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POPULATION DENSITY OF THE FLORIDA SCRUB LIZARD *(SCELOPORUS WOODI)* IN MANAGED FLORIDA SCRUB AND LONGLEAF PINE SANDHILL HABITATS

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***Abstract.*—Studies investigating managed landscapes are of increasing importance, as fragmentation is a known cause of biodiversity loss. From June to September 2012, we sampled populations of the rare, endemic Florida Scrub Lizard (*Sceloporus woodi*) across the Ocala National Forest (ONF) to compare lizard density across two managed habitat types. Florida Scrub habitat in the ONF is clearcut and roller-chopped, whereas Longleaf Pine habitat is managed via prescribed burning. We sampled 10 stands of Florida Scrub (2–3 y post disturbance) and 10 stands of Longleaf Pine (1 y post-disturbance) for lizards. We compared lizard density between the interior of each habitat patch and the associated natural surface road habitat surrounding each habitat patch. To compare microhabitat conditions between stand types, we also gathered vegetation and substrate data. Lizards occurred in higher density in recently burned Longleaf Pine than in roller-chopped scrub. Stands of roller-chopped scrub showed a noticeable absence of lizards. Higher lizard density along roads suggests that lizards use natural surface roads extensively. Scrub and longleaf stands differed in several microhabitat conditions, which may be related to differences in density. Further research is needed to examine the effects of disturbance frequency, patch size, and isolation on the overall persistence of the Florida Scrub Lizard population in the ONF.**

Key Words.—clearcutting; management; Ocala National Forest; prescribed fire; rollerchopping; sandhill

INTRODUCTION

Xeric pine forests such as Florida Scrub (FSC) and Longleaf Pine-Wiregrass Forest (LLP) provide good examples of disturbance dependent habitats. Florida Scrub is characterized by a high number of endemic species (Neill 1957; Auffenberg 1982; Christman and Judd 1990) and is typically comprised of a single overstory species, Sand Pine (*Pinus clausa*), with an understory composed of oak species (*Quercus myrtifolia, Q. geminata, Q. chapmanii*), Fetterbrush (*Lyonia lucida*) and palmetto (*Serenoa* spp.; Jackson 1972; Greenberg et al. 1994). Longleaf Pine (*Pinus palustris*) is the dominant overstory species in LLP, with an understory consisting of patches of Turkey Oak (*Quercus laevis)* occurring amid broad areas of Wiregrass (*Aristida beyrichiana*; Wells 1928; Wells and Shunk 1931). Recently disturbed FSC has a low canopy and an abundance of open sand. Disturbed LLP typically has an intact canopy but is also characterized by an open park-like understory. Historically, these intrinsic microhabitat conditions were naturally created via high-intensity wildfires (Greenberg et al. 1994) that occurred every 10–20 y (Myers 1990).

In recent decades, however, wildfire suppression has allowed for the maturation on a landscape-scale of xeric forests (Greenberg et al. 1994; Tiebout and Anderson 1997; Tiebout and Anderson 2001). In addition to anthropogenic pressures (Fogarty 1978; Enge et al. 1986; Greenberg et al. 1994) and land use changes (Gilliam and Platt 1999), wildfire suppression has contributed to the loss and degradation of FSC and LLP (Frost 1993) forests. In particular, FSC is considered to be an endangered ecosystem (Noss et al. 1995; Peters and Noss 1995) and LLP has been subjected to a vast reduction from its original range (about 1–3% of original range remaining; Outcalt 2000). In the absence of wildfire, similar open, sandy microhabitat conditions are now created primarily via anthropogenic management practices (i.e., clearcutting and prescribed burning; Greenberg et al. 1994; Tiebout and Anderson 2001) in many of the remaining patches of FSC and LLP. This raises questions about how management affects the intrinsic microhabitat structure and spatiotemporal configuration of managed stands, and how these factors affect populations of species adapted to the microhabitat of recently disturbed xeric pine forest **(**Campbell and Christman 1982; Mushinsky 1985; DeMarco 1992; Anderson and Tiebout 1993).

The Florida Scrub Lizard, *Sceloporus woodi* (Fig. 1) is a small, terrestrial lizard endemic to the xeric pine forests of peninsular Florida (Campbell and Christman

FIGURE 1. Female *Sceloporus woodi* observed on burned wood at Kerr Island longleaf pine stand in the Ocala National Forest, Florida, USA. (Photographed by Lauren K. Neel).

