and disappears at a high rate and species must migrate among suitable patches to avoid extinction. The growth rate and persistence of the metapopulation depends upon intrinsic attributes of the species such as habitat specificity and migration behavior (Hanski, 1998). Since *S. woodi* has strict habitat requirements and a low vagility, long-term viability of the metapopulation in the ONF will depend on the availability of suitable open habitat (e.g. clearcuts, prescribed burns, etc.) with patches in close proximity to enhance connectivity.

ISOLATION BY DISTANCE

If a pattern of genetic IBD is discovered, then this implies non-random mating and restricted gene flow among populations (Wirth & Bernatchez, 2001). In the ONF, *S. woodi* does not exhibit IBD (Fig. 2a). On the contrary, I measured a slightly negative relationship between geographic and genetic distance (i.e. lizards separated by 20 km were as genetically similar or more similar than lizards only 2 km apart). This may not be surprising as a recent study of *S. woodi* showed that though significant genetic IBD was detected, ecological metrics (e.g. patch area, relative isolation) were more predictive of genetic structuring than geographic distance (Hokit et al., 2010). The main difference

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between their study and the present is likely the influence of human disturbance in the ONF.  The commercial logging results in a more dynamic habitat that has led to the observed genetic patchiness in *S. woodi*.

The ONF also has the added complexity and disturbance of roads.  Previous studies have shown that roads can generate genetic differentiation in rodents (Gerlach & Musolf, 2000), marsupials (Lee, Seddon, Corley, Ellis, Johnston, de Villiers, Preece & Carrick, 2010), large mammals (Dixon, Oli, Wooten, Eason, McCown & Cunningham, 2007; Epps, Palsboll, Wehausen, Roderick, Ramey & McCullough, 2005), insects (Keller & Largiader, 2003; Keller et al., 2004), amphibians (Marsh, Page, Hanlon, Corritone, Little, Seifert & Cabe, 2008), and reptiles (Clark, Brown, Stechert & Zamudio, 2010). Pairwise combinations of populations were separated based upon whether they were on the same or opposite side of the road.  As evidenced by homogeneity in regression slopes, the relationship between geographic and genetic distance is not altered by the presence of SR-40.

Construction on SR-40 began in 1926 and was finished in 1927 (FDOT), leaving over 80 years (approximately 62 generations; Jackson & Telford, 1974) to potentially restrict movement between northern and southern populations of *S. woodi*.  If we assume a scenario in which SR-40 is the only barrier to dispersal (i.e. northern lizards can mate with northern lizards only and southern lizards can mate with southern lizards only), we would expect to detect significant genetic differentiation across the road.  This would not be unheard of seeing that I examined differentiation over short distances (2 km) between populations separated by SR-40 (40N & FEE; CN & CS).  AMOVA allows the researcher to partition the total variance into covariance components at different

hierarchical levels (Excoffier, Smouse & Quattro, 1992). The AMOVA indicates that partitioning populations into clusters based on the presence of SR-40 only explains 0.02% of the genetic variation in *S. woodi*. This leaves 2 explanations: (1) SR-40 is not a barrier to dispersal and lizards are able to traverse the road and exchange genetic material or (2) there is not significant gene flow taking place in any area of the forest including across SR-40. The results lend more support to the latter. Measures of *Fst* and IBD demonstrate that there is a substantial degree of genetic isolation across the forest regardless of SR-40. Furthermore, in over 16 years, wildlife biologists with the Unites States Forest Service (USFS) have never spotted *S. woodi* alive or dead on SR-40 (personal comm. Carrie Sekerak).

The Florida Department of Transportation has initiated a widening project to increase portions of SR-40 from two lanes to four lanes. During construction, the USFS has received approval to add wildlife passages along SR-40 to promote animal movement across the road ([www.sr40pde.com](www.sr40pde.com)). Previous research has demonstrated that crossing structures such as overpasses and underpasses can be effective at reducing wildlife roadkills, enhancing connectivity, and reducing genetic structuring around roads (Corlatti et al., 2009; Glista, DeVault & DeWoody, 2009). Anecdotal evidence suggests that lizards do not cross SR-40. Though populations separated by the road do show significant differentiation (*Fst*), the results also indicate significant isolation in all areas of the forest. My best interpretation is that the leading cause of genetic isolation for *S. woodi* is overgrown, mature forest. It is possible that lizards are not seen crossing SR-40 because there is little suitable habitat near the road. While wildlife passages may be valuable for increasing connectivity across the road, access to these passages (i.e. suitable

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habitat) is crucial if they are going to be successful.  Before and after studies to examine

the effects of roads or effectiveness of wildlife passages are ideal (Glista et al., 2009;

Keller et al., 2004) but few exist.  These results will be valuable to later evaluate the

effectiveness of the wildlife passages to increase connectivity and to see how

metapopulation structure might vary temporally.

