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The Role of Habitat Management in Shaping Predation, Animal Color, and Gene Flow in a Metapopulation of Florida Scrub Lizards (*Sceloporus Woodi*)

Richard William Orton

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THE ROLE OF HABITAT MANAGEMENT IN SHAPING PREDATION, ANIMAL COLOR,
AND GENE FLOW IN A METAPOPOPULATION OF FLORIDA SCRUB LIZARDS
(SCELOPORUS WOODI)

by

RICHARD W. ORTON

(Under the advisement of Lance D. McBrayer)

ABSTRACT

Anthropogenic disturbance is known to affect biological diversity at the community, species, and genetic levels. Habitat fragmentation, in particular, has been shown to impact predator abundance and distribution, impede dispersal, and augment genetic drift. In small populations, which often result from habitat fragmentation, the effects of human disturbance may be disproportionately expressed. Small populations are more susceptible to selection pressures and random drift because genetic and phenotypic frequencies can become rapidly fixed, in comparison to larger populations. In turn, fixation of maladaptive alleles or morphs can accelerate extinction. For example, cryptic color polymorphism can be maintained by apostatic selection, where detection of prey is dependent on the relative frequencies of color morphs. In the event that a conspicuous color morph becomes fixed, the probability of detection by visual predators is likely to increase, thus increasing probability of local extinction. Furthermore, events that alter habitat structure and substrate composition may also increase exposure of cryptic animals to visual predators because crypsis is substrate-dependent. A color morph that is cryptic against one visual background may be conspicuous against a different visual background. Subpopulations of *Sceloporus woodi*, a cryptic species of lizard, occupy managed stands of sand pine scrub and longleaf pine habitats in the Ocala National Forest. These subpopulations are subjected to prescribe burning, fire suppression, and clear-cutting. Here, I show that habitat

alteration, due to management in the Ocala National Forest, results in differential predation between sampling locations. As a result, significant variation in dorsal color is observed across the metapopulation. Furthermore, subpopulations appear to experience little genetic drift, perhaps due to gene flow facilitated by anthropogenically-maintained corridors.

INDEX WORDS: Habitat fragmentation, Predation, Crypsis, Selection, Adaptation, Genetic drift, Habitat-management

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(SCHELOPORUS WOODI)

by

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Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

STATESBORO, GEORGIA

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by

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Electronic Version Approved:

July 2017

DEDICATION

Dedicated in the loving memory of my father, Richard Deyo Orton

1 August, 1953 – 6 March, 2017

“Life is not easy for any of us. But what of that? We must have perseverance and above all, confidence in ourselves. We must believe that we are gifted for something and that this thing must be attained.”

- Marie Curie

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Research in the Ocala National Forest was conducted under protocol with the Institutional Animal Care and Use Committee (IACUC permit #I150112), the State of Florida Fish and Wildlife Conservation Commission (permit #LSSC-15-00027), and the U.S. Forest Service (USFS permit #SEM540).

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CHAPTER 1

HABITAT MANAGEMENT AFFECTS PREDATION IN A FRAGMENTED LANDSCAPE

ABSTRACT

Crypsis reduces the probability of detection in prey animals by concealing the visual signal of the animal within the local visual background. However, because crypsis is a background-specific adaptation, animals cryptic in one visual background may become conspicuous in another visual background. Thus, events which alter habitat structure and substrate composition are likely to affect rates of predation on cryptic animals. Populations of *Sceloporus woodi*, a cryptic diurnal lizard, occupy clear-cut stands of sand pine scrub and prescribe-burned longleaf pine habitat within the Ocala National Forest. Here, I use a combination of clay models resembling *S. woodi* and spectral analysis to examine the effects of spatial heterogeneity on rates of predation. The proportion of attacked models placed in the field was greatest on open sand and deadwood in sand pine scrub habitat. The dorsal color of models greatly contrasted open sand and dead wood, but had similar reflectance values to leaf litter, suggesting that models were cryptic on leaf litter. However, the contrast between models and leaf litter did not vary between stands. Moreover, the proportion of attacked models decreased as the age of sand pine scrub stands increased, and was low in stands of longleaf pine. It is likely that the proportion of attacked models relates to increased exposure of open sand and decreased amounts of leaf litter, immediately following clear-cutting. These findings suggest that habitat management can affect predation intensity on cryptic species.

INTRODUCTION

Predation is often of interest to studies of phenotypic evolution because predation reduces fitness and predators can act directionally on specific phenotypes (Lima and Dill 1990). For example, animals with colors and patterns that blend with the visual background (i.e. match the color of substrate), termed ‘crypsis,’ are often found in environments with high rates of predation imposed by visual predators (Kettlewell 1965; Endler and Basolo 1998). The common inference is that cryptically-colored animals are more likely to avoid visual detection by predators than conspicuous individuals, barring aposematic coloration, and are thus more likely to survive and reproduce (Storfer et al. 1999; Stuart-Fox et al. 2003; Troscianko et al. 2016). However, studies investigating crypsis often only infer predation to be the driving selection pressure behind colors that resemble the local visual background (but see Farallo and Forstner 2012).

Crypsis has been noted in multiple taxa including amphibians (Storfer et al. 1999), mammals (Hoekstra and Nachman 2003), moths (Endler 1984) and reptiles (Stuart-Fox et al. 2004; Rosenblum 2006; Stuart-Fox and Moussalli 2009; Farallo and Forstner 2012). The dorsal color of reptiles, particularly, is thought to be under strong selection pressure for crypsis because diurnal reptiles experience intense selection from visual predators, such as birds (Norris and Lowe 1964; Kettlewell 1973). Geographic variation in the dorsal color of cryptic reptiles is also documented (Norris and Lowe 1964; Sweet 1985; Fox et al. 2004; Rosenblum et al. 2006; Farallo and Forstner 2012), and because crypsis is a substrate-specific adaptation (Merilaita et al. 1999; Ruxton et al. 2004), geographic variation in the dorsal color of reptiles may result from spatial heterogeneity in substrate coupled with selection pressure from visual predators. In the past, ecological transition zones harboring reptiles have provided arenas for testing hypotheses regarding cryptic coloration, substrate, and predation (Rosenblum et al. 2006; Farallo and

Forstner 2012) because populations across these zones occupy habitats that vary in environmental characteristics, such as substrate type (Gleason 1917). Thus, events that lead to variation in substrate type, natural or anthropogenically-influenced, may feasibly lead to variation in animal color in the presence of visual predators.

Populations of the Florida scrub lizard (*Sceloporus woodi*) within the Ocala National Forest (ONF) of central Florida, provide an ideal opportunity in which to study the impacts of geographic variation in substrate on predation. In the ONF, populations of *S. woodi* are exposed to avian predators, such as the Florida scrub jay (*Aphelocoma coerulescens*) (Breininger et al. 2006), and are fragmented between longleaf pine (LLP) and sand pine scrub (SPS) habitats (Jackson 1973; Enge et al. 1986). Longleaf pine and SPS within the ONF contrast in several environmental variables (Wells 1928; Jackson 1973; Greenberg et al. 1994), including dominant substrate type (Kaunert and McBrayer 2015). Additionally, the ONF is an anthropogenically-altered landscape that relies upon management practices to maintain successional habitats characteristic to LLP and SPS, where LLP is prescribe-burned on an annual or bi-annual cycle and stands of SPS are clear-cut following at least forty years of succession (Enge et al. 1986; Greenberg et al. 1994; Tiebout and Anderson 1997). However, in place of clear-cutting, fire is suppressed in stands of SPS, allowing for increases in vegetation density and thus, changes to dominant substrate type over time (Tiebout and Anderson 2001). The timing and type of management practice in the ONF likely exaggerates differences in substrate composition between LLP and SPS, as well as between different stands of SPS. Consistently, stands of LLP and SPS within the ONF are in various stages of succession.

In this study, we used clay models to test the effects of substrate type and management practice on predation in *S. woodi* between two contrasting habitats. Without prior knowledge of

color polymorphism in *S. woodi*, we used uniformly-colored clay models, placed on substrates of various color, to quantify the contingency of predation on model-substrate contrast. Our methods followed several published studies that have successfully used clay models to examine the influence of selection from predation (Pfennig et al. 2001; Wuster et al. 2004; Husak et al. 2006; Steffen 2009). Clay models provide an advantage for studying the impacts of color on predation, by removing individual variation such as size and behavior (Paemelaere et al. 2013). We predicted that attacks from visually oriented predators would be dependent on the degree to which models contrasted substrate and that the proportion of attacked models would vary between LLP and SPS due to differences in dominant substrate. We also predicted that management practice would affect the proportion of attacked models because disturbance can alter substrate composition (Auerbach et al. 1997; Dinnage 2009).

MATERIALS AND METHODS

Clay models

We constructed models (Figure 1a) by molding a thin layer (1-2mm) of pre-tinted oil-based modeling clay (Roma Plastilina; Van Aken International, Rancho Cucamonga, CA, USA), around commercially available plastic lizard replicas. The replica lizards [snout-vent length (SVL) = 60mm] were within the size range of the average adult male *S. woodi* (mean = 55mm SVL; range= 50-65mm SVL). We modeled our clay replicas (N = 380) after male *S. woodi* because the species is sexually dimorphic and males are thought to incur higher rates of predation than females. Males have reduced dorsal patterning and bright blue throat badges, which are thought to play a role in sexual selection but may inadvertently attract predators (Husak, 2006). The dorsal side and color badges of clay models were painted with acrylic paint (Liquitex, Cincinnati, OH, USA) to match the coloration of adult male *S. woodi*. The color of models was selected by eye prior to the experiment, and was later verified with a spectrophotometer after the completion of the experiment. Additionally, we constructed control models shaped as spheres from the same clay as lizard models, painted with the same paint used for the dorsal surface of clay lizard models.

Field Placement

We placed a total of 380 clay models and 32 controls among five longleaf pine (LLP) and five sand pine scrub (SPS) stands between June 2015 and June 2016 (Figure 2). Models were placed in typical basking and foraging locations of *S. woodi* and would thereby be available to natural predators such as birds of prey (e.g. *Falco columbarius*) and Florida scrub jays (*Aphelocoma coerulescens*). Forty models were spaced 10-20m apart within each stand to

characterize encounter rates of *S. woodi* in the Ocala National Forest (R. Orton, personal observation). In order to test for predation and crypsis of *S. woodi*, we placed models on the three dominant substrates (open sand, deadwood, and leaf litter) in each stand (Kaunert and McBrayer, 2015). These substrates contrast in color and are typical substrates for *S. woodi* activity (Kaunert and McBrayer, 2015). Models were randomly placed on the different substrates to represent the proportion of each substrate within stands. Statistical analysis of this sampling method matched published data on substrate abundance within each habitat type (Kaunert and McBrayer, 2015). Models were left in the field for 72 undisturbed hours to allow predators sufficient time to locate models but to avoid acclimation of predators to the models. Models were retrieved between the 73rd and 74th hour and scored as “attacked” or “not attacked” according to the presence or absence of tooth or beak marks retained in the malleable clay, which were easily differentiated from one another (Figures 1b and 1c).

Spectrophotometric measurements

We used a bifurcated fiber optics probe (Ocean Optics, Dunedin, FL, USA) connected to an Ocean Optics Flame spectrometer and a xenon light source (Ocean Optics) to measure the spectral reflectance of model dorsal color, open sand, and leaf litter. The fiber optic probe was held with a standard probe holder at 1mm from the surface of all substrates and models and at 45°. All measurements were recorded with Ocean View software v1.5.2 (Ocean Optics) and were taken relative to a certified 99% diffuse white reflectance standard. Dark current and white standard measurements were taken before each spectrophotometric reading. To reduce noise, the average of two scans with a boxcar width of two was used for each measurement.

Spectrophotometric Analysis and Visual Model Use

Approximately 97% of attacks to clay models were from avian predators. Thus, we used AVICOL software (Gomez 2006) to analyze spectral data because the AVICOL analysis integrates cone sensitivity curves which provide the sensitivities to wavelengths for each of the four single cone types that birds possess (Bowmaker et al. 1997). In AVICOL, Vorobyev and Osorio's (1998) physiological model was used because it accounts for chromatic and achromatic contrast between colors as perceived by an organism with tetrachromatic vision. This model is accepted to be consistent with the capabilities of avian vision (Osorio 1999; Osorio et al. 1999; Endler and Mielke 2005) and considers the chromatic and achromatic properties as independent sources of visual stimulation (Vorobyev and Osorio 1998).

Achromatic contrast is crucial for distinguishing between small objects or objects visualized from large distances (Osorio et al. 1999; Lind and Kelber 2011). For example, achromatic contrast might be expected to be important for avian predators that search for prey while midflight or while perched on tree branches. Initially, we analyzed both chromatic and achromatic contrast, but found achromatic contrast to be a more reliable measure. Thus, we focused our spectrometric analysis on achromatic contrast. The contrast between colors of two different samples is expressed as a just noticeable difference (JND) value, where a JND value = 1 is the critical value for discrimination between two colors or objects of varying brightness (Gomez, 2006).

We also collected 15 samples of sand and 15 samples of leaf litter from each habitat type (3 from each of 5 stands) and brought them back to the lab where we recorded spectrophotometric measurements. Three spectrophotometric measurements were taken on each sample and averaged. This sample average was then averaged across the other two samples of the same substrate type collected from the same stand to obtain a measure of reflectance for a

particular substrate type from a particular stand. We also took measurements of three lizard models (to ensure accuracy of measurements) and found the difference in reflectance measurements between models to be negligible (0.4 to 0.6 just noticeable difference, JND units). Because the difference in reflectance between the three lizard models was negligible and all models were colored with identical paint, there was no need to measure the spectral reflectance of additional models. The average from the three lizard model spectral measurements was then used to determine the contrast against each substrate type from each stand where models were placed. Difficulty in accurately measuring the reflectance of dead wood due to its irregular shape, prevented spectrophotometric measurements and thus deadwood was excluded from model-substrate contrast analyses.

Cameras

Cameras (Browning model BTC-5, Browning Arms Co, Morgan, UT, USA) were deployed to aid in predator identification and to potentially observe predation events. Four camera traps were deployed at each stand for the same 72 hours as our models. The camera traps were focused on one model per substrate type and one camera trap was focused on a random model. The camera traps were set to take five photographs in rapid succession following the triggering of the camera sensor. Also, cameras were set to take one photograph every minute from 0600 to 2030 hours. The photographs were downloaded and reviewed in the lab between field data collection sessions.

Statistical Analysis

All statistical tests were performed using the JMP v12 statistical package (SAS Institute, Cary, NC, USA). Chi-square tests were used to determine if the proportion of attacked models was contingent on habitat and/or substrate type. When cell counts violated the assumptions of

Chi-square tests, we used a Fisher's exact test (FET). Chi-square tests were also used to test if the proportion of attacked models on different substrate types differed within habitat type and between LLP and SPS. Because the distribution of JND values and attack rate did not meet the assumptions of normality, a nonparametric linear rank regression (Hettmansperger 1998; Hollander 1999) was used to determine if the proportion of attacked models was dependent upon the degree to which the dorsal color of models contrasted the color of substrate. A Wilcoxon test was used to determine if the spectral values of the substrate types differed between LLP and SPS. Because the ONF is an anthropogenically-managed landscape, a Chi-square test was used to determine if attack rate was associated with the age of stands (management practice). All stands were classified as "1-3 CC" (less than four years post clear-cut), "4-6 CC" (four to six years post clear-cut), "7 CC" (more than six years post clear-cut), or "1-2 Burned" (one to two years post prescribe burn). Last, a Chi-square test was used to determine if our method for placing models represented the relative proportions of each substrate type in LLP and SPS.

RESULTS

The color of models was similar to the color of adult male *S. woodi* (6.97 JND). Of the 380 models placed in the ONF, 35 (9.2%) were attacked. Of these, a single model was attacked by a mammal and the remaining 34 were attacked by avian predators. We excluded the mammal attack from our analyses because the prey detection systems of mammals and birds are expected to drastically differ, and our focus was on the visual detection of prey. Five of 380 models were lost either through experimental error, or from being carried away by a predator, and were excluded from analysis. Statistical tests were run both including and excluding the single mammal attack; exclusion of the mammal attack made no difference in any of the results presented below. Zero of the 32 controls were attacked, and were thus excluded from analyses.