1982; McCoy and Mushinsky 1992; Tiebout and Anderson 1997, 2001). *Sceloporus woodi* is rare (Wood 1990; McCoy and Mushinsky 1992) and is listed as Threatened by the Florida Committee on Rare and Endangered Plants and Animals (Moler 1992). *Sceloporus woodi* has limited vagility (Jackson 1973; Clark et al. 1999; McCoy et al. 2004) and has a maximum dispersal distance of ≤ 750 m (Tiebout and Anderson 1997; Hokit et al. 1999).

Sceloporus woodi historically occupied xeric forests across the Florida peninsula, but many populations are now believed be extinct or dangerously close to extinction (Enge et al. 1986; DeMarco 1992). The majority of research on *S. woodi* has been conducted in FSC (DeMarco 1992; McCoy and Mushinsky 1992; Anderson and Tiebout 1993; Greenberg et al. 1994; Tiebout and Anderson 2001). However, the species also occurs in stands of LLP (Jackson 1973; Williams and McBrayer 2015), but has been relatively understudied in this forest type. Today, management activities (i.e., clearcutting and roller-chopping in FSC, prescribed fire in LLP) provide the disturbance regimen, and presumably the appropriate microhabitat conditions that *S. woodi* requires (i.e., open sand; Anderson and Tiebout 1993).

However, clearcutting FSC does not mimic the landscape-level scale of the natural wildfire regime. Instead, the result is a patchy network of suitably managed FSC stands. In a relatively short period of time (approximately 5–7 y following a disturbance event; Tiebout and Anderson 1997, 2001), natural succession deteriorates open sand microhabitat conditions for *S. woodi* in FSC, forcing individuals to disperse to other recently disturbed stands throughout the landscape. Due to its limited vagility (Tiebout and Anderson 1997; Hokit et al. 1999), *S. woodi* does not disperse through mature stands of scrub (Greenberg et al. 1994; Hokit et al. 1999) or other habitats that do have suitable amounts of open canopy and open sand (Fernald 1989). Thus, both intrinsic microhabitat structure and spatiotemporal variables such as patch size and isolation (Fabry 2007) can affect scrub lizard dispersal, patch colonization, and overall metapopulation persistence (Hokit et al.1999).

Scrub lizards are known to use natural surface roads, trails, and firebreaks in the ONF (Johnson 2000; Fabry 2007). These habitats may provide dispersal corridors (Greenberg et. al. 1994; Johnson 2000) and/or permanent open sand habitat (Johnson 2000; Tiebout and Anderson 2001). While several studies have investigated the effects of management on scrub lizard habitat use (Anderson and Tiebout 1993; Greenberg et al. 1994; Tiebout and Anderson 2001; Fabry 2007), no study has compared microhabitat structure and lizard population density between recently disturbed stands of FSC and LLP. Also, no study has investigated lizard densities along natural surface road habitat.

The purpose of this study was to compare scrub lizard density between managed stands of FSC and LLP (managed-habitat types). Furthermore, we compared lizard density between the interior area of stands and the associated natural surface road habitat (sub-habitat types). Finally, microhabitat conditions (e.g. vegetation, substrate) were quantified to compare differences between managed-habitat types and to document correlations with observed trends in lizard abundance within stands. Elucidating differences in population density and microhabitat structure between these managed habitats could influence future forest management practices and conservation efforts for the Florida Scrub Lizard.

MATERIALS AND METHODS

Study area.—The Ocala National Forest (ONF) is centrally located on the Mt. Dora sand ridge in parts of Marion, Lake, Putnam, and Seminole counties in Florida, USA. Despite recent local extinctions elsewhere (Enge et al. 1986; DeMarco 1992), viable populations of scrub lizards are still present in the xeric pine forests of the ONF (Enge et al. 1986; DeMarco 1992; Tiebout and Anderson 2001; McCoy et al. 2004). The largest remaining contiguous patch of FSC habitat in Florida is encompassed by the ONF (Greenberg et al. 1994; Tiebout and Anderson 2001) where mature stands of Sand Pines are clearcut for wood pulp harvest (U.S. Forest Service 1985; Tiebout and Anderson 2001) on 30–40 y cycles (Greenberg et al. 1994). Clearcutting destroys Sand Pines and other aboveground vegetation, and in the ONF, is often followed by the practice of roller-chopping. This secondary process destroys remaining roots, stumps, and debris and mixes them with the sandy soil to promote rapid decomposition (Tiebout

and Anderson 2001). The majority of ONF LLP stands are managed on a rigorous biennial prescribed burning cycle (Kathy Bronson, pers. comm.). Nearly every stand of ONF FSC and LLP has an associated road, trail, or firebreak that intersects and/or borders the stand interior (Kathy Bronson, pers. comm.).