**Table 2.1** Microsatellite summary statistics for all 7 populations.

| Population | Sample Size | Expected Heterozygosity | Observed Heterozygosity | Avg. No. Alleles |
|---|---|---|---|---|
| 40N | 21 | 0.6311 | 0.7476 | 5.60 |
| BS | 20 | 0.7754 | 0.7600 | 7.80 |
| CS | 23 | 0.7756 | 0.7597 | 7.00 |
| KI | 18 | 0.7188 | 0.6841 | 6.80 |
| SS | 20 | 0.7597 | 0.7200 | 7.00 |
| FEE | 20 | 0.7800 | 0.7700 | 8.00 |
| CN | 17 | 0.7633 | 0.7412 | 7.00 |

**Table 2.2** Pairwise estimates of *Fst* (below diagonal) and geographic distance (above diagonal) in km.

| | 40N | BS | CS | KI | SS | FEE | CN |
|---|---|---|---|---|---|---|---|
| 40N | | **14.1\*** | **5.95\*** | 20.8 | **14.5\*** | **2.01\*** | **6.00\*** |
| BS | **0.043\*** | | **16.7** | 36.0 | **29.8** | **14.2\*** | 18.5 |
| CS | **0.077\*** | **0.010** | | 21.3 | 15.7 | **4.53\*** | **2.11\*** |
| KI | 0.009 | 0.007 | **0.038** | | 6.28 | **22.0\*** | 19.2 |
| SS | **0.074\*** | **0.015** | **0.012** | 0.024 | | 15.9 | 13.7 |
| FEE | **0.096\*** | **0.032\*** | **0.030\*** | **0.069\*** | **0.014** | | 5.30 |
| CN | **0.074\*** | 0.002 | **0.018\*** | **0.048** | 0.014 | 0.009 | |

**BOLD** indicates significance using a Fisher's exact G test ($P \leq 0.05$)

\* Indicates significance after Bonferroni correction ($P \leq 0.002$)

**Table 2.3** AMOVA with 2 groups and 7 populations. Populations were designated in the "North Group" if they were North of SR-40 or "South Group" if they were situated South of SR-40.