The proportion of attacked models was significantly different between LLP and SPS ($X^2 = 12.632$, $P = 0.0004$) (Figure 3a). More specifically, the proportion of attacked models on open sand ($X^2 = 4.045$, $P = 0.0443$) and on deadwood ($X^2 = 4.757$, $P = 0.0292$) was significantly different between LLP and SPS, but the proportion of attacked models on leaf litter was not significantly different between LLP and SPS ($X^2 = 0.893$, $P = 0.3448$) (Figure 3b). Furthermore, the proportion of attacked models was contingent on substrate type within SPS ($X^2 = 6.810$, $P = 0.0332$) and combined LLP and SPS (across the ONF) ($X^2 = 10.876$, $P = 0.0043$) but not significantly contingent on substrate type within LLP. This result may be due to the overall low number of attacks in LLP (4.10%). For attacks within LLP, the proportion of attacked models was not contingent on substrate type ($P = 0.5911$, FET).

The proportion of attacked models across the ONF was dependent on the achromatic contrast between models and their associated substrate ($R^2=0.321$, $F_{(1,18)} = 10.097$, $P = 0.0052$) (Figure 4b) but not chromatic contrast ($R^2 = 0.0716$; $F_{(1,18)} = 1.3892$; $P = 0.2539$). A Wilcoxon

test was then used to determine if the contrast between models and substrate types differed between LLP and SPS, and there was no difference in spectral contrast (between models and their substrates) for open sand ($Z = -0.054$, $P = 0.6139$) or leaf litter ($Z = -1.095$, $P = 0.2731$) (Figure 4b). However, the placement of models upon different substrates significantly differed between LLP and SPS ($X^2 = 49.062$, $P < 0.001^*$), with the frequency of models placed on leaf litter being greater in LLP and the frequency of models placed on open sand higher in SPS. Data published by Kaunert and McBrayer (2015) confirms that placement of models was in relative proportion to the available substrate types in LLP and SPS. Last, the proportion of attacked models was contingent upon management practice ($X^2 = 27.568$, $p < 0.001^*$) (Figure 5). The proportion of attacked models was highest in 1-3 CC stands (.217) intermediate in 4-6 CC stands (.137), non-existent in 7 CC stands (0), and low in 1-2 Burned stands (.041).

Camera traps placed near models captured over 104,400 minutes of photographs, yet no predation events were recorded on cameras. However, camera traps did capture the presence of multiple taxa including lizards (*S. woodi*, *Aspidescelis sexlineatus*, and *Plestiodon* spp.), birds (*Melanerpes carolinus*, *Paucaea aestivalis*, *Meleagrus gallopavo* [Figure 1d]), and mammals (*Podomys floridanus*, *Odocoileus virginianus*, and *Sus scrofa*) near our clay models. Of the species photographed by our camera traps, *M. gallopavo* was the most common (captured in six different photographs) followed by *P. floridanus* (captured in three different photographs). All lizards and birds were captured by camera traps before 2130 and all mammals were captured between 2130 and 0600 when most lizards would be inactive. Of the 35 attacked models, only one was placed with an accompanied camera trap. This model was attacked by an obvious mammalian predator (likely *Procyon lotor* or *Didelphis virginiana*, based upon the distance between incisors [2.0 cm]), however, the associated camera trap was disturbed before the attack.

The camera trap was retrieved with the lens flush against the substrate, hence, the predation event was not captured on camera.

DISCUSSION

In the ONF, selection from visually-oriented predators appears to be reduced in LLP compared to SPS. Differences in the proportion of attacked models between habitat types likely relates to differences in prey detection by avian predators between LLP and SPS. For example, the contrast between substrates and models significantly affected rates of attacks in SPS, but there were no differences between the proportion of attacked models placed on sand, deadwood, or leaf litter in LLP. Furthermore, the proportion of attacked models placed on sand and deadwood in SPS were significantly greater than the proportion of attacked models placed on sand and deadwood in LLP, even though contrast between models and substrates did not vary between LLP and SPS. If prey detection by visual predators were similar between LLP and SPS, it would be expected that the patterns and proportions of attacked models would be similar for both habitat types, regardless of total number of attacked models. However, this is not the case in our study, suggesting that visual predators with different mechanisms of prey detection (or foraging strategy) reside in LLP and SPS.

The results of our study also compliment evidence that substrate type plays a significant role in the detection of prey by visually-oriented predators (Kettlewell 1965; Endler 1984; Farallo and Forstner 2012). Across the ONF, the proportion of attacked models was contingent on substrate type, where models placed on sand and deadwood were attacked more often than models placed on leaf litter. This pattern of attacks is likely manifested in the contrast between models and different substrates, suggesting that models are more cryptic against leaf litter than open sand or dead wood. Our results indicate a positive relationship between the proportion of attacked models and the contrast between models and substrate, suggesting that there is selective pressure for crypsis on *S. woodi* across the ONF.

The theory of adaptive coloration predicts that cryptic individuals are more likely to survive than individuals with dorsal coloration that contrasts local substrate (Cott 1940; Endler 1984). Hence, selection is expected to lead to cryptic phenotypes in environments where predation from visual predators is high. *A-posteriori* spectrophotometric measurements revealed that the average contrast between our models and three adult male *S. woodi* was 6.97 JND. This value was similar to the average contrast between models and leaf litter (6.87 JND), and no models placed on leaf litter in SPS were attacked. Thus, there appears to be selection pressure on the dorsal color of *S. woodi* to resemble leaf litter. This inference is supported with published data that substrate selection is greatly affected by predation risk (Stein and Magnuson 1976; Ruxton et al. 2004) and *S. woodi* encounter rates in SPS are highest on leaf litter despite the dominant substrate in SPS being open sand (Kaunert and McBrayer, 2015)

In LLP, where predation intensity from visual predators appears to be relaxed, it is possible that populations exhibit a wider range of dorsal coloration. However, in addition to predator evasion, animal colors and patterns also affect thermoregulation (Endler 1978), which is vital for ectothermic organisms (Kettlewell 1973; Kingsolver and Wiernasz 1991; Bittner et al. 2002; Strugariu and Zamfirescu 2011). In environments with reduced selective pressure from visual predators, it is possible that thermoregulatory selective pressures drive dorsal coloration (Gibson and Falls 1979; Andren and Nilson 1981). Recent data indicates that thermal quality of habitat significantly varies between LLP and SPS (Neel 2016). Hence, it is plausible that tradeoffs in selective pressures between LLP and SPS in the ONF causes geographic variation in dorsal coloration of *S. woodi*. Future work will measure the spectral reflectance of dorsal color in a large sample size of *S. woodi* from LLP and SPS to test for color polymorphism and background color-matching.

Additionally, management practices in the ONF appear to affect predation. In addition to significant differences in the proportion of attacked models between LLP and SPS, the proportion of attacked models significantly differed by stand age. Both LLP and SPS are fire-dependent ecosystems, however, fire is suppressed in SPS and replaced with clear-cutting (CC) and roller-chopping (RC) in the ONF (Greenberg et al., 1994; Tiebout and Anderson, 2001). Clear-cutting in SPS exposes bare sand and deadwood, and decreases vegetation (Tiebout and Anderson, 1997). However, as SPS stands mature, vegetative density (and leaf litter) increases and the amount of open sand decreases (Tiebout and Anderson, 1997; Tiebout and Anderson, 2001), reducing the chances of visual detection of prey items that are cryptic against leaf litter. Meanwhile, LLP undergoes prescribed burns on a bi-annual schedule (Tiebout and Anderson, 2001), maintaining LLP in a state of early to mid-succession (Wells and Shunk 1931) where open sand and leaf litter are both common and extensively used by *S. woodi* (Kaunert and McBrayer 2015). Management practices such as prescribed burning and/or clearcutting have direct impacts on substrate composition and abundance, hence, likely affecting predation rates on *S. woodi*. However, it is also possible that management affects the abundance and spatial distribution of potential avian predators in the ONF.

Changes in avian species abundance and richness often result from anthropogenic disturbance (Herkert 1994; Gray et al. 2007). In particular, avian populations tend to be detrimentally affected by habitat fragmentation (Robinson and Robinson 1999; Stratford and Stouffer 1999). For example, habitat fragmentation was shown to decrease gene flow and increase the need for greater dispersal distance for *A. coerulescens* (Coulon et al. 2010). Furthermore, *A. coerulescens* prefers habitat with open sand and young scrub oaks (Fitzpatrick and Woolfenden 1984) which is characterized by recently-disturbed SPS (Breininger et al. 1995;

Breining et al. 2006). The highest *A. coerulescens* abundance that was anecdotally observed in the ONF was in a 1-3 CC stand (Figure 2; SPS 5), which happened to be the location of the highest predation rate on our models. It is plausible that the relative abundance and spatial distribution of *A. coerulescens* is a determining factor of predation rate in our study.

Management practices in the ONF are also likely to affect the spatial distribution of wild turkeys (*Meleagris gallopavo*), as impacts from anthropogenic disturbance are documented in other understory species (Barlow et al. 2006). Cameras did not record any predation events, though we were able to use these data to identify several potential avian predators observed near attacked models. The most common potential avian predator recorded by our camera traps were *M. gallopavo*, and most often in stands of LLP. *M. gallopavo* forage terrestrially where the advantage of cryptic coloration to prey may be overridden by the close proximity of the predator. The relative abundance of terrestrially-foraging avian predators, such as *M. gallopavo*, may describe the lack of variation in predation rate between substrate types within LLP. Furthermore, the primary diet of *M. gallopavo* consists of seeds and berries, and only on occasion are *M. gallopavo* expected to consume small lizards (Rumble and Anderson 1996). Hence, the dietary preference of *M. gallopavo* may account for the overall low attack rate in LLP. Further study on avian density and spatial distribution within the ONF may be needed to fully understand variation in predation rate between LLP and SPS.

In conclusion, avian predation on *S. woodi* appears to be related to substrate type, habitat type, and management practice in the ONF. Differences in predation between LLP and SPS are likely directly and/or indirectly related to management practice and suggest that polymorphism in *S. woodi* may be apparent between LLP and SPS. Though evidence indicating the effects of selective pressure from visual predators on cryptic coloration is well-documented, experiments

elucidating the impact of management practice on predation is not. In species where survival is dependent on environmental factors that are subject to management practices, there may be unintended consequences due to those practices.

Table 1.1 A list of each sample location (stand) with the habitat type, management practice, proportion of attacked models per substrate type in each stand, and total proportion of attacked models for each stand. The categories of management combine the type of management (burned vs clear cut and roller chopped) and time since last disturbance. Categories: 1-2 Burned = 1-2 years post burn in LLP ; 7 CC = 7+ years post clear cut in SPS; 4-6 CC = 4-6 years post clear cut in SPS; 1-3 CC = SPS stands 1-3 years post clear cut (CC).

Habitat Type	Stand	Management Practice	Leaf Litter	Open Sand	Dead Wood	Total
Longleaf Pine	Riverside	1-2 Burn	0	0	0	0
	Island	1-2 Burn	0	0	0	0.03
	Norwalk Island	1-2 Burn	0.05	0.25	0.17	0.14
	Kerr Island	1-2 Burn	0	0	0	0
	Salt Springs	1-2 Burn	0	0	0.14	0.10
Sand Pine Scrub	Island	7 CC	0.10	0	0	0
	Hughes Island	3-6 CC	0	0.33	0.12	0.15
	SPS1	3-6 CC	0	0	0.22	0.13
	SPS2	1-2 CC	0	0.13	0.29	0.15
	SPS3	1-2 CC	0	0.38	0.20	0.25
	SPS4					
	SPS5					

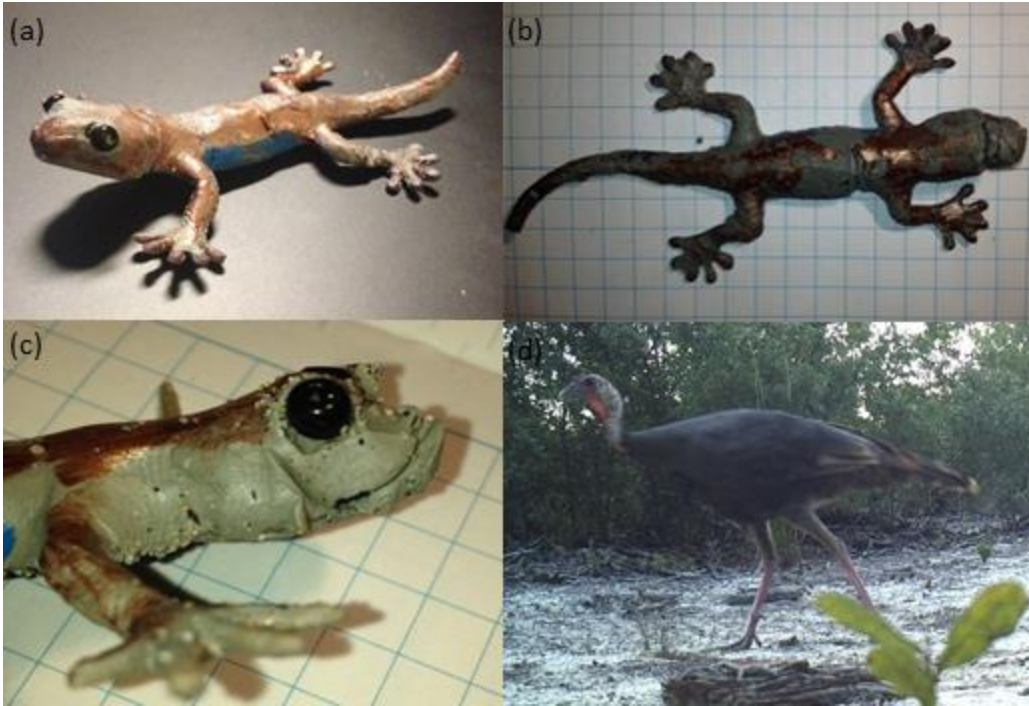


Figure 1.1. (a) Photograph of a clay model. (b) Photograph of a clay model which was attacked multiple times by an avian predator on the head and torso, or by multiple avian predators. Models which were attacked multiple times were only counted as a single attack due to uncertainty in the number of predators. (c) Close-up of a model attacked by an avian predator on the head. Data collected from field traps suggest the model may have been attacked by *M. gallopavo*. (d) Photograph captured by a camera trap showing a wild turkey (*M. gallopavo*) near one of our models placed on deadwood (in foreground).