Selection of managed stands of FSC and LLP.—We selected 10 FSC and 10 LLP sites based on current ONF management practices (ONF Seminole Ranger District office; Kathy Bronson, pers. comm.; see below), and the presence of adjacent natural surface road habitat. We only sampled stands with associated natural surface road habitat, and avoided stands bordering development such as paved roads. Selected FSC stands were clearcut and roller-chopped in 2009 or 2010 (2–3 y prior to study). These stands maximized the potential for the establishment of lizard populations considering the colonization window imposed by FSC understory succession (≤ 5 y post-disturbance; Tiebout and Anderson 1997, 2001) and the fact that stands managed ≤ 1 y post-disturbance have a lower probability of dispersing lizards locating and colonizing a FSC stand (Tiebout and Anderson 1997).

The selected LLP stands were burned in 2011 (1 y prior to study), and thus were considered to be most suitable because most ONF LLP stands are burned biennially. We selected stands that were burned in 2011 because stands burned in 2012 were burned only a few months prior to sampling, and a limited number of LLP stands were burned solely in 2009 or 2010. Therefore, we considered LLP stands burned in 2011 to be the most comparable to the sampled FSC stands because they were of the most suitable age for lizard colonization and microhabitat similarities, yet represented a unique forest type and management regimen in the ONF. Site locations are identified in Appendix 1.

Lizard sampling.—We surveyed the interior of each stand, and the associated intersecting and/or bordering natural surface roads, trails, and firebreaks (all are henceforth referred to only as roads), to determine differences in lizard density between managed-habitat types and between sub-habitat types. We defined the road as the actual road surface as well as 0.5 m of the bordering vegetation on either side because lizards are likely to use the road edge as refuge. We defined the interior of each stand as the remaining area of the stand, excluding a 25 m buffer zone extending from the edge of the road into the interior. Lizards we observed within the 25 m buffer zone were not included in analyses to avoid confounding samples between sub-habitat types.

All lizard surveys took place between 0900 and 1400 from 9 June to 9 September 2012. On each survey day, we measured several climatic variables: cloud cover, soil temperature in the sun and shade, and air temperature in the sun and shade approximately 1 m above the ground. We took all ambient temperature readings with a handheld infrared temperature gun (Model MT-2U, Raytek Corporation, Santa Cruz, California, USA).

We captured lizards by noose or by hand. Upon capture, we recorded location, time of capture, detection method, substrate used when first observed, lighting condition where first observed, and detection distance when first observed. We recorded detection distance to determine differences between managed-habitat types or between sub-habitat types. We gave each lizard a unique identification mark via toe-clipping, and a unique color pattern painted on the dorsum, to easily avoid the inclusion of any recaptured animals. After processing, we released lizards at the site of capture.

Sampling effort within stand interiors.—A single individual (MDK) performed line transects to sample each stand interior for lizards. Preliminary sampling indicated that when walking a consistent speed and using a 3-m sampling width, lizard density could be rapidly and reliably surveyed for 4.6% of the interior of any stand (total area of each stand was known; Appendix 1). We spaced transects at least 25 m apart and traversed the longest distance of each stand to maximize any variation within the stand. In smaller stands, we sampled at least two shorter transects (together comprising 4.6% of total interior area). Sampled stands of LLP were either discrete stands or portions of a larger stand surrounded by a natural surface road. We measured all spatial data and line transects using a handheld Garmin Etrex Legend GPS (Garmin International Ltd., Olathe, Kansas, USA).

Sampling effort for natural surface roads.—To compare lizard density between road and interior habitats, we sampled 100% of the area of associated road habitat. Sampling 100% of the area of stand interiors would have been logistically impossible. However, 100% of the area of road habitat could be sampled rapidly. We also recorded encounter rates (lizards observed per minute sampled) along roads and within stand interiors.

Vegetation and substrate sampling.—We recorded vegetation and substrate characteristics to assess the microhabitat conditions within each stand. Point samples were taken along line transects. We used four 50-m transects per stand that we randomly selected because asymptotic values were reached at 200 m for various vegetation and substrate types. We took point samples every 2 m using a 2.5-m pole marked at 0.5-m increments to estimate the vegetation height, vegetation patch width, and substrate patch width. For each point sample, we recorded the substrate type (open sand, OS; pine litter, PL; leaf litter, LL; mixed litter, ML; or coarse