| Source of Variation | Sum of Squares | Variance Components | Percentage Variation |
|---|---|---|---|
| Among Groups | 4.417 | 0.00045 | 0.02341 |
| Among Populations within Groups | 21.440 | 0.06491 | 3.36197 |
| Within Populations | 481.531 | 1.86524 | 96.61462 |
| Total | 507.387 | 1.93060 | |
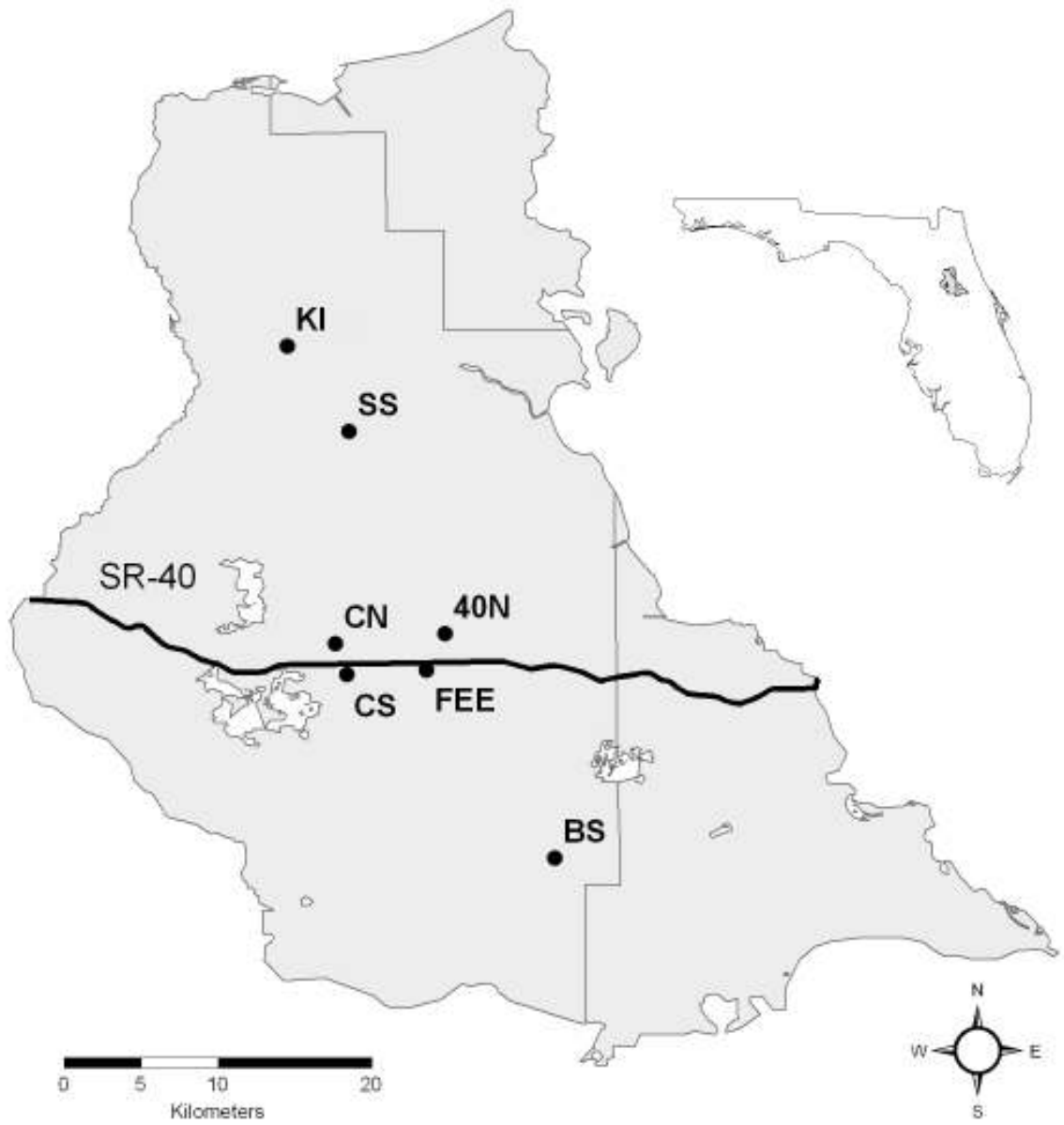
**Fig. 2.1** Populations where lizards were caught throughout the Ocala National Forest, FL. Locations of populations were achieved via handheld GPS units and the map was created using ArcGIS 9.3.
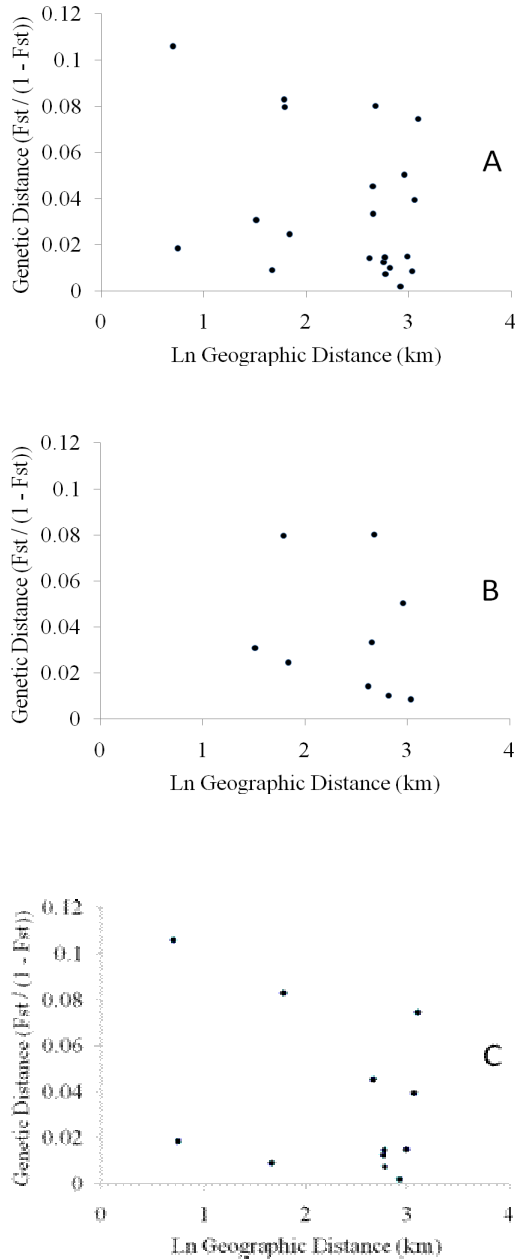
**Fig. 2.2** Isolation by distance tests comparing genetic and geographic distance among all combinations of populations. A, all Pairwise comparisons ignoring the presence of SR-40 (i.e. all possible comparisons). B, all Pairwise comparisons that are on the same side of the road. C, all Pairwise comparisons separated by the road. There is no statistical difference in slope (ANCOVA, $P = 0.98$) or $R^2$ among regressions.

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