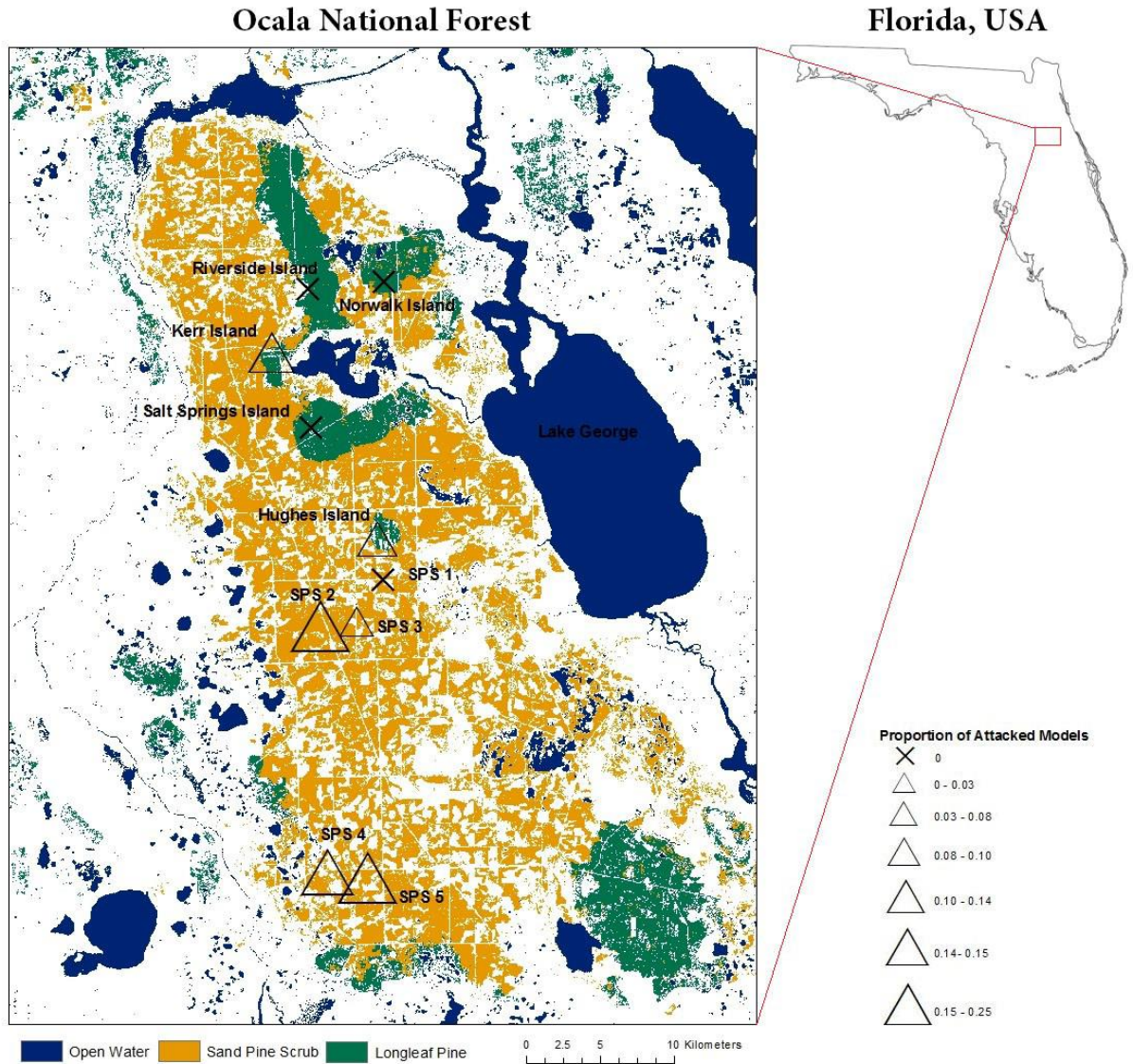


Figure 1.2. Sample locations (stands) and total proportion of attacked models over 72 hours at each stand in the Ocala National Forest. Hollow triangles represent the total proportion of attacks and are in relative proportion to one another, with an “X” representing zero attacks.

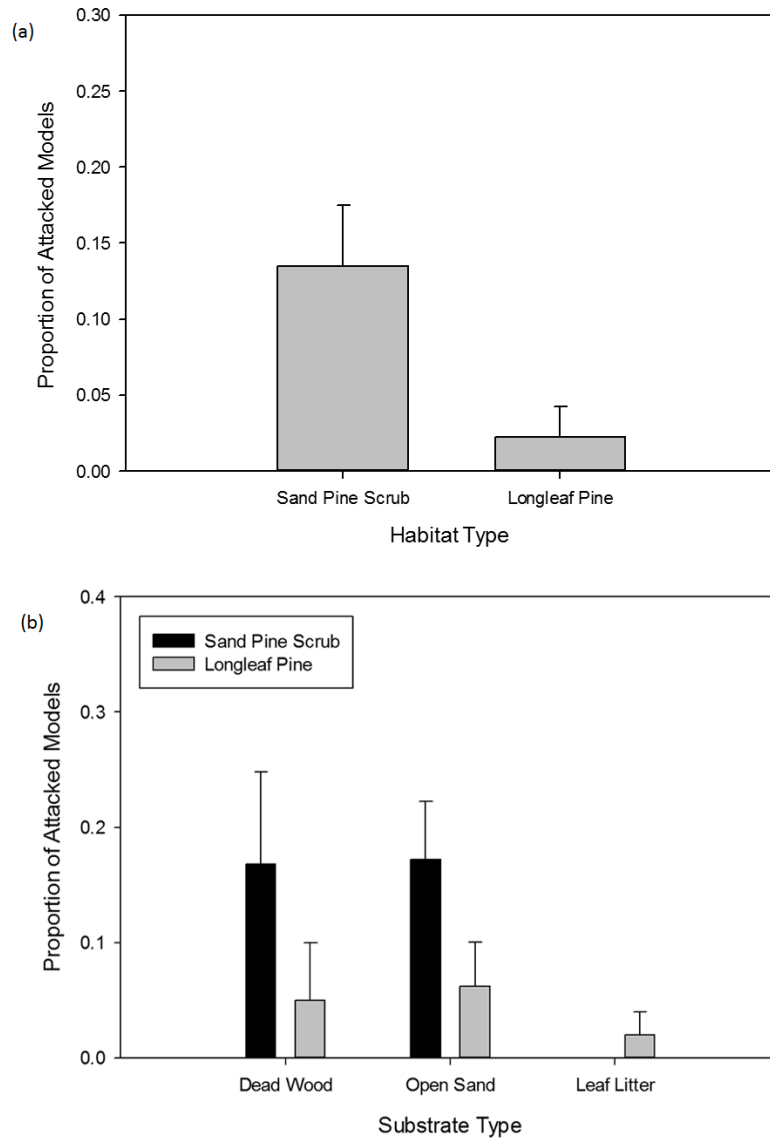


Figure 1.3. (a) Difference in proportion of attacked models between longleaf pine and sand pine scrub (+/- 1 standard error). (b) Difference in proportion of attacked models among substrates for LLP and SPS (+/- 1 standard error). Differences in the proportion of attacked models placed on deadwood and sand were significantly higher in SPS. However, differences in the proportion of attacked models on leaf litter did not differ between LLP and SPS.

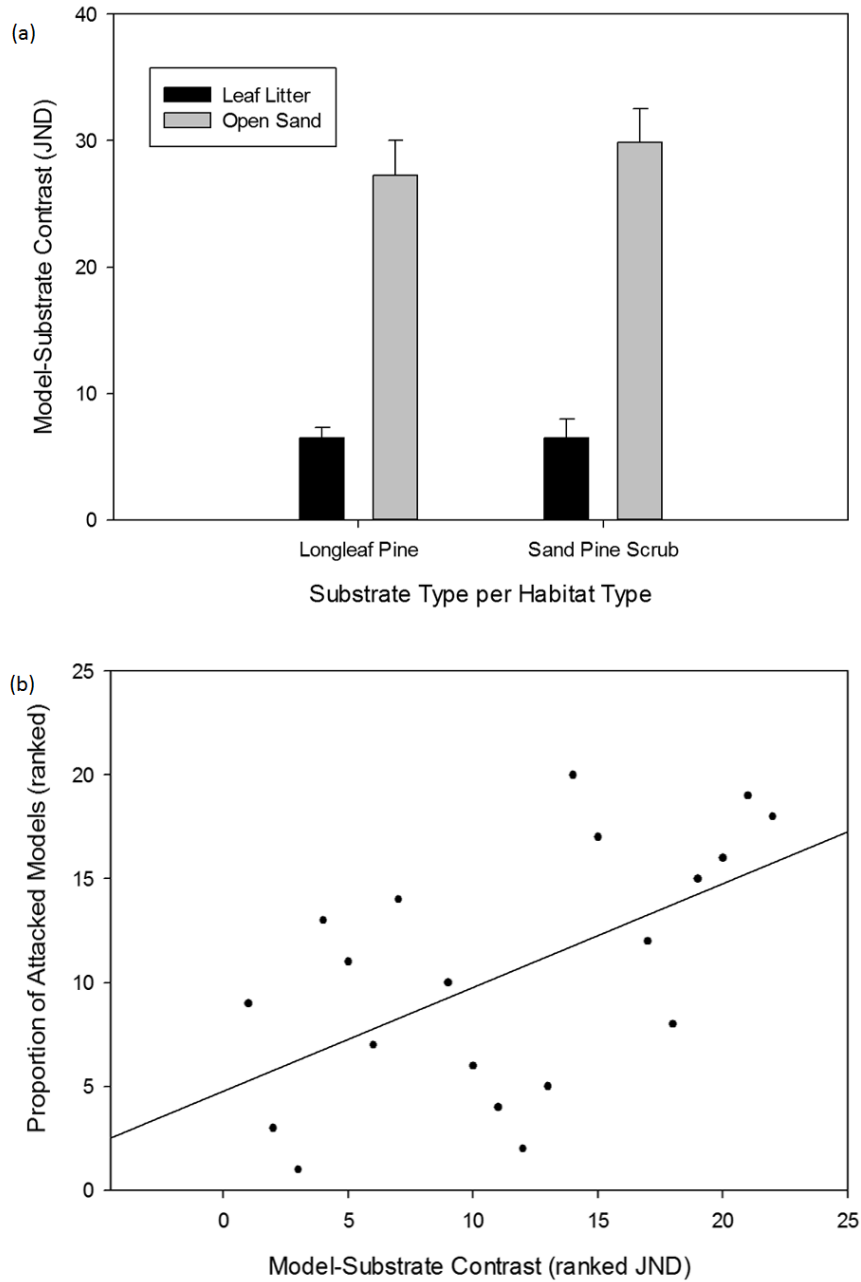


Figure 1.4. (a) Achromatic contrast (measured in just noticeable difference) between models and leaf litter and models and open sand in LLP and SPS. (b) Relationship (ranked regression) between model-substrate contrast (measured in just noticeable difference) and proportion of attacked models ($R^2=0.321$, $F_{(1,18)} = 10.097$, $P = 0.0052$).

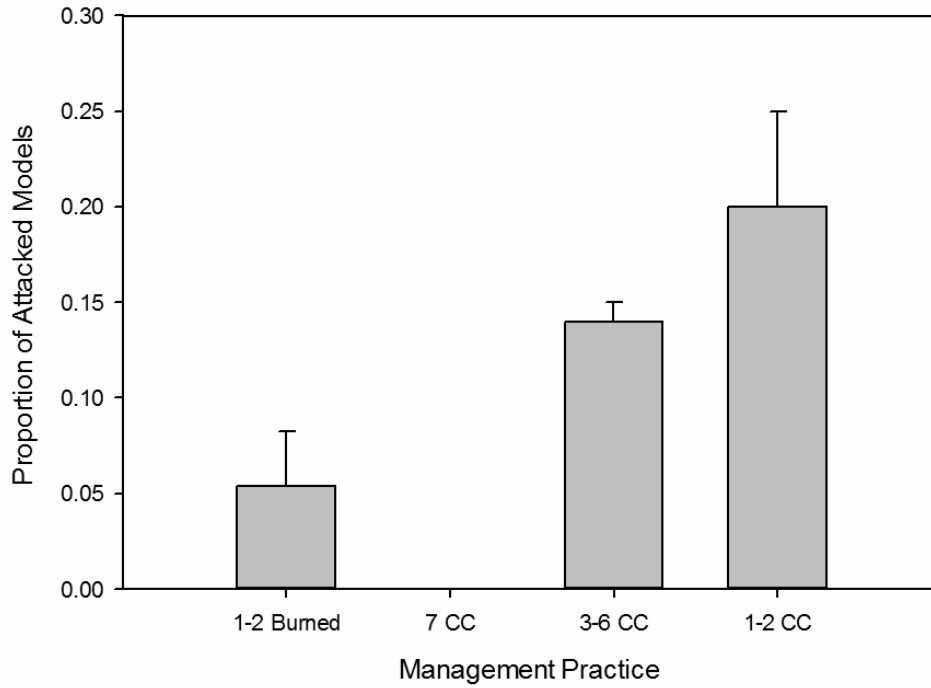


Figure 1.5. Proportion of attacked models by management practice of the stand. 1-2 Burned = one to two years post prescribe burn; 7 CC = seven years post clear-cut; 3-6 CC = three to six years post clear-cut; and 1-2 CC = one to two years post clear-cut.

CHAPTER 2

THE RESPONSE OF ADAPTIVE COLORATION TO DIFFERENTIAL PREDATION IN A
MANAGED LANDSCAPE

ABSTRACT

Animal colors and patterns are often viewed as adaptive responses to predation. However, little is known about variation in the adaptive response of color to different rates of predation. Furthermore, few quantitative studies have examined the role of predation in the maintenance of sexual dichromatism. Here, I use a combination of calibrated photographs, spectrometry, and antipredator behavior data to examine the influence of spatial heterogeneity in predation intensity on protective coloration in *Sceloporus woodi*. *Sceloporus woodi* is a cryptic and sexually dimorphic lizard, which occupies managed stands of longleaf pine and sand pine scrub habitats in the Ocala National Forest. Previously, these stands were shown to vary in rates of attacks on lizard clay models, potentially related to management practice. The results of this study reveal that variation in color within populations of *S. woodi* across the Ocala National Forest decreased as predation intensity increased. Moreover, the dorsal color of lizards more closely resembled the color of substrates in stands with increased rates of predation, suggesting an increased value for crypsis in high-predation environments. Variation in dorsal color was more impacted for females than for males, and data collected in the field suggest that behavioral dimorphism and sexual dichromatism may be related to predation pressure. Because management in the Ocala National Forest alters habitat structure and substrate composition, it is

likely that habitat management impacts animal color through variation in exposure to visual predators.

INTRODUCTION

Predation is a driving force of the evolution of morphology and behavior (Cott 1940; Schall and Pianka 1980; Endler 1991; Eklov and Svanback 2006), which interact with one another and the local environment to reduce selective pressure imposed by predators (Heatwole 1968; Forsman and Appelqvist 1998). A classic manifestation of this interaction is the occurrence of protective coloration and its relationship with escape behavior and microhabitat use (substrate) (Endler 1980; Caldwell 1982; Endler 1984; Bond and Kamil 2002; Rosenblum et al. 2004). For example, stripes, bands, and uniform coloration are thought to aid prey species in flight from predators following detection (Jackson et al. 1976; Pough 1976; Creer 2005), and geometric patterns reduce visual detection by concealing prey animals within their visual backgrounds (Endler 1978; Cooper and Allen 1994; Johannesson and Ekendahl 2002; Ruxton et al. 2004; Troscianko and Stevens 2015). In turn, selection pressure is likely to vary between different visual backgrounds and different forms of adaptive color.

Examples of adaptive responses in animal color and pattern are common, especially in regard to geographic (Storfer et al. 1999; Stuart-Fox and Ord 2004; Hoekstra et al. 2005; Rosenblum 2006) and intersexual variation (Badyaev and Martin 2000). Crypsis, in particular, is often associated with examples of local adaptation because crypsis is substrate-dependent (Norris and Lowe 1964; Endler 1980), and substrates often vary across space (Gleason 1917). The common inference among local adaptation studies is that dorsal color is an adaptive response to selection pressure imposed by visual predators. However, there are few quantitative studies that examine sexual dichromatism as a response to selection pressure from visual predators (but see Stuart-Fox and Ord 2004), despite empirical evidence correlating sexual dimorphism with predation (Reimchen and Nosil 2004), and color polymorphism with variation in antipredator

defense behavior (Jackson et al. 1976; Pough 1976; Creer 2005). Furthermore, with the exception of the stickleback (genus *Gasterosteus*), there appears to be little known about the effects of differential predation intensity on animal color, even though the intensity of predation can vary between sexes and across space (Hagen and Gilbertson 1973; Moodie et al. 1973).

In addition to naturally-occurring geographic variation in rates of predation, habitat alteration from anthropogenic disturbance can affect predation intensity (Whittingham and Evans 2004). Practices, such as clear-cutting and prescribe burning, often affect substrate composition and habitat structure (Prescott et al. 2000). In turn, these changes can have direct consequences on exposure to visual predators and the availability of refugia. For example, an event which removes leaf litter from a habitat occupied by animals that are cryptic on leaf litter, may leave that population conspicuous on the resulting substrate. Habitat alteration may also remove refuge, thus increasing exposure of animals to visual predators and potentially affecting animal behavior (Coull and Wells 1983; Dill and Houtman 1989; Huffaker 1991).

Fragmented populations of the Florida scrub lizard (*Sceloporus woodi*) in the Ocala National Forest (ONF) provide an ideal opportunity in which to study the impacts of predation intensity on protective coloration. Different populations face varying degrees of predation intensity by avian predators (see Orton and McBrayer unpublished), potentially due, at least in part, to management practice. Because populations occupy longleaf pine (LLP) and sand pine scrub (SPS) habitats (Enge et al. 1986), which contrast in substrate composition (Kaunert and McBrayer 2015), the relationships between environment and protective coloration can be thoroughly examined. Furthermore, sexual dichromatism in *S. woodi* dorsal pattern is ideal for testing the relative impacts of predation intensity on different forms of protective coloration, potentially with respect to the maintenance of sexual dichromatism.