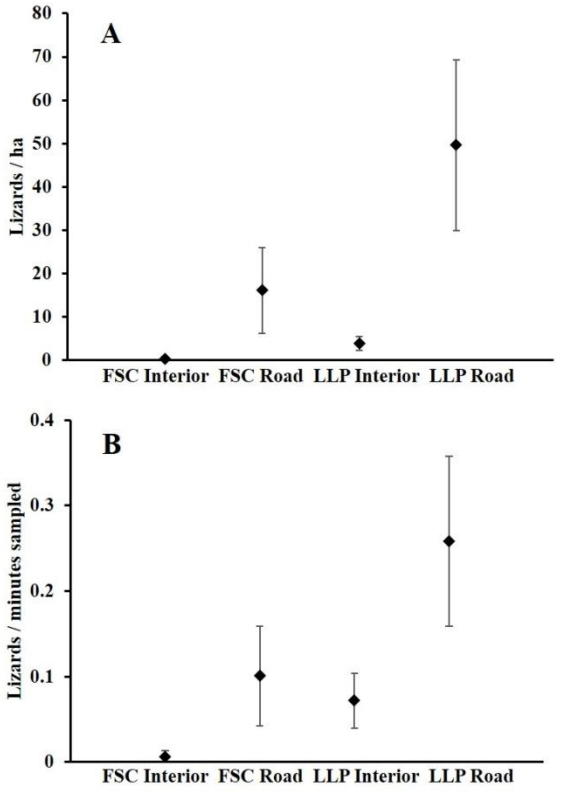

FIGURE 2. A.) Densities of Florida Scrub Lizards (*Sceloporus woodi*) within stand interiors and along roads in Florida Scrub (FSC) and Longleaf Pine Sandhills (LLP). B.) Encounter rates of Florida Scrub Lizards (*Sceloporus woodi*) within stand interiors and along roads in Florida Scrub (FSC) and Longleaf Pine Sandhills (LLP). Symbols are the means and the vertical lines are 95% confidence intervals.

woody debris, CWD), and the vegetation type (annuals, shrubs, pines, oaks [ground-dwelling oaks], Turkey Oaks [tree-like oaks], Wiregrass [WG], grass, palmetto [PALM], and open [areas void of aboveground vegetation regardless of substrate type]).

Statistical analyses.—We analyzed lizard density using a split-plot ANOVA with managed-habitat type as the main plot, sub-habitat type as the subplot, and sampled stand as the random effect. Because sampling effort and stand size might be confounded, this design allows us to gauge this via the random effects. We used correlation analyses and non-parametric alternatives (Spearman's Rank tests) to examine relationships between lizard abundance within stands and microhabitat characteristics as well as between lizard abundance within stands and total stand area. We used one–way ANOVAs, matched pair tests, and non-parametric alternatives (Mann-Whitney U-test, Wilcoxon signed rank test) to compare encounter rate, detection distance, microhabitat conditions, and total area between managed-habitat type and between sub-habitat types. We used a contingency table analysis to compare lizard captures by substrate type. We used the standard alpha level of $P < 0.05$ throughout.

RESULTS

Managed-habitat type and sub-habitat type effects.—Lizard density was significantly higher in LLP than in FSC ($F_{1,18}$ = 10.19, P = 0.005; Fig. 2A, Appendix 2). Each LLP stand interior and surrounding road were occupied by scrub lizards. However, only 30% of FSC stand interiors, and 70% of FSC roads were occupied by lizards; when road and interior habitats were combined, only 70% of all FSC sites surveyed were occupied by lizards. Lizard density was significantly higher along road habitat than within stand interior habitat ($F_{1,18}$ = 31.29, $P < 0.001$; Fig. 2A). There was a significant interaction between managed-habitat type and sub-habitat type ($F_{1,18}$ = 7.41, P = 0.014) but no significant effect due to individual stands ($F_{18,18}$ = 1.12, P = 0.416).

Across the entire ONF, there was a significantly larger total area of biennially burned LLP stands than FSC stands that met the management criteria for this study ($F_{1,313}$ = 29.21, $P < 0.001$). The sampled areas of stand interior varied considerably within managed-habitat types (FSC: 114,529–799,948 m²; LLP: 103,223–3,400,955 m²). Yet, the sampled stands of FSC and LLP did not significantly differ in total interior area (Z = -1.47, df = 19, P = 0.140). Roads occupied significantly less area than stand interior habitat (S = 105.00, df = 19, $P < 0.001$).

Encounter rate and detection distance.—Encounter rates were significantly higher along roads than within the stand interior in both LLP (t = 3.74, df = 9, P = 0.005; Fig. 2B) and FSC (S = -20.50, df = 9, P = 0.031; Fig. 2B). Detection distance of lizards did not differ in any managed-habitat type or sub-habitat type comparisons. There was no significant difference in detection distance between LLP and FSC stands (Z = 1.08, df = 19, P = 0.279) or between the roads surrounding LLP and the roads surrounding FSC (Z = 0.09, df = 19, P = 0.921). There was no difference in detection distance between the interior of LLP and the roads surrounding LLP (Z = 0.94, df = 9, P = 0.350), or between the interior of FSC and the roads surrounding FSC (Z = 1.30, df = 9, P = 0.193).

Lizard captures by substrate type.—Microhabitat use differed between managed-habitat types and sub-habitat types (Fig. 3). In FSC, we captured lizards on litter (50%) and open sand (33%) more than downed wood (9%), trees (4%), or other vegetation (4%). In LLP, we captured lizards on litter (37%) and trees (36%) more than open sand (24%) or downed wood (3%). These differences in captures among substrates in FSC and

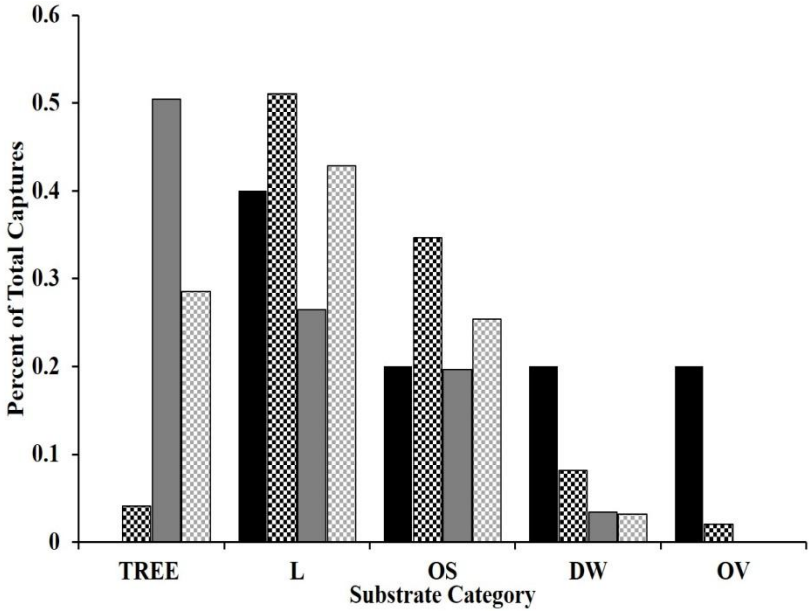

FIGURE 3. Captures of Florida Scrub Lizards (*Sceloporus woodi*) by substrate type within stand interiors (solid bars) and along roads (checkered bars) in Florida Scrub (FSC; black bars) and Longleaf Pine Sandhills (LLP; gray bars). Abbreviations are substrate types: TREE = on a tree, L = litter, OS = open sand, DW = dead wood (i.e. coarse woody debris, branches, etc.) OV = other vegetation.

LLP were significant ($\chi^2_{4,\ n\ =\ 356} = 34.17$, $P < 0.001$).

We captured lizards on pines and Turkey Oaks with equal frequency (50%) in FSC (n = 2). We captured lizards on pines (71%) more than Turkey Oaks (29%) in LLP (n = 109). Captures by tree type did not differ significantly between FSC and LLP ($\chi^2_{(1,\ n\ =\ 111)} = 0.40$, $P = 0.527$).

Within the interior of stands (FSC + LLP), we captured lizards on trees (40%) and litter (33%) more than open sand (21%), downed wood (5%), or other vegetation (0.7%). Along roads (FSC + LLP), we captured lizards on litter (43%), open sand (27%), and trees (25%), more than downed wood (4%) or other vegetation (0.5%) and these captures by substrate differed significantly between stand interiors and roads ($\chi^2_{4,\ n\ =\ 356} = 9.63$, $P = 0.047$). We captured lizards on pines (77%) more than Turkey Oaks (23%) within stand interiors (n = 56) and on pines (64%) more than Turkey Oaks (36%) along roads (n = 55), but differences were not significant between stand interiors and roads ($\chi^2_{1,\ n\ =\ 111} = 2.30$, $P = 0.130$).

***Microhabitat conditions.*—**Between FSC and LLP, FSC had significantly more open sand ($F_{1,18} = 45.75$, $P < 0.001$; Fig. 4), coarse woody debris (Fig. 4), oaks ($F_{1,18} = 168.75$, df = 19, $P < 0.001$; Fig. 4), and open ground ($Z = 2.73$, df = 19, $P < 0.006$; Fig. 4). Longleaf Pine had significantly more litter ($Z = -3.74$, df = 19, $P < 0.001$; Fig 4), Turkey Oaks ($Z = -3.07$, df = 19, $P = 0.002$; Fig. 4) and Wiregrass (Fig. 4). Only two microhabitat conditions were significantly correlated with lizard abundance within stands.