Here, I use a combination of calibrated photographs, spectrometry, and behavioral data collected in the field to examine the influence of spatial heterogeneity in substrate composition and predation intensity on protective coloration. First, I document phenotypic variation between habitat types and between sexes, and correlate ranges in dorsal color with predation intensity. Next, I show that, despite the absence of classical local adaptation in the ONF, populations subjected to increased pressure from visual predators more closely match the color of local substrates than populations subjected to relaxed predation intensity. Last, I show that escape behavior correlates with crypsis and that microhabitat (substrate) use varies between male and female *S. woodi*. Because management practices alter substrate composition and habitat structure, it appears that management in the ONF impacts adaptive color in *S. woodi*.

MATERIALS AND METHODS

Sample collection

Lizards were collected from LLP and SPS stands within the ONF between early May and late August 2016, and were captured by hand or hand-held noose. Lizards were then transported to the laboratory at Georgia Southern University where they were housed under standard conditions for an acclimation period of 72 to 86 hours prior to collecting any measurements. All lizards were housed individually on sand and provided light (on a 12L:12D photoperiod) from commercially available 75 W incandescent and ultraviolet lamps. This not only provided light, but a temperature gradient of 32 to 28 degrees Celsius to allow adequate thermoregulation (Cowles and Bogert 1944). Water and food were provided *ad libitum*. Lizards were only disturbed immediately before taking photographs or spectrometric measurements. Lizards were removed from their enclosures between 1200 and 1400 hours and measurements were recorded within 60 seconds of capture. Because temperature has been documented to affect coloration in *Sceloporus* (Sherbrooke et al. 1994), the internal temperature of each adult individual was measured immediately following any photograph or reflectance measurement, using a cloacal thermometer. Only measurements of lizards that were within the range of operative temperatures were analyzed. Photographs were taken after approximately 72 hours of acclimation and spectrometry measurements were taken following approximately 24 hours after photographing lizards.

Calibrated Photographs

I digitally photographed individual lizards (n=126) under standardized lighting conditions in a windowless room, illuminated only by overhead fluorescent tubes. No source of auxiliary

lighting was used for any photograph and all photographs were taken from a standard distance of 0.5 meters. Lizards were photographed using a Fujifilm S20 Pro digital camera (Fujifilm, Minato, Tokyo, Japan) with a Fujinon super EBC 6x zoom lens for all photographs. This 35mm camera has an effective pixel count of 6.2 megapixels and allows for manual exposure and light metering. The camera was manually adjusted for white balance and fluorescent lighting, and a standardized ISO sensitivity, shutter speed, and lens aperture (ISO = 200, shutter-speed 1/25th second exposure time, and F/6.0 aperture) were used. I photographed all individuals at a resolution of 6 megapixels and a compression ratio of 1:4 (fine quality setting) before saving all images as 1280 x 960 JPEG files. The dorsal surface of each lizard was photographed against a Color-aid basic gray scale (Color-aid, Hudson Falls, New York, USA) to allow calibration and equalization in Adobe Photoshop. The average dorsal brightness was then measured using the blur and average tools in adobe Photoshop, measuring the dorsal area from the neck to the hip for both the right and left sides (divided by the spinal column). The measurements for the left and right dorsal brightness were then averaged together to obtain the mean dorsal brightness for each individual.

Spectrometry

I used a bifurcated fiber optics probe (Ocean Optics, Dunedin, FL, USA) connected to an Ocean Optics Flame spectrometer and a xenon light source (Ocean Optics) to measure the spectral reflectance of lizard dorsal color, longleaf pines (*Pinus palustris*), sand pines (*Pinus clausa*), turkey oaks (*Quercus laevis*), open sand, and leaf litter. The fiber optic probe was held with a standard probe holder 1mm from the surface of all substrates and lizards at 45°. All measurements were recorded with Ocean View software v1.5.2 (Ocean Optics) and were taken relative to a certified 99% diffuse white reflectance standard. Dark current and white standard

measurements were taken before each spectrophotometric reading. To reduce noise, the average of two scans with a boxcar width of two was used for each measurement.

Fifteen samples of each substrate from each habitat type (3 from each of 5 stands) was collected and brought back to the lab where I measured spectral reflectance. Three spectrophotometric measurements were taken on each substrate and each lizard, then respectively averaged. Substrate sample averages were then averaged across the other two samples of the same substrate type collected from the same stand to obtain a measure of reflectance for a particular substrate type from a particular stand. For all lizards I took three readings, one measurement from three body positions: between the shoulders, mid dorsum, and between the hips. These three measurements were then averaged together to obtain the mean dorsal reflectance for each lizard.

Spectrophotometric Analysis

AVICOL software (Gomez 2006) was used to analyze spectral data because it takes into account the spectral sensitivities for each of the four single cone types that birds possess (Bowmaker et al. 1997) and birds are thought to be the dominant predator of *S. woodi* (see Orton and McBrayer unpublished). In AVICOL, Vorobyev and Osorio's physiological model (1998) was used because it accounts for both chromatic and achromatic contrast between colors as perceived by an organism with tetrachromatic vision. This model is accepted to be consistent with the capabilities of avian vision (Osorio 1999; Osorio et al. 1999; Endler and Mielke 2005). This model also considers chromatic and achromatic properties as independent sources of visual stimulation (Vorobyev and Osorio 1998).

Achromatic contrast is thought to be especially important for avian predators because it is crucial for distinguishing between small objects or objects visualized from large distances (Osorio et al. 1999; Lind and Kelber 2011), such as when avian predators are midflight or perched in trees. Additionally, I found through a previous experiment, that achromatic contrast was a more reliable indicator of attack rates for models placed on terrestrial substrates. Conversely, chromatic contrast is thought to be important for visual detection of prey by avian predators when searching for prey items against a background of color, such as a tree or leaf litter (Lind and Kelber 2011). Thus, the relative importance we placed on achromatic and chromatic contrast varied according to substrate. For example, achromatic contrast was considered a more important measure of contrast between lizards and sand. The contrast between colors of two different samples is expressed as a just noticeable difference (JND) value, where a JND value = 1 is the critical value for discrimination between two colors or objects of varying brightness (Gomez 2006).

Field Measurements

Quantification of lizard responses when approached by a researcher is a standard method for studying antipredator behavior in lizards (Rand 1964; Cooper 2003). This measurement, termed ‘approach distance,’ was collected for lizards in both LLP and SPS. Between early May and late August 2016, I measured approach distance and beginning substrate type for each lizard encountered in the field between 0830 and 1830 hours. Approach distance for lizards which were confidently detected before flight were recorded. Approach was conducted by traversing straight paths toward lizards at a steady walking pace, wearing the same clothing for each measurement. Approach distance was measured by marking the initial location of the lizard before flight, our location (distance from the lizard) at the point of flight, and the substrate which

upon the lizard was initially observed. SVL was recorded for each lizard because larger lizards are known to accelerate faster than smaller lizards (Huey and Hertz 1984), thus likely to affect approach distance. All approach distance measures were then standardized by SVL before analyses.

Statistical analysis

All statistical tests were performed using the JMP v12 statistical package (SAS Institute, Cary, NC, USA). First, differences in lizard dorsal color between sex and between habitat type (LLP and SPS) were tested using a two-way nested ANOVA with stand (sampling site) nested within habitat type, to account for any added variation due to the effect of stand. Because values for dorsal color were not normally distributed, data was log transformed. A Spearman's rank correlation was used to test for a significant association between the range of dorsal colors within each stand with predation intensity. Predation intensity was measured in a previous experiment (see Orton and McBrayer unpublished) as the proportion of attacked clay models per stand. To determine the range of dorsal color, I subtracted the lowest value (measured as the sum of the percentage of red, green, and blue) from the highest value, for each stand. The value for each stand was then paired with the predation intensity value for that same stand.

Second, three-way ANOVAs were used to test for local adaption, using sex, habitat type, and substrate type as factors. Just noticeable difference values met the assumptions of normality and equal variance after cube root transformation. Separate three-way ANOVAs were used for chromatic contrast and achromatic contrast because avian predators interpret these visual stimuli differently are thought to be of importance for different substrate types (Osorio et al. 1999). Significant interaction terms were explored using a Tukey-Kramer HSD test (Tukey 1953; Kramer 1956; Hayter 1984).

Next, a three-way ANOVA was used to test for differences in approach distance between sex, habitat type, and substrate type. Approach distance, measured in meters, was standardized by lizard SVL. Last, I tested if the percentage of detected lizards per substrate type was contingent on sex. Because substrates vary between LLP and SPS, I tested for differences in detection between males and females within each habitat type using separate Chi-square tests. Post hoc analyses were performed using adjusted residuals, as in (Delucchi 1993). The terms ‘encounters’ or ‘microhabitat use,’ are used interchangeably in this study.

RESULTS

Phenotypic Variation

The results of this study reveal significant variation between the dorsal color of males and females ($F_{(1,3)} = 44.9765$; $P < 0.0001^*$) and between LLP and SPS ($F_{(1,3)} = 25.8597$; $P < 0.0001^*$) (Figure 1). Furthermore, the range in color variation is also associated with predation intensity ($\rho = -0.81$; $p = 0.0015$) (Figure 2), with the range in dorsal color being ten percent more constricted for SPS populations than for LLP populations. Additionally, the range in dorsal color for LLP females is 12 percent more restricted than that of LLP males, and SPS females are 37 percent more restricted in their range of dorsal color than are SPS males.

Crypsis

Spectrophotometric data indicate that differences in contrast between the reflectance of lizard dorsal color and substrate vary between different substrate types, habitat types, and sex (Table 1). Globally, both males and females match the color of leaf litter more closely than open sand ($F_{(7,98)} = 24.42$; $p < 0.0001$). However, lizards collected from SPS are altogether more cryptic than lizards collected from LLP for terrestrial substrates ($F_{(7,98)} = 5.92$; $p = 0.0168$) (Figure 3a) and vertical perches ($F_{(11,68)} = 3.78$; $p = 0.0059$) (Figure 3b). In regard to sexual dichromatism, there was a no intersexual variation determined for either terrestrial substrate in SPS ($F_{(7,98)} = 0.13$; $p = 0.72$) (Figure 4a). However, in LLP, there is a significant interaction between all three factors for terrestrial substrates, where females in LLP match the color of leaf litter more closely than males in LLP ($F_{(7,98)} = 5.08$; $p = 0.0301$) (Figure 4b). Additionally, there was no intersexual variation in crypsis for vertical perches in SPS ($F_{(11,68)} = 2.38$; $p = 0.1001$)

(Figure 4c), but in LLP, where predation is relaxed, females tend to match the color of vertical perches more closely than do males in LLP ($F_{(11,68)} = 10.77$; $p = 0.0016$) (Figure 4d).

Escape Behavior and Microhabitat Selection

The approach distance for lizards found in SPS was significantly shorter than that of lizards in LLP ($F_{(1,92)} = 12.9878$; $P = 0.0005$). However, in LLP, females encountered on leaf litter had a shorter approach distance than males on leaf litter and when either sex was encountered on open sand ($F_{(1,92)} = 9.6414$; $p = 0.0025$) (Figure 4a). In SPS, there was no intersexual variation for either terrestrial substrate ($F_{(1,92)} = 1.757$; $p = 0.1883$) (Figure 4b). Furthermore, the detection percentages of lizards on different substrates was contingent on habitat type ($X^2 = 101.136$; $p < 0.0001^*$), as well as sex in both LLP ($X^2 = 11.079$; $P = 0.0113$) (Figure 5a) and SPS ($X^2 = 7.084$; $P = 0.0290$) (Figure 5b). In LLP, a higher percentage of males (as compared to females) was detected on *Q. laevis* and open sand, while a higher percentage of females was detected on *P. palustris* and leaf litter. The highest percentage of females was detected on leaf litter and the highest percentage of males was detected on *Q. laevis* in LLP. In SPS, the percentage of lizards detected on *P. clausa* was higher for males than for females and the percentages of lizards detected on leaf litter and open sand were slightly, but not significantly, higher for females than for males. However, for both sexes, the highest percentage of lizards was detected on open sand in SPS.

Management

Nesting stand (sampling location) within habitat type revealed that 19.056 percent of variation in dorsal color is due to the effect of individual stands within each habitat type ($F_{(10,110)} = 3.2662$; $p = 0.0010^*$). Last, spectrophotometric data show that the degree to which lizards

match substrate within a sampling location varies by management practice and the time since last disturbance, for both terrestrial substrates ($F_{(4,167)} = 2.8605$; $p = 0.0252$) (Figure 6a) and vertical perches ($F_{(4,167)} = 2.7159$; $p = 0.0299$) (Figure 6b).

DISCUSSION

The results of this study are consistent with long-standing views that animal color and pattern can be an adaptive response to predation (Poulton 1890). These data indicate that the color variation observed within a population is associated with local predation intensity and that predation likely plays a role in the maintenance of sexual dichromatism. Analyses of calibrated photographs show that the range in dorsal color gradually decreases as predation intensity increases, and that this range is more constricted for females than for males, particularly in environments where predation intensity is increased. Additionally, spectrophotometric data reveal that in environments of increased predation, intersexual variation is reduced and both sexes demonstrate crypsis for multiple substrates. This data coincides well with data collected in the field, where in environments of increased predation, neither antipredator behavior nor microhabitat use varied between males and females. These findings are similar to results published in studies of differential predation in fish, where sexual dichromatism becomes absent with increased predation, and defensive morphology and behavior become more pronounced (Moodie 1972; Hagen and Gilbertson 1973; Maan et al. 2008). However, the data for the current study were collected in an anthropogenically-managed landscape, where habitat alteration appears to affect color variation.

In response to decreased predation, a wider array of 'safe' colors and patterns are expected to satisfy the adaptive response to predation, while potentially increasing fitness for other selection pressures that affect color, such as thermoregulation (Stuart-Fox and Moussalli 2009). Conversely, environments of intense predation may increase the value of visually matching the local background, thus constricting the range of 'safe' colors (as reviewed by Endler 1995). A previous study suggests that predation intensity in SPS is approximately two and a half

times greater than in LLP (see Orton and McBrayer unpublished). Likewise, lizards in SPS not only more closely resemble the color of local substrates, but the range of color variation within these populations is much narrower. Additionally, intersexual variation in crypsis is significantly reduced, if not absent in populations of *S. woodi* inhabiting environments of increased predation.

Crypsis is also considered, in general, to be a background-specific adaptation, where increased fitness in one microhabitat leads to decreased fitness in a different microhabitat. Because most animals occupy heterogeneous environments, crypsis may lead to restrictions in microhabitat use or provide little benefit. However, in a recent model, Merilaita et al. (1999) demonstrated that crypsis can be optimized as a compromise between the requirements of multiple visual backgrounds. The current study may lend complimentary and empirical support to their findings because in environments of increased predation, *S. woodi* tend to simultaneously match the color of multiple substrates. Likely, only a narrow range of color is sufficient in resembling multiple visual backgrounds.

Moreover, my data show that the range in dorsal color for females is always more constricted than the range in dorsal color for males. In particular, the impact of increased predation intensity on dorsal color range is three times greater for females than it is for males, and in LLP, only females appear to be cryptic for any substrate. It has been previously suggested that sexual dimorphism can be an adaptive response to predation (Reimchen and Nosil 2004), though most studies attribute sexual dimorphism to sex-specific pressures that relate to fecundity (Schulte-Hostedde et al. 2002), niche partitioning (Slatkin 1984; Shine 1989), and sexual selection (Andersson 1994). Sexual dichromatism, for example, is traditionally taught to result from sexual selection (Darwin 1859) and many contemporary studies provide complimentary support to this view (Andersson 1994; Badyaev and Martin 2000; Stuart-Fox and Ord

2004). Even in aposematic species, the brightness of male color appears to be influenced by mate acquisition (Maan and Cummings 2009). However, because cryptic coloration and reduced ornamentation are thought to result from natural selection (Endler 1980), intersexual variation in drab color and geometric patterns (disruptive coloration) imply that selective pressures from predators vary between males and females (as reviewed by Badyaev and Hill 2003). It is possible that sexual dichromatism in *S. woodi* arises from sex-specific responses to selection pressure.