The abundance of lizards found within LLP stands was positively correlated with open sand ($r_s = 0.78$, df = 8, $P = 0.008$) and negatively correlated with litter ($r_s = -0.78$, df = 8, $P = 0.008$). The abundance of lizards found within FSC stands were not significantly correlated with any microhabitat condition. The abundance of lizards found within LLP stands was positively correlated with the total area of LLP interior ($r_s = 0.68$, df = 8, $P = 0.032$). The abundance of lizards found within FSC stands was not correlated with the total area of FSC interior ($r_s = -0.07$, df = 8, $P = 0.851$).

DISCUSSION

This study yielded important data for the future management and conservation of Florida Scrub Lizards in the ONF. Despite having significantly less of the microhabitat conditions favored by *Sceloporus woodi* (Abrahamson 1984a, b; Greenberg et al. 1994), stands of managed LLP had significantly higher lizard density than FSC. The high lizard density in LLP has not been reported in previous studies of habitat preference of *S. woodi* (Abrahamson 1984 a,b; Greenberg et al. 1994). Florida Scrub stands had lower lizard density and a noticeable absence of lizards from 30% of sampled FSC stands. These data highlight that open sand habitat created via clearcutting and roller-chopping FSC may not alone provide sufficient habitat for *S. woodi*

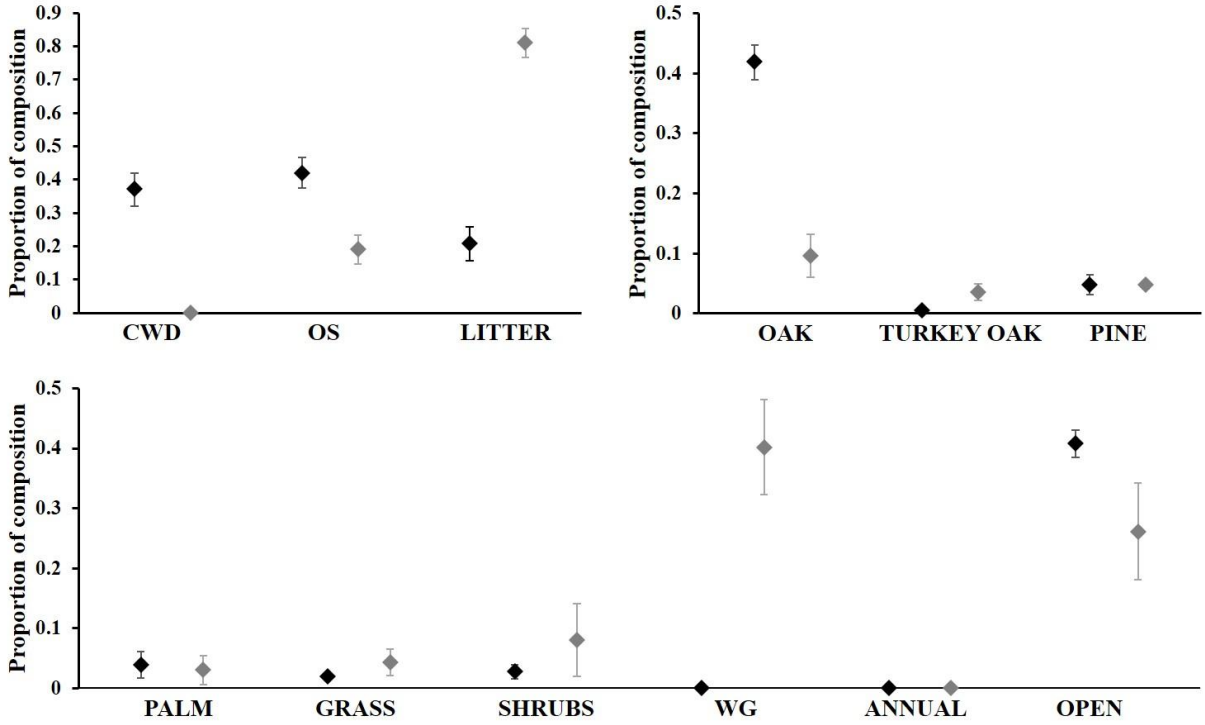

FIGURE 4. Differences in vegetation and substrate composition between Florida Scrub sites (FSC; black symbols) and Longleaf Pine Sandhills (LLP; gray symbols). Symbols are the means and the vertical lines are 95% confidence intervals. Abbreviations are CWD = coarse woody debris, OS = open sand, PALM = palmetto, WG = Wiregrass, Open = no aboveground vegetation.