Interestingly, both male and female juvenile *S. woodi* are dorsally-patterned. It is during an ontogenetic shift, when males lose their dorsal pattern and develop conspicuous blue throat badges (Stiller and McBrayer 2013), which are thought to play a role in testosterone-driven behaviors such as mate acquisition and territorial defense (Moore 1984; Salvador et al. 1997). Cox et al. (2005) showed that by removing the primary source of circulating testosterone from male *Sceloporus undulatus*, ornamentation fades and dorsal pattern becomes observable. Testosterone has been empirically demonstrated to increase activity, locomotor performance, and home range size in male (Sinervo et al. 2000), but not female, *Sceloporus* lizards. These behaviors result in increased movement on behalf of the lizard (Salvador et al. 1996) which can diminish any benefit provided by cryptic coloration. The loss of dorsal patterning in male *S. woodi*, perhaps by design, is accompanied by an increase in approach distance, which suggests that the development of uniform coloration may be associated with flight from predators.

Solid colors (Creer 2005), stripes (Brodie 1992), and contrasting bands (Shine and Madsen 1994; Lindell and Forsman 1996) assist prey species in rapid escape from predators by limiting a visual predator's ability to accurately determine the movement, direction, and speed of a prey animal (as reviewed by Stevens and Merilaita 2009). Solid colors and high contrast

stripes are frequently observed in animals that rely on rapid escape behavior to evade predators (Ruxton 2004; Creer 2005), such as colubrid snakes (e.g., Titcomb et al. 2014) and zebras (e.g., How and Zanker 2014). Because the benefit of these patterns is dependent on flight, it is assumed that the visual environment has little impact on their evolution and maintenance. Conversely, the success of crypsis is largely dependent on the local visual environment as well as the ability of the prey animal to remain sedentary because crypsis blends the visual signal of the animal with a still background (Endler 1978). Thus, more sedentary animals, such as ambush foragers, stand to gain more from the benefit of crypsis than do highly active animals, such as male *S. woodi*.

Alternatively, female *S. woodi* may incur a greater advantage provided by cryptic coloration than males because gravidity is known to decrease flight efficacy in different lizard species (Miles et al. 2000; Shine 2003). Gravidity in reptiles can also lead to increased basking needed to achieve adequate body temperatures required by gestation (Shine 2006). Unintendedly, however, increased basking can result in elevated predation risk (Shine 1980). Thus, cryptic colors and patterns would potentially allow females increased exposure to visual predators, and decrease their need to rely on flight. I found that females, when approached on leaf litter in LLP, allowed me to approach much closer than the males encountered on leaf litter. I also found that females in LLP had a shorter approach distance when on leaf litter, a substrate for which they are cryptic, than they did for open sand where they are conspicuous. Conversely, males initiated flight at a set approach distance, regardless of whether being encountered on sand or leaf litter in LLP. It may be important to note that approach distance did not vary between males and females for either substrate in SPS, where both sexes appear to be equally cryptic on both terrestrial substrates. These data anecdotally support the

hypothesis that crypsis is dependent on an animal's ability to remain sedentary (Ydenberg and Dill 1986; Broom and Ruxton 2005; Martin et al. 2009), and suggest that crypsis only benefit *S. woodi* when they are encountered on a substrate for which they are cryptic.

In lieu of increased risk of predation, cryptic animals are often more confined in their use of microhabitats than animals that rely on escape to evade predators (Stein and Magnuson 1976; Donnelly and Dill 1984; Merilaita et al. 2001; Ruxton 2004; Skelhorn and Ruxton 2011). For example, (Harvey and Weatherhead 2006) found that gravid rattlesnakes are more selective in their choice of microhabitat than males and non-gravid females, opting for microhabitats which provided improved refuge. Despite lacking frequencies for gravidity, I did find that females in LLP were more selective in their choice of substrate than were males, and were most often encountered on substrates for which they are cryptic, such as leaf litter and *P.*

palustris. Interestingly, this pattern was not found in SPS, where males and females were encountered at similar rates on both leaf litter and open sand. However, there is marked variation in *S. woodi* use of substrates between habitat types. I suspect that this variation is, at least in part, due to management practices in the ONF.

Stands of SPS and LLP habitat are managed with different strategies in the ONF. In SPS, any fire regime is suppressed and replaced with clear-cutting and LLP is maintained with prescribe burning on a biannual schedule (Tiebout and Anderson 1997). Immediately following a clear-cut in SPS, vertical perches and vegetation are removed from the core of stands, leaf litter is reduced, and open sand is greatly exposed (Tiebout and Anderson 2001). However, as a response to fire suppression in SPS, vegetation density increases unabated. The result of this management strategy creates a mosaic of stands in various stages of succession in SPS. Meanwhile, prescribe burning in LLP is thought to preserve habitat features characteristic

of early to mid-succession habitat (Wells 1928). In particular, stands of LLP offer vertical perches and proportionately more leaf litter than open sand. Thus, substrate availability, influenced by management, likely plays a role in variation in predation intensity between stands.

In a previous study, I found that the proportion of attacks on clay models resembling *S. woodi* was contingent on management, where predation appeared to be greatest immediately following clear-cutting, moderate in stands of LLP, and non-existent in stands seven years post clear-cut (see Orton and McBrayer unpublished). We see here, that not only is color variation affected by variation in predation intensity, but that twenty percent of the variation in dorsal color is described by sampling location within each habitat type. Specifically, the degree of crypsis within each stand varies according to management practice in the ONF. Freshly clear-cut stands, where predation appears to be greatest, harbor the most cryptic populations. In comparison, LLP stands and more mature stands of SPS harbor lizards which are less cryptic, with the exceptions of females, which appear to maintain crypsis against leaf litter but not open sand. This variation is likely due to the effects of habitat alteration on microhabitat availability, influencing selection pressure on animal color. Because differential microhabitat use and selection is likely to influence the dynamics and maintenance of phenotypic polymorphism (Farallo and Forstner 2012) and sex-specific variation in microhabitat use may contribute to the evolution of sexual dichromatism (Slatkin 1984; Merilaita and Jormalainen 1997), management practices that alter habitat structure and substrate composition may have unintended consequences on evolutionary trajectory.

Table 2.1. Results of a three-way ANOVA, testing the effects of substrate, sex, and habitat on crypsis in *S. woodi*.

Factor	Terrestrial Substrates		Vertical Perches	
	F _(11,68)	p	F _(7,98)	p
Substrate	24.42	<0.0001**	12.8	<0.0001**
Habitat	5.92	0.0168*	3.78	0.0259*
Sex	2.8	0.1	4.99	0.029*
Substrate x Habitat	0.01	0.97	1.08	0.344
Habitat x Sex	0.52	0.47	10.77	0.0016**
Substrate X Sex	0.13	0.72	0.19	0.83
Substrate x Habitat x Sex	5.08	0.031*	2.38	0.1001

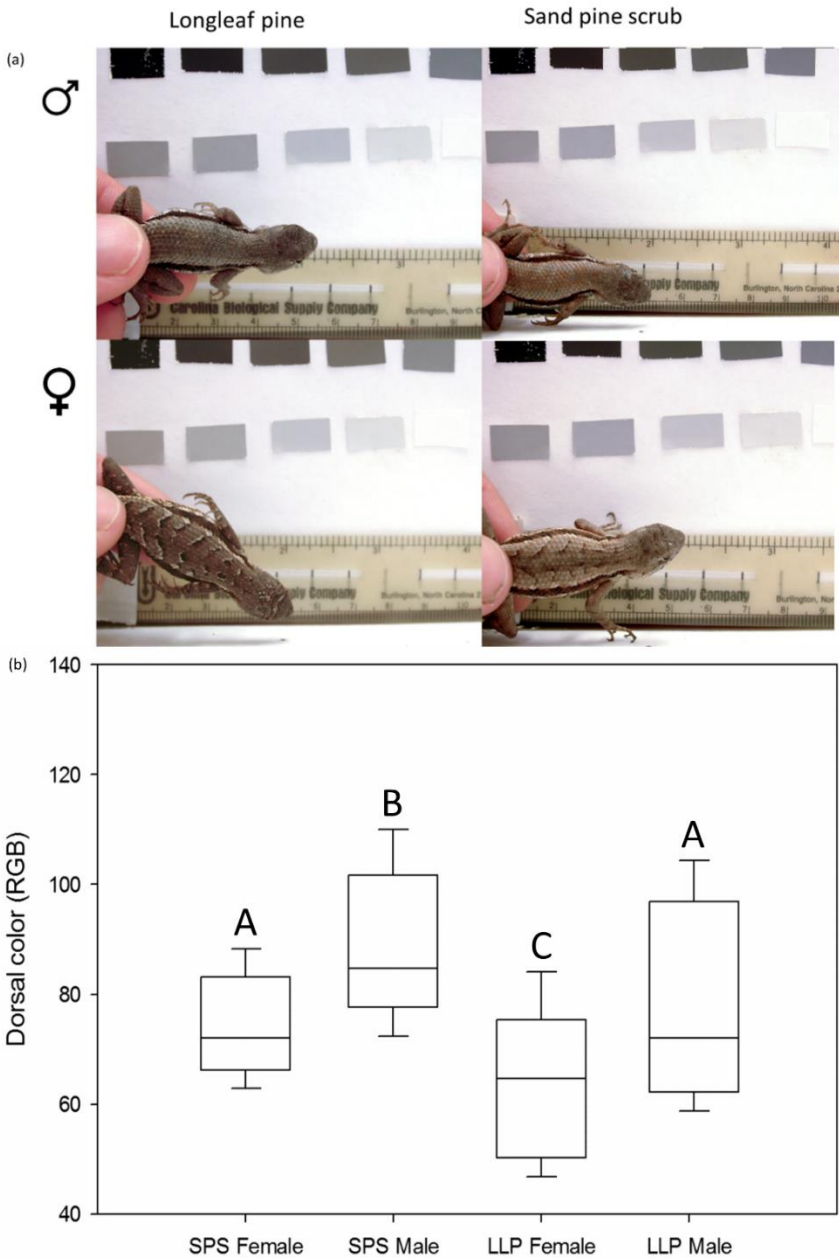


Figure 2.1. (a) Calibrated photographs for each sex from both habitat types. (b) Results from a two-way ANOVA of mean dorsal color (+/- one standard error) for each sex from both habitat types. Results are significant between sex ($F_{(1,3)} = 25.8597$; $P < 0.0001^*$) and habitat type ($F_{(1,3)} = 44.9765$; $P < 0.0001^*$). Post hoc analyses Tukey-Kramer HSD test.

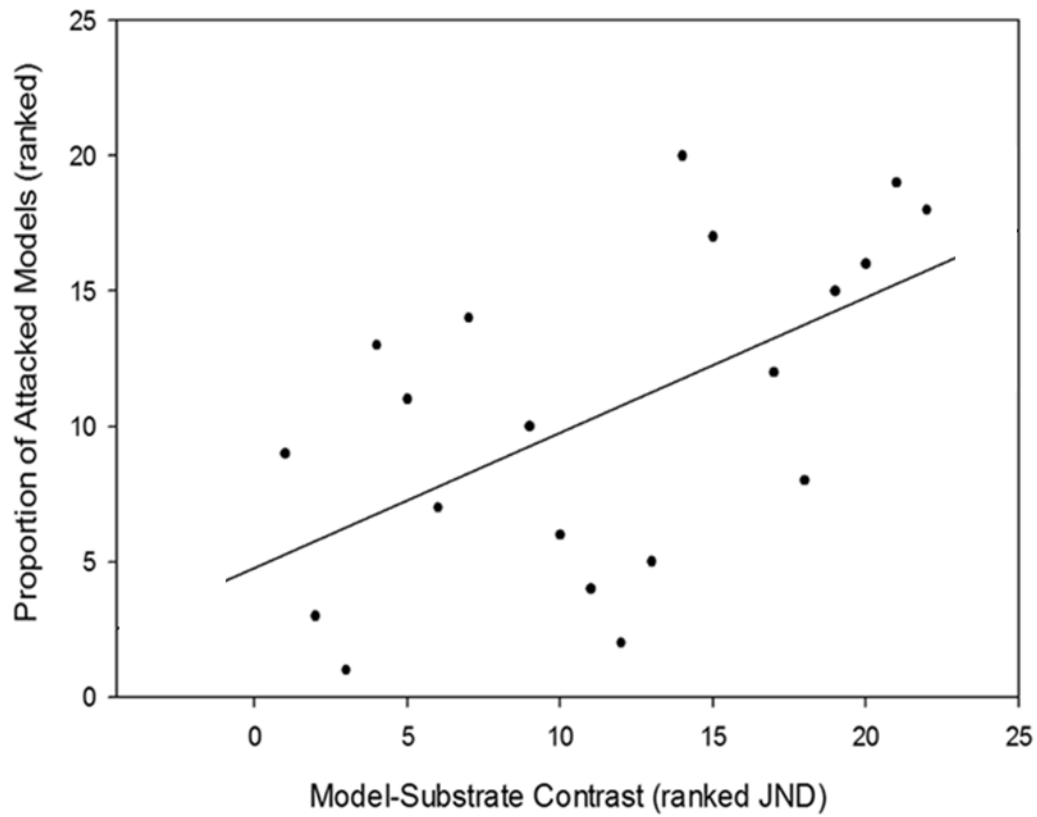


Figure 2.2. Spearman's rank correlation (with line of best fit) showing that the range in dorsal color is dependent on the predation intensity at each stand ($\rho = -0.81$; $p = 0.0015$)

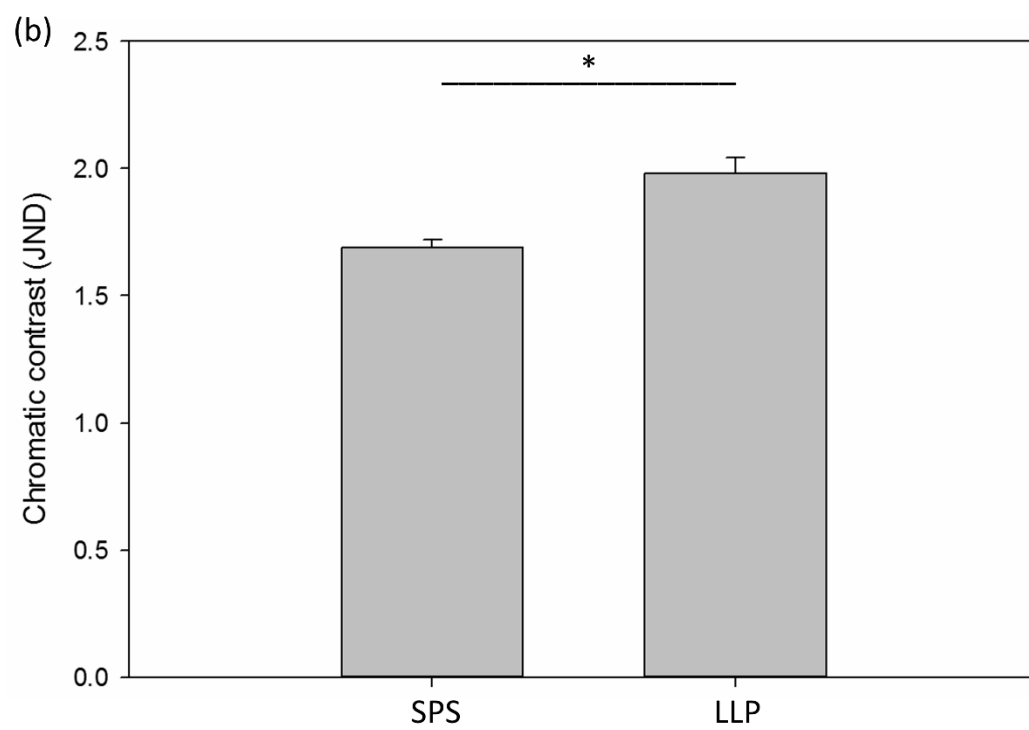
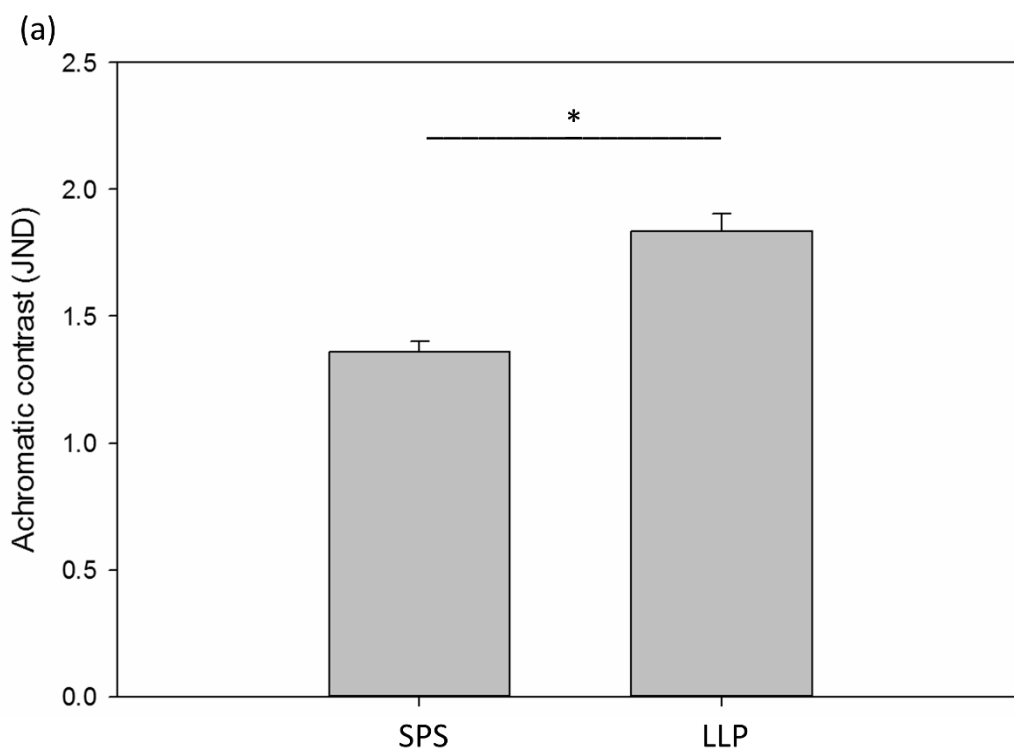


Figure 2.3. Global comparison of crypsis between habitat types for terrestrial substrates (a) ($F_{(7,98)} = 5.92$; $p = 0.0168$) and vertical perches (b) ($F_{(11,68)} = 3.78$; $p = 0.0059$).

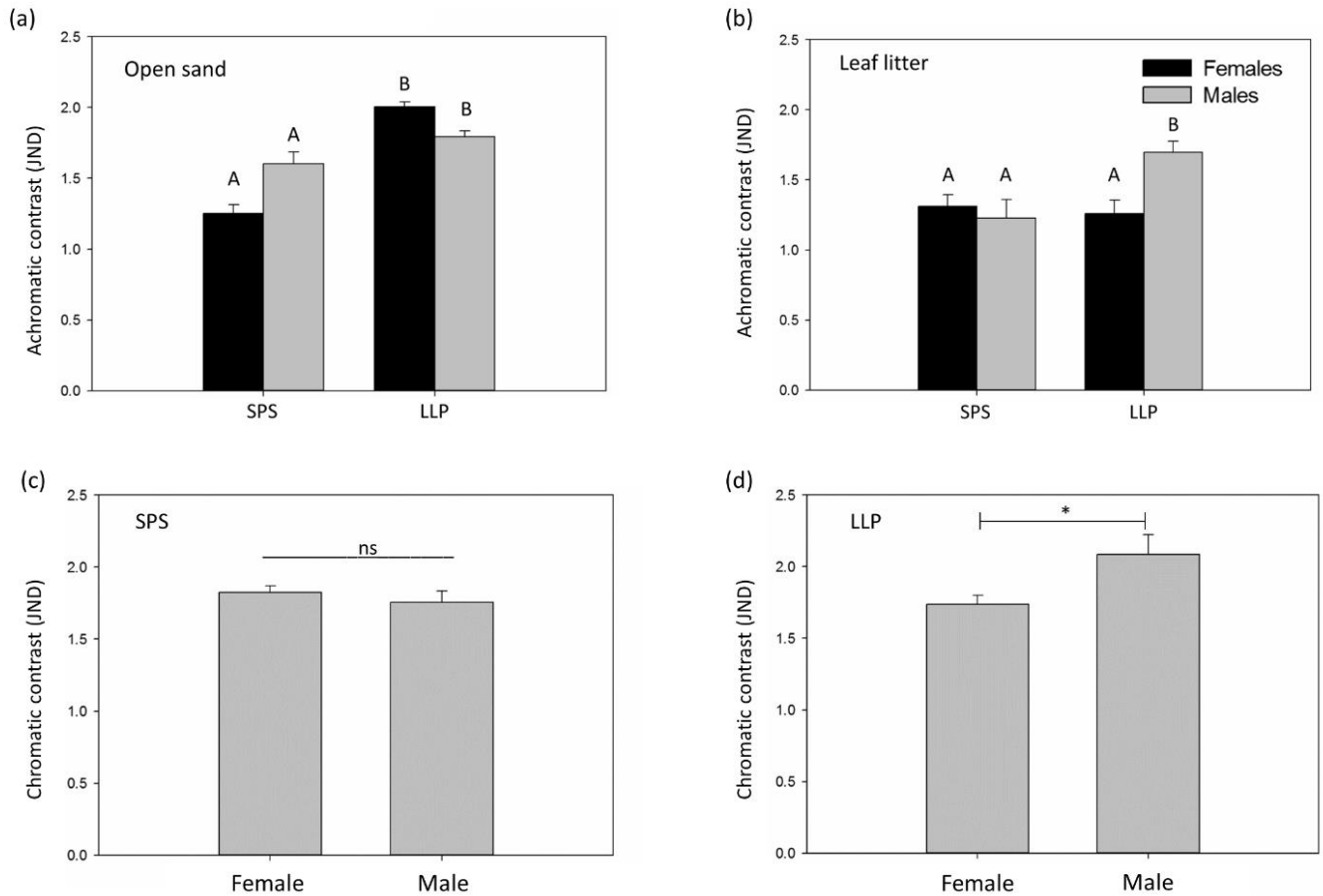


Figure 2.4. Mean contrasts against substrates for males and females collected from both LLP and SPS; open sand (a), leaf litter (b), vertical perches in SPS (c) and vertical perches in LLP (d). Significant results from three-way ANOVA displayed in table 1. Post hoc analyses Tukey-Kramer HSD test.

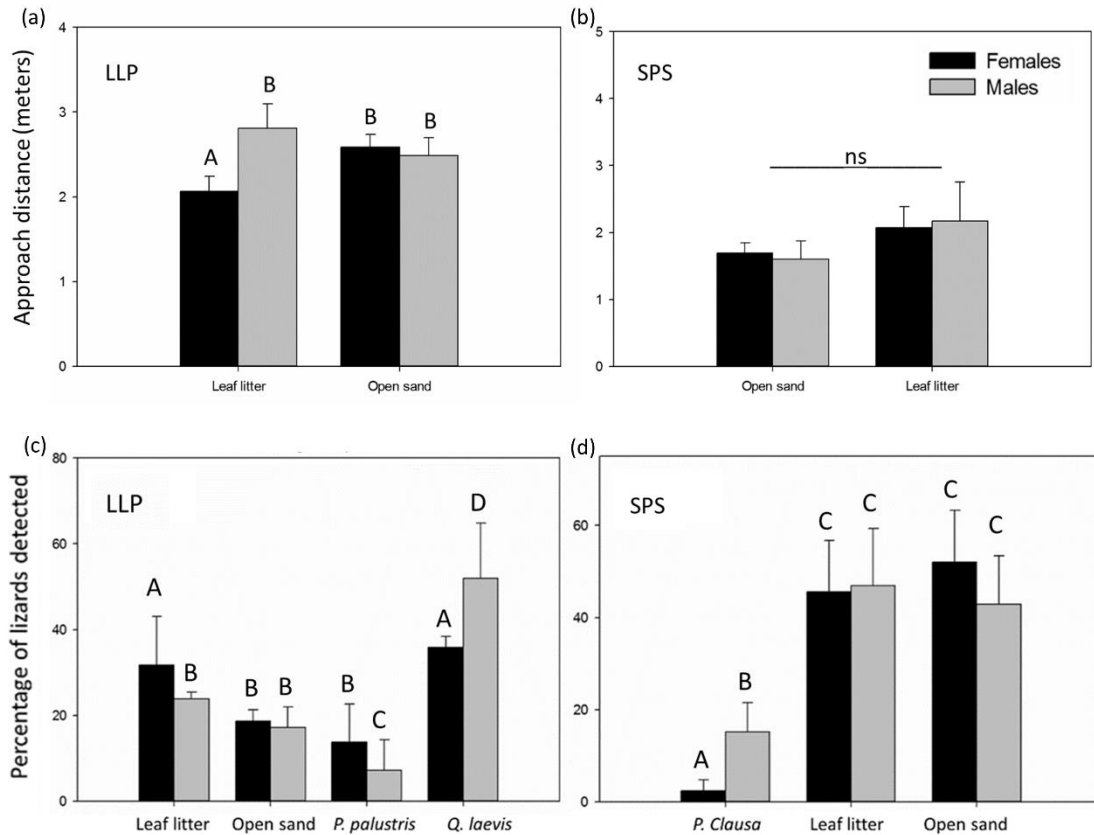


Figure 2.5. Mean approach distance (+/- one standard error) for males and females encountered on terrestrial substrates in LLP (a) and SPS (b). Females in LLP had a shorter approach distance when encountered on leaf litter and a shorter approach distance than males encountered on either substrate ($F_{(1,93)} = 10.2213$; $P = 0.0019$). However, there were no differences in approach distance between sexes or substrate in SPS. Mean percentage of both male and female lizards detected for each substrate in SPS (a) and LLP (b) (+/- one standard error). Detection was contingent on sex in LLP ($X^2 = 11.079$; $P = 0.0113$) and SPS ($X^2 = 7.084$; $P = 0.0290$). Post hoc analyses performed using adjusted residuals.

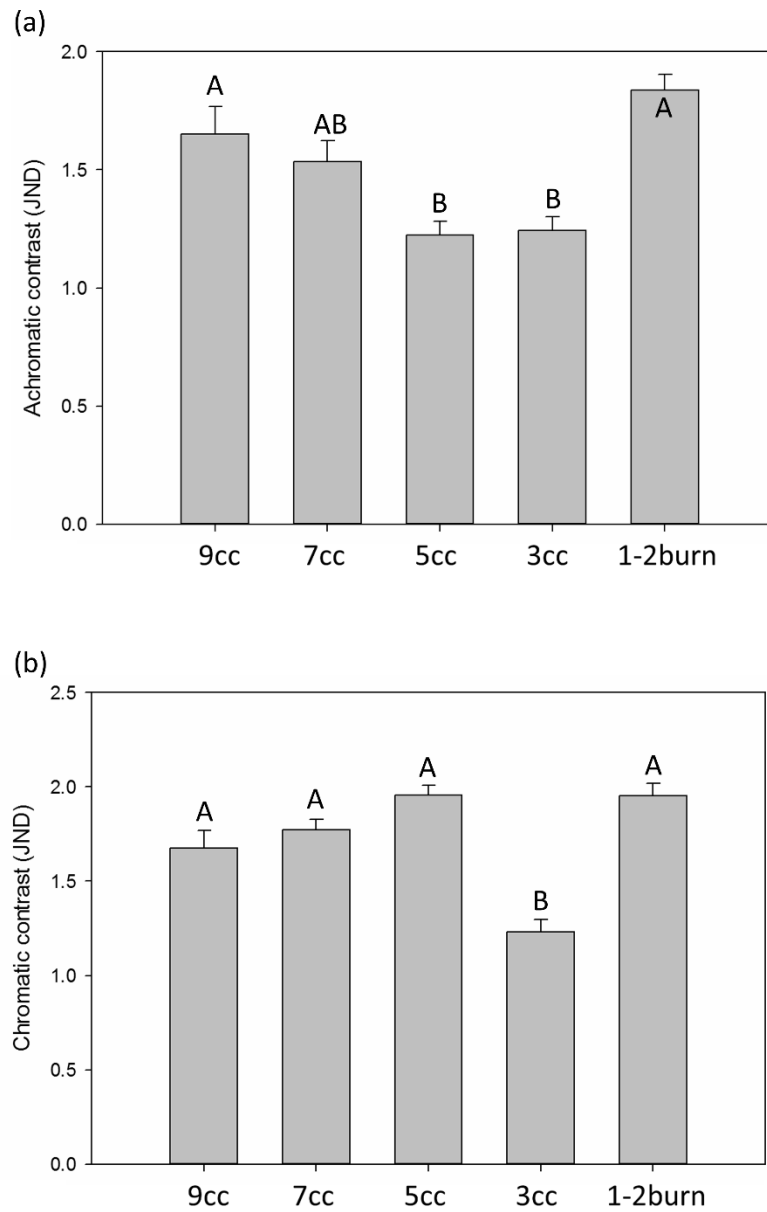


Figure 2.6. Global comparison of contrast against terrestrial substrates (a) ($F_{(4,167)} = 2.8605$; $p = 0.0252$) and vertical perches (b) ($F_{(4,167)} = 2.7159$; $p = 0.0299$) between stands at various stages of succession: 9cc = nine years post clear cut; 7cc = seven years post clear cut; 5 cc = five years post clear-cut; 3 cc = three years post clear-cut; 1-2 burn = one to two years post burn in LLP habitat. Post hoc analyses by Tukey-Kramer HSD test.

CHAPTER 3

ANTHROPOGENICALLY-MAINTAINED CORRIDORS FACILITATE GENE FLOW IN A
METAPOPULATION OF FLORIDA SCRUB LIZARDS, *SCELOPORUS WOODI*

ABSTRACT

Anthropogenic disturbance has the potential to influence dispersal and population size by altering habitat quality and connectivity, therefore impacting important demographic processes. Thus, species with limited vagility and specific habitat preferences may be particularly susceptible to landscape-altering events. Subpopulations of Florida scrub lizards (*Sceloporus woodi*) within the Ocala National Forest (ONF) are subjected to prescribed fire, fire suppression and clear-cutting. Stands of longleaf pine within the ONF are maintained on a biannual cycle of prescribed burning and harbor large populations of *S. woodi*. Meanwhile, clear-cut stands of sand pine scrub (SPS) only temporarily provide suitable habitat for *S. woodi*. I predict that *S. woodi* disperse from stands of SPS as vegetation density increases in the absence of a natural fire regime. The objective of this study is to quantify temporal and spatial genetic diversity in *S. woodi* populations in the ONF and assess any correlation with habitat management practices. To this end, I used microsatellite markers to quantify genetic variation in *S. woodi* at two time points separated by approximately six generations, and spatial analyses to test for correlations between landscape metrics and genetic diversity. Microsatellite markers revealed a weak population genetic structure that was better described by a least cost path than Euclidean distance. I also found that temporal shifts in genetic diversity are correlated with several patch metrics, such as habitat quality and proximity. These data suggest that corridors can facilitate gene flow in a

fragmented landscape, and thus, may have implications for the management of species of concern.

INTRODUCTION

Understanding population-level responses to habitat alteration and anthropogenic disturbance is a leading concern of conservation biology (Hanski and Thomas 1994; Sanderson et al. 2002; Keller and Bollmann 2004; Foley et al. 2005). Commonly, alteration of landscapes result in habitat fragmentation, where subpopulations of a larger metapopulation, are presented with isolation effects, area effects, and changes to habitat quality (Hanski 1998; McKinney and Lockwood 1999; Keller and Bollmann 2004). These effects can lead to populations that decline with decreases in habitat extent, resulting in an acceleration of genetic drift (Frankham 1995). Increased genetic drift can then lead to rapid declines in effective population size, resulting in inbreeding depression and eventually extinction (Frankham 2005). Typically, the assumption is that area and isolation effects are the dominant influences on metapopulation dynamics, though other measures of habitat quality may also explain significant variance in patch extinction and colonization (Hanski 1991; Hanski and Thomas 1994; Kindvall 1996). If habitat variables other than area and connectivity have significant effects on metapopulation dynamics, then effective conservation may entail more than simply maintaining a suitable metapopulation geometry.