(Anderson and Tiebout 1993; Tiebout and Anderson 2001). The higher lizard density and higher encounter rate along road habitat suggests that scrub lizards are using roads extensively, if not exclusively, in some areas. The significant interaction between managed-habitat type and sub-habitat type is due to both the low lizard density in FSC and the significantly higher densities found along road habitats across both FSC and LLP (Fig. 2A).

Scrub lizard abundance is positively correlated with open sand (Jackson 1972; Hokit et al. 1999; Tiebout and Anderson 2001) and negatively correlated with woody debris and litter (Anderson and Tiebout 1993). Yet in this study, less open sand, more litter, and a higher lizard density was present in LLP, but not in FSC. This variation suggests that the reduced open sand and increased litter in LLP still provides suitable intrinsic microhabitat conditions and/or that *S. woodi* use additional cues to select habitat (Fabry 2007). The importance of litter in LLP is reflected in scrub lizard use of trees and understory debris (litter + downed wood; Williams and McBrayer 2015). In LLP, litter and trees were used more than any other substrates, while in FSC, litter and open sand were the most used substrates. Hence, *S. woodi* has different microhabitat preferences between FSC and LLP.

In LLP, trees may allow lizards to avoid Wiregrass, which dominates the LLP understory (40%; Wells 1928; Wells and Shunk 1931) and is absent from FSC. Wiregrass is a poor refuge from thermal extremes and predators (Burrow et. al. 2001; Tchabovsky et. al. 2001; Smith and Ballinger 2001) and can inhibit both predator and prey detection by *S. woodi* (Jackson 1972). Trees represent the coolest substrate in LLP, and may also offer similar microclimate as open sand found in FSC (Williams and McBrayer 2015). In contrast, litter and downed wood represented the warmest substrates in LLP (Williams and McBrayer 2015). Hence, scrub lizards may differentially use litter vs. trees for thermoregulation in LLP during different parts of the day (Adolph 1990; Adolph and Porter 1993, 1996; Smith and Ballinger 2001).

Despite overall lower lizard density, FSC stands may harbor high density of scrub lizards if managed in proximity to other occupied stands of managed FSC or LLP. A small (about 147,000 m²) FSC stand was sampled using the same protocols described above in May 2013. We found 14 lizards within the interior of this stand, which is the highest density of any FSC stand surveyed in this study. This stand is located along a Forest Service road with a history of sequential FSC clearcutting and roller-chopping management along its length. Thus stands along this road have high connectivity with other neighboring FSC stands. Many

of the neighboring stands along the road have had high lizard abundances over the past 10 y (Roger A. Anderson, unpubl. data). Therefore, while microhabitat conditions undoubtedly influence population density, connectivity among managed stands may also be a strong determinant of the density of Florida Scrub Lizards (Johnson 2000; Hokit et al. 2001; Fabry 2007).

Temporal and spatial differences between FSC and LLP management may explain the higher lizard density in LLP (Fabry 2007). The biennial burning cycle of LLP in the ONF reduces the possibility for litter buildup and succession that results in cluttered understory. Instead, an open habitat is maintained (Kathy Bronson, pers. comm.). Conversely, FSC stands are typically clearcut once and then allowed to undergo natural succession, without any subsequent management for 30–40 y (Greenberg et al. 1994). Within 5–7 y after clearcutting and roller-chopping, regeneration of Sand Pines and the understory has largely obliterated the once plentiful patches of open sand (Tiebout and Anderson 1997, 2001). Without additional FSC management after 5–7 y, the available time for dispersing lizards to colonize, and then proliferate, in new early successional stages of FSC is severely limited. Whereas in LLP populations, the higher frequency of fire disturbance maintains the microhabitat conditions needed for populations to both persist and to increase in size (Fabry 2007).

The LLP management regimen benefits *S. woodi* populations via functionally increasing patch size and connectivity among LLP stands. Large stands of LLP are separated into compartments and managed by alternating the burning year of adjacent compartments. This management regimen maintains the total LLP patch area and the connectivity of adjacent LLP stands. Thus, the management of LLP differs considerably from the current FSC management. Recent FSC management has resulted in smaller, more isolated stands of FSC, which is a poor combination for scrub lizard populations. Differences in management practices between LLP and FSC stands are likely to have major effects on the overall scrub lizard population size in the ONF. Scrub lizard patch occupancy is reliably predicted by patch size and isolation (77% accuracy; Hokit et al. 2001). Patch size has also been shown to be positively associated with scrub lizard abundance (Fabry 2007) survivorship, recruitment, and male growth rate in FSC stands (Hokit and Branch 2003).