The probability of metapopulation persistence in fragmented landscapes is dependent on gene flow between subdivided populations as this allows for rescue or recolonization of declining or extinct populations and prevents inbreeding effects in small populations (Thomas and Hanski, 1997). A proposed method for moderating the negative effects of habitat fragmentation is the preservation of linear landscape elements (corridors) which can facilitate gene flow between patches. However, the utility of corridors on metapopulation persistence is debated, as the ecological value of corridors is highly variable (Simberloff et al. 1992) and relies on species behavioral characteristics, landscape composition and structure, patch size, and

environmental variation (Hokit 2010). The benefit of corridors may be further complicated when landscapes are continually subject to habitat alteration that can affect metapopulation persistence. However, relatively little attention has been paid to the issue of connectivity for transient habitats, and thus the benefit provided by corridors for metapopulations inhabiting these landscapes.

The Ocala National Forest (ONF) of central Florida, is a highly transient landscape where different habitat types are managed with contrasting management practices, such as prescribe burning in longleaf pine (LLP) versus the combination of fire-suppression with clear-cutting in sand pine scrub (SPS). The ONF also harbors a large metapopulation of Florida scrub lizards (*Sceloporus woodi*), which occupy stands of SPS and LLP within the ONF (Enge 1986; Kaunert and McBrayer 2015). These lizards are both habitat specialists and limited in their dispersal capacity, thus are likely to be substantially affected by events which alter patch geometry. However, stands of SPS and LLP within the ONF are connected by a vast network of anthropogenically-maintained sand corridors, which facilitate human traffic and may have the potential to influence gene flow between subpopulations of Florida scrub lizards.

Previous genetic analyses revealed that scrub lizard population structure was highly significant and that fixed differences or significant frequency shifts in mtDNA haplotypes were observed between most sampling locations separated by more than a few hundred meters of poor quality habitat (Clark et al. 1999; Tucker et al. 2014). These findings support the initial conclusion, formulated from landscape studies (Demarco 1992), that populations of Florida scrub lizards are effectively isolated by zones of unsuitable habitat. Additionally, computer simulations suggest that fire suppression in the ONF significantly reduces connectivity between subpopulations (Tiebout and Anderson 1997). However, to date, no study has examined

temporal changes in scrub lizard genetic diversity in response to habitat alteration in the ONF, nor has any study tested the effect of sand corridors on connectivity between stands.

An important use of genetic monitoring is the detection of demographic processes within populations, such as genetic bottleneck and founder events, which can influence the trajectory of metapopulation persistence (Schwartz et al. 2007). Additionally, recent improvements in molecular genetic tools, coupled with advances in statistical programs, have led to the field of landscape genetics, which aims to provide information about the interaction between landscape characteristics and microevolutionary processes such as gene flow and genetic drift. Here, I combine a genetic monitoring approach with landscape genetics analyses in order to provide insight into population-level response to alteration of habitat over time. I used five polymorphic microsatellite markers to quantify genetic variation within and among scrub lizard subpopulations at two time points, and spatial analyses to assess the relationship between landscape features and demographic processes that can lead to genetic drift and inbreeding depressions. The aim of this study was to estimate the impact of different management practices on demographic processes and determine the importance of corridors in facilitating gene flow within a metapopulation of the Florida scrub lizard.

METHODS

Study System

The major emphasis of forest management in the ONF is on sustained timber production, which calls for the suppression of fire in stands of SPS (Anderson and Tiebout 1993). In place of a natural fire regime, SPS stands are clear-cut for timber harvest and then roller-chopped (Anderson and Tiebout, 1993). Meanwhile, LLP stands are prescribe burned on an annual or biannual schedule. The contrasting management strategies of different stands within the ONF create a fragmented landscape structure with stands of habitat constantly in different successional stages. Species such as the Florida scrub lizard, which simultaneously exhibit low vagility and high habitat specificity for early successional habitat, are subjected to increased influence by habitat alteration events (Templeton, 2001). The Ocala National Forest is purported to support the current highest abundance of the species (Enge 1996), however, continual anthropogenic influence on the ONF may be greatly affecting patterns of genetic diversity by increasing isolation and altering habitat suitability (Tucker et al 2014). Population sizes of scrub lizards varies throughout the season with peaks measured at 124 individuals per hectare, coinciding with the first appearance of juveniles (McCoy et al. 2004).

Sample collection

Tucker et al., captured lizards by noose from two LLP and five SPS stands in the ONF during the 2010 active season (2014). Tissue (toe or tail clip) was collected from individuals using a noninvasive method and preserved in 70 percent ethanol. In the 2016 active season, I collected tissue from an additional 100 lizards captured amongst two of the same five SPS stands and the same two LLP stands sampled in 2010. Three of the five SPS stands were not occupied

by scrub lizards in 2016. However, we successfully extracted nuclear DNA from preserved toe clips collected from one additional LLP stand in 2010 that was not included in the microsatellite analyses by Tucker et al., (2014). This stand was sampled once again in 2016, providing two SPS stands and three LLP stands which were sampled in both 2010 and 2016. I also sampled an additional 106 lizards collected from four new SPS stands, which were only applied in the analyses of patch metrics, and are not included in any reported statistics related to temporal fluctuations (*e.g.* changes in heterozygosity or allelic richness).

Nuclear DNA was extracted from all toe clips, for 2010 and 2016, using a DNeasy blood and tissue extraction kit following the manufacture's protocol (Quiagen; Boston, MA, USA). Individual scrub lizards were then genotyped for five species-specific microsatellite loci using polymerase chain reaction (PCR) and genotyping protocols described in Tucker et al., (2014). Approximately eight percent of all samples, including samples collected in 2010, were PCR-amplified and genotyped a second time to ensure repeatability scoring.

Statistical analysis

To test for the possibility of null alleles at each locus, I used the software program MICRO-CHECKER version 2.2.3 (Van Oosterhout et al. 2004). To calculate F statistics, observed and expected heterozygosity, and to test exact probabilities for Hardy-Weinberg and genotype linkage disequilibrium, GENEPOP version 4 (Rousset 2008) was used. Estimation of genetic differentiation was then quantified with pairwise F_{st} values calculated for all combinations of stands using a standard analysis of variance (ANOVA) as in Weir and Cockerham (Weir and Cockerham 1984). Significance was determined with a Fisher's exact G-test. Allelic richness was corrected for sample size and then estimated using FSTAT version

2.9.3.2 (Goudet 1995). I then used software program BOTTLENECK (Cornuet and Luikart 1996) to test for recent bottleneck events, using the TPM (two phase model; (Dirienzo et al. 1994)) with 70 percent stepwise mutation model (SMM) and 30 percent infinite allele model (IAM). Deviations between the observed and expected frequency distribution were tested using a Wilcoxon's signed rank test. BOTTLENECK was run for 10,000 iterations.

Data for patch metrics were obtained directly from spatial data provided by USDA ONF division. Because each sampled stand has a clear and defined boundary, patch area was equated to the area of each stand, measured in hectares. The habitat quality for each patch was measured as function of time of last disturbance, because empirical evidence suggest that scrub lizards prefer habitat features characteristic to young LLP and young SPS habitat (Tiebout and Anderson 2001). Stand proximity was measured in a GIS (ArcMap 10.4; Redlands, CA, USA) as the cumulative straight-line distance from a focal stand to all known occupied stands. Stand proximity shifted between time points based on the timing of clear-cuts. If a stand was occupied in 2016, this stand was also assumed to be occupied in 2010 if the stand was clear-cut prior to that date. Relationships between patch metrics (stand area, stand age, stand proximity) and genetic diversity were then tested using separate linear regressions followed by a Bonferroni adjustment (Rice 1989) to alpha to account for multiple simultaneous tests on a single dependent variable.

To assess if corridors facilitate gene flow, I tested an alternative model of Least Cost Path (LCP) against the null model of Euclidean Distance (D_E). Euclidean Distance was measured as the shortest straight-line distance between each pair of sampled stands using ArcMap and land cover data obtained from the Florida Geographic Data Library (FGDL) for the ONF. To estimate LCP, habitat types were classified according to the likelihood of occupation by scrub

lizards. Several previous studies indicate that scrub lizards prefer open xeric habitat and are unlikely to occupy densely vegetated habitat, and do not occupy hydric habitat (Demarco 1992; Tiebout and Anderson 1997; Hokit et al. 1999). Data collected in the field corroborate these indications and further suggest that scrub lizards do not occupy even moderately disturbed habitats, such as campgrounds. Thus, I assigned resistance values in ArcMAP accordingly: open sand = 1; longleaf pine = 3; xeric oak scrub = 5; mature sand pine scrub = 6; flat woods = 7; high impact urban = 9; and open water = restricted. Least Cost Path was then calculated as the shortest distance between a pair of sampled stands that accrued the lowest resistance value. Significant correlations of IBD and LCP with genetic distance (F_{st}), were tested using Mantel's tests (Mantel, 1967).

RESULTS

A total of 300 lizards collected from five sampling locations at two time points and four additional locations at one time point were genotyped for five polymorphic microsatellite loci. Out of 140 tests for linkage disequilibrium, four tests were found to be significant. However, none of the significant pairings were consistent for any loci among populations, thus we assumed no linkage disequilibrium. Two tests deviated from Hardy-Weinberg Equilibrium (HWE), however, these deviations occurred for the same locus (SW614-A1) in the same stand (Kerr Island) for both time points. Despite that allele mis-scoring is thought to be common, often due to the presence of ‘stutter bands’ (Hoffman and Amos 2005), there was no evidence of mis-scoring or allelic dropout.

Global F_{st} across all individuals and subpopulations for 2016 was 0.013, compared to a 2010 global F_{st} of 0.034. The average number of effective alleles per subpopulation ranged from 6.2 to 10.6 in 2010 and 6.8 to 8 in 2016 and the average allelic richness per subpopulation ranged from 4.8 to 5.2 in 2010 and 4.7 to 6 in 2016. Fluctuations in effective number of alleles and allelic richness varied between 2010 and 2016 depending on sampling location. The BOTTLENECK analysis revealed a single significant heterozygote excesses, indicative of a recent bottleneck that occurred at Crash South (CS) in 2010 ($p = 0.03125$). Additionally, BOTTLENECK detected a single heterozygote deficiency for sampling location Crash North (CN) at 2010 ($p = 0.03125$), suggesting a recent population expansion. I also found that stand age and stand proximity were significantly associated with allelic richness ($F_{(1,15)} = 9.00$; $r^2 = 0.38$; $p = 0.0090$ and $F_{(1,15)} = 9.63$; $r^2 = 0.39$; $p = 0.0073$, respectively) but that stand area was not. Euclidean distance was not associated with genetic distance in either 2010 or 2016.

However, I found that LCP was associated with genetic distance in 2016, ($r = 0.61$; $p = 0.0110$), but not for 2010.

DISCUSSION

Microsatellite analyses revealed that genetic differences between subpopulations of scrub lizards in the ONF decreased between 2010 and 2016, while genetic diversity increased within four of the five stands sampled at both time points. Moreover, spatial analyses showed that genetic diversity within stands is correlated with stand age and proximity to other occupied stands, and that gene flow between stands is associated with sand corridors. These results, together with observations of both a single heterozygote deficiency and a single heterozygote excess in 2010, suggest that gene flow can rescue subpopulations from demographic processes that can lead to genetic drift. The decrease in genetic distance between subpopulations is likely explained by this genetic rescue followed by admixture. Thus, the results of this study support the argument that anthropogenically-maintained corridors can benefit metapopulations by facilitating gene flow, particularly in the case of scrub lizards in the ONF.

Continual alteration of landscapes affect landscape metrics, such as habitat quality and connectivity, which impact the population genetic structure of metapopulations (Puth and Wilson 2001). Temporal fluctuations in genetic diversity have been thoroughly studied in salmonid fishes and these studies often reveal that shifts in genetic differentiation occur due to changes in gene flow and genetic drift (Nielsen et al. 1999; Planes and Lenfant 2002) Kanda and Allendorf 2001. These temporal fluctuations in genetic differentiation can also change quickly due to demographic instability (Slatkin 1977; Whitlock and McCauley 1990), which can be caused by changes to landscape structure and patch geometry (Gilpin 1991; Hansen and Loeschcke 1996; Tessier and Bernatchez 1999; Jensen et al. 2005). Genetic drift is often accelerated with reductions in habitat extent, and is reduced with increased connectivity (Frankel and Soulé 1981; Stockwell et al. 2003) (Stockwell et al. 2003). Between 2010 and 2016, the scrub lizard

metapopulation in the ONF experienced a fifty percent reduction in genetic differentiation, suggesting an increase in gene flow, and thus increased connectivity between subpopulations.

Empirical data and theory tend to suggest that the likelihood of colonization increases as connectivity increases and that the probability of local extinction increases as patch area decreases (Kindvall and Ahlen 1992; Thomas and Harrison 1992; Moilanen and Hanski 1998) (Thomas et al. 1992; Thomas & Jones 1993). This area-and-isolation paradigm (Hanski 1998) has been validated by a small group of case studies in various taxa such as plants and invertebrates (Kindvall & Ahlén 1992; Hanski & Thomas 1994) and it is commonly argued that additional variables, such as habitat quality, contribute little explanatory power to models of metapopulation dynamics (Hanski 1994; Moilanen and Hanski 1998; but see (Verboom et al. 1991). However, a recent meta-analysis of a wide variety of animal groups in fragmented landscapes demonstrated that patch size and isolation, the two key factors explaining population dynamics in island models, explained relatively little variation in stand occupancy (Prugh et al. 2008). Instead, the authors concluded that habitat type and quality was more closely associated with stand occupancy. Additionally, Tiebout and Anderson (1997) found that scrub lizard dispersal in the ONF, is likely related to the timing of disturbance in addition to patch geometry. Thus, demographic processes of habitat-specific species, such as the Florida scrub lizard, are likely to be affected by environmental variables in addition to patch geometry (Bennett 1983).

Florida scrub lizards occupy a narrow range of young successional habitats (Christman et al. 1979; Anderson and Tiebout 1993) that provide open sand and exposure to direct sunlight (Campbell and Christman 1982; Mushinsky 1985; DeMarco 1992; Tiebout and Anderson 2001). In the ONF, such habitats only occur immediately following disturbances such as clear-cutting in SPS and prescribe burning in LLP (Anderson and Tiebout 1993; Anderson and Tiebout 1994).

Interestingly, while stands of SPS are managed with a combination of fire suppression and clear-cutting in the ONF, stands of LLP habitat are maintained with prescribe burning on an annual or biannual cycle. Observations (Tiebout and Anderson, personal observation) suggest that stands of SPS in the ONF remain suitable only until seven to nine years post clear-cut. Thus, populations of scrub lizards occupying stands of LLP are consistently exposed to suitable habitat while SPS populations have to cope with temporal variation in the number, quality and spatial arrangement of stands (Fahrig 1992). The results of the current study indicate that genetic diversity within stands is associated with stand age, or in the ONF, quality of habitat.

Populations sampled in LLP showed no signs of population bottlenecks or founder events for either 2010 or 2016. However, a heterozygote deficiency and a heterozygote excess were detected in two stands of SPS. The heterozygote deficiency was detected for the population sampled at Crash North (CN) in 2010, which was clear-cut and roller chopped in 2009. Because scrub lizards do not occupy mature sand pine scrub (DeMarco 1992; McCoy and Mushinsky 1994; Tiebout and Anderson 1997), it is highly unlikely that CN could have been colonized for more than one generation prior to sampling. Thus, the population sampled at CN in 2010 was potentially the founding population. My data show that the population sampled at CN in 2010 also had an 8.5 percent lower average allelic richness and a slightly lower heterozygosity than the population sampled in 2016. This is expected of a founding population because a smaller proportion of the total genetic variation within a metapopulation is expected to be carried by a small group of individuals. Coupled with recent conclusions that heterozygote deficiencies can indicate recent admixture (Barson et al. 2009), it is likely that the population sampled at CN in 2010 was experiencing genetic rescue from a recent founder event. In species with relatively short generation times, new migrants can quickly rescue a population experiencing genetic drift

(Brown and Kodricbrown 1977), especially when the founding population size is small (Keller et al. 2001).

Though recent clear-cuts in the ONF may temporarily provide suitable habitat for scrub lizards, increases in vegetation density are expected to reduce habitat extent and quality in SPS stands, in turn reducing population size. Two of the original stands sampled by Tucker et al (2014) did not harbor lizards in 2016. As of 2016, these two stands were 15 years post clear-cut. Furthermore, sampling at CS in 2016, which was then nine years post clear cut, was heavily confined to sand corridors bordering the stand. Though the exact mechanisms of dispersal from aging stands of SPS and subsequent colonization are unknown (McCoy and Mushinsky 1994; Greenberg et al. 1994), several recaptures along the border at CS suggest that scrub lizards may temporarily occupy corridors adjacent to stands of declining habitat quality. Colonization of and dispersal along sand corridors may then lead to outbreeding with the metapopulation, reducing genetic drift within a declining subpopulation. Software program BOTTLENECK detected a genetic bottleneck for the population sampled at Crash South (CS) in 2010, when habitat quality was expected to be in the beginning stages of decline. However, there was no indication of a genetic bottleneck for CS in 2016. Furthermore, a large increase in allelic richness was observed between 2010 and 2016, suggesting potential genetic rescue due to increased gene flow (Kolbe et al. 2008).

Similar results were found in a network of populations of Rocky Mountain Apollo butterflies, which, following a population bottleneck varied in their loss of genetic diversity and recovery due to different levels of connectivity (Jangjoo et al. 2016). Unfortunately, I was limited to two stands of SPS in temporal analyses due to sampling design. However, like the results found in Jangjoo et al.'s (2016) study, allelic richness was strongly associated with

connectivity (proximity) and increases in allelic richness followed each potential demographic rescue. Additionally, previous studies on scrub lizard demography have concluded that demographic rescue and recolonization are likely to occur among patches that are in close proximity or are linked by suitable habitat (Tiebout and Anderson 1997; Hokit et al. 1999). Both CN and CS share a high proximity to other occupied stands in the ONF. Furthermore, previous experiments indicate that the addition of a single immigrant to a population experiencing genetic drift can have a substantial impact, with fitness improved by over 50 percent in a single generation (Spielman and Frankham 1992). For example, Madsen et al (1999) introduced male *Vipera berus* (a species of European adder) into a declining and isolated population, where, within only a few generations, inbreeding effects had been completely assuaged and the population was expanding (Madsen et al. 1999). Because female scrub lizards lay two to three clutches each breeding season, it is feasible that genetic rescue of declining subpopulations can occur quickly if stands are not isolated.

Typically, anthropogenic disturbance increases habitat fragmentation and reduces gene flow between populations (Templeton et al. 2001). However, in some cases, human disturbance has been shown to increase gene flow (Neve et al. 2008) by increasing connectivity. For example, using a model of least cost path, Coulon et al. (Coulon et al. 2004; Coulon et al. 2010) determined that genetic similarity between roe deer populations within a fragmented landscape was correlated with connectivity provided by wooded corridors. The positive association between least cost distance and genetic distance among scrub lizard subpopulations in the ONF suggests that anthropogenically-maintained corridors, which facilitate human traffic in the ONF, also facilitate the dispersal of scrub lizards between neighboring stands. However, only in 2016 was any model of geographic or cost distance associated with genetic distance, potentially due to

increased genetic differentiation caused by a recent genetic bottleneck and founder event at CS and CN, respectively.

The persistence of metapopulations depends on the balance between colonization and extinction dynamics (Harrison and Taylor 1997 (Johst et al. 2002)). Because temporal variation in habitat structure affects the probability of colonization and extinction within metapopulations (Wiens 1997), species inhabiting transient landscapes, such as the ONF, should be carefully monitored. In particular, species with limited vagility may be at high risk of extinction in fragmented landscapes because dispersal between stands is necessary when habitat becomes unsuitable. Considering the low dispersal documented for Florida scrub lizards, both empirical and theoretical evidence indicate that scrub patches within ridges are distinct demographic units (Hokit et al. 1999). Though the Florida scrub lizard is not yet recognized as endangered, the species is included on Florida's list of Species of Greatest Conservation Concern (United States Fish Wildlife Service 1991; McCoy and Mushinsky 1992; Florida Fish and Wildlife Conservation Commission 2005). The apparent inability of scrub lizards to disperse through maturing stands of SPS previously raised the question of how the ONF scrub lizard metapopulation was able to persist in the 'managed mosaic of transient successional stages dominated by older seres'. Results of the current study suggests that the low-traffic sand corridors facilitate scrub lizard gene flow. Thus, in the absence of any fire regime in stands of SPS within the ONF, it is likely vitally important to maintain these sand corridors because connectivity in a metapopulation allows demographic rescue.

Table 3.1. Pairwise estimates of F_{st} with stands sampled in 2010 (below diagonal) and 2016 (above diagonal). * indicates significance using Fisher's exact G-test (alpha level of 0.05).

	Crash North	Crash South	Salt Springs	Hughes Island	Kerr Island
Crash North		0.03*	0.047*	0.023*	0.012*
Crash South	0.018*		0.069*	0.011*	0.014
Salt Springs	0.014	0.012*		0.016	0.016*
Hughes Island	0.026*	0.0696*	0.072*		0.012*
Kerr Island	0.048*	0.0379*	0.024	0.106*	

Table 3.2. Allelic richness (Ar), expected heterozygosity (He) and observed heterozygosity (Ho) for each stand sampled in 2010 and 2016. In four of the five stands, allelic richness increases.

Stand	Ar		He		Ho	
	2010	2016	2010	2016	2010	2016
Crash North	5.17	5.61	0.76	0.78	0.74	0.72
Crash South	5.13	5.69	0.77	0.75	0.76	0.79
Salt Springs	5.17	4.65	0.76	0.71	0.72	0.67
Hughes Island	4.88	5.17	0.68	0.71	0.70	0.67
Kerr Island	5.17	5.89	0.71	0.72	0.68	0.73

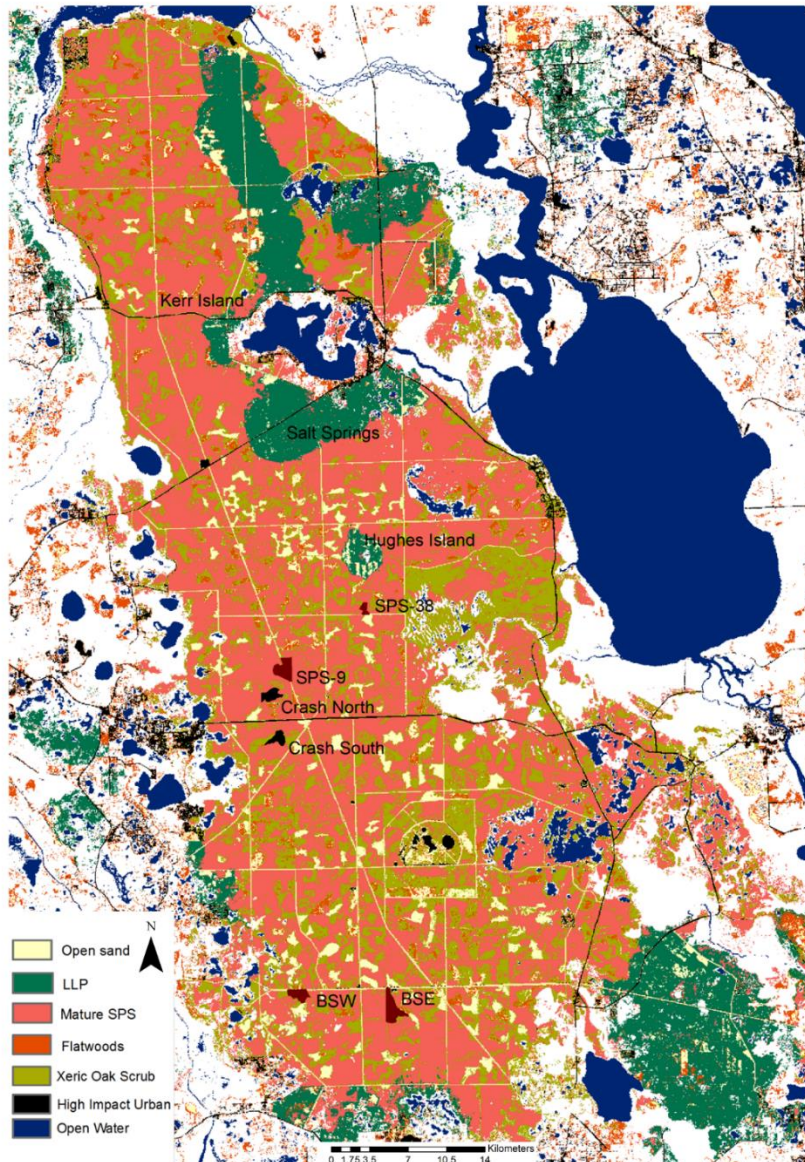


Figure 3.1.

Location of SPS and LLP sites where Florida scrub lizards were sampled in the ONF. Stands highlighted in black were sampled in 2010 and 2016, while stands highlighted in red were only sampled in 2016. Stands of LLP are in green and are labeled by name. The different habitat types and qualities are colored according to the legend. Stand names correspond to stand names in tables 1 and 2.

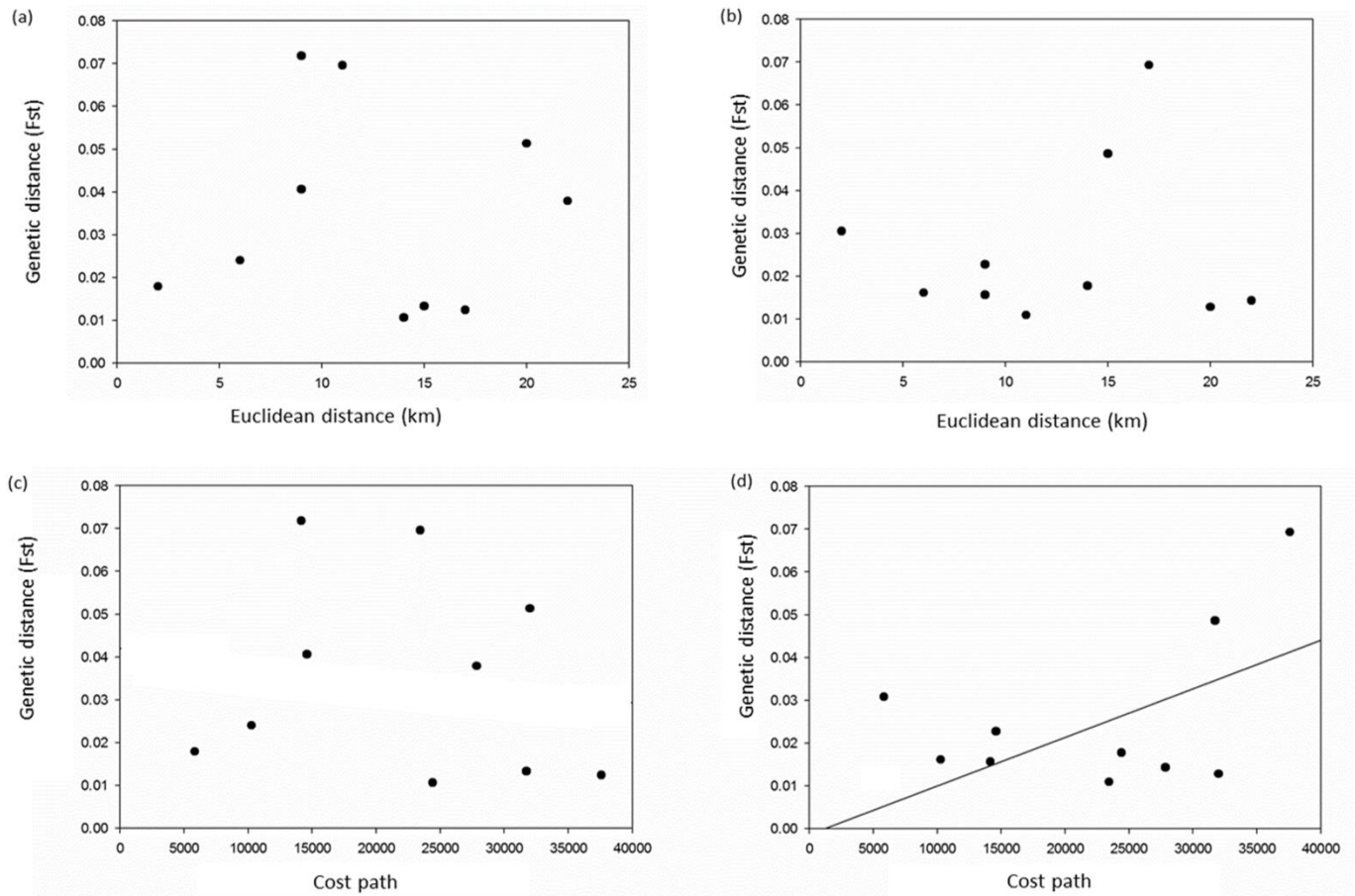


Figure 3.2. Associations between Euclidean distance and least cost path with genetic distance.

Populations sampled in 2010 (figures 2a and 2c) and populations sampled in 2016 (figures 2b and 2d).

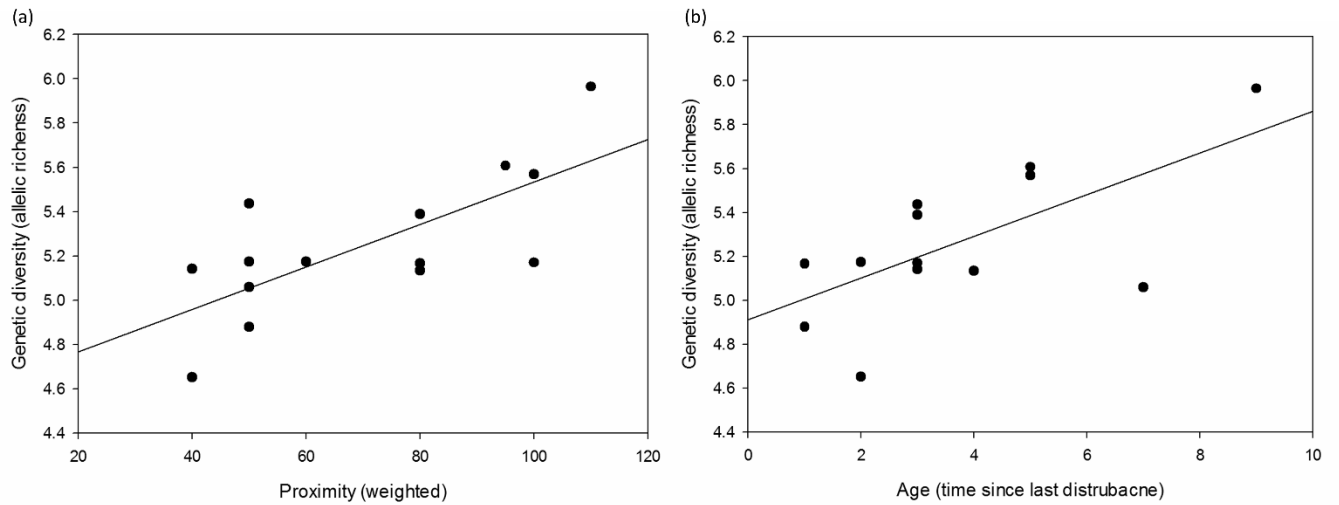


Figure 3.3.

Multiple linear regressions between patch geometry (proximity and age) and genetic diversity (allelic richness). As proximity to other stands increases, the genetic diversity within a focal stands also increases. Also, there is a positive correlation between the time since last disturbance and genetic diversity within a focal stand. All sampling locations for 2010 and 2016 are included. Tests are significant at Bonferroni correction (adjusted alpha level 0.0125).

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