This study supports earlier hypotheses that scrub lizards use ONF natural surface roads extensively (Johnson 2000; Tiebout and Anderson 2001; Fabry 2007). Species with different life-history traits respond differently to road characteristics (e.g., surface type, road width, traffic volume; Rico et al. 2007; McGregor et al. 2008; Brehme et al. 2013). For some species, roads fragment patches of suitable habitat, create population sinks, and/or provide corridors for invasive species (Forman et al. 2003; Fahrig and Rytwinski 2009; Taylor and Goldingay 2010). However, for *S. woodi*, roads increase connectivity between suitable habitat patches and food resources (Johnson 2000; Forman et al. 2003; Fabry 2007), albeit the current high degree of isolation of many FSC stands makes actual dispersal events highly unlikely if not impossible because of the limited vagility exhibited by *S. woodi*. The microhabitat of natural surface roads with low traffic volume provides *S. woodi* with additional permanent habitat (Johnson 2000; Tiebout and Anderson 2001) and/or dispersal corridors (Greenberg et al. 1994; Johnson 2000; Brehme et al. 2013).

Additional research should investigate the use of natural surface roads by *S. woodi*. Studies should attempt to elucidate the role that ONF roads play in lizard habitat use, as well as in the underlying mechanism of scrub lizard dispersal. Many low-use natural surface roads are being decommissioned across the ONF (Kathy Bronson, pers. comm.). Hence the use of these roads by *S. woodi* should be investigated, along with any effects of road removal on scrub lizard dispersal and/or metapopulation persistence.

Management suggestions and conclusions.—Due to the higher connectivity and frequency of local disturbance (Fabry 2007), LLP stands tend to have dense populations of scrub lizards, whereas FSC stands do not. As such, LLP stands may serve as extinction-resistant source populations. Longleaf Pine stands could permit dispersal to neighboring FSC sinks, which will deterministically become extinct (Pulliam 1988; Pulliam and Danielson 1991) within 5–7 y post-disturbance (Tiebout and Anderson 1997 2001). Depending on the historical fire cycle, LLP may have provided expansive habitat in the proper spatial arrangement for *S. woodi* to intermittently occupy FSC. However, this hypothesis is untestable. Conversely, the current LLP management regimen may be creating more suitable and/or more connected habitat, while current FSC management is limiting connectivity and temporal availability of suitable habitat. This hypothesis could be tested by clustering managed FSC stands in a particular spatial ($\leq$ 750 m) and temporal ($\leq$ 5 y post-disturbance) pattern. Such management should increase dispersal, inter-patch connectivity, genetic diversity, and metapopulation persistence (Doak et al. 1992; With and King 1999; Hokit and Branch 2003; Fabry 2007). Finally, managing stands along established corridors (i.e., well connected, low-use, natural surface roads with a known abundance of lizards) will increase connectivity between stands (Huey 1941), promote dispersal, genetic diversity, and metapopulation persistence (Hokit et al. 1999; Fabry 2007).

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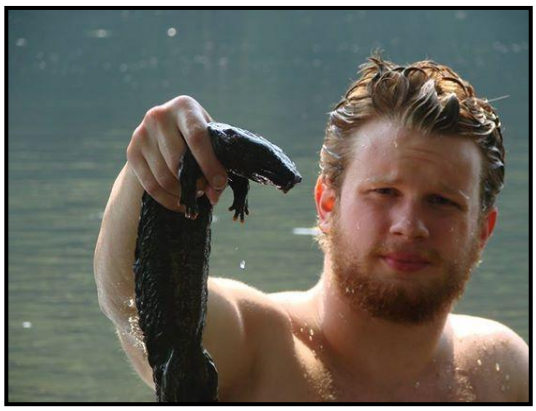

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Appendix 1. Site names, locations, and sampling details of sites used to quantify variation in population density of *Sceloporus woodi*. Coordinates represent the approximate center of each stand. LLP = Longleaf Pine Sandhill, FSC = Florida Scrub. GPS coordinates were taken using datum WGS 84. Total area of the stand interior, and the total circumference of road surrounding the stand shown.

Site	Name	Latitude	Longitude	Interior (m^2)	Road (miles)
LLP1	Hughes Island	29°15'12.16"	81°44'56.06"	3,400,955	6
LLP2	Penner North	29°29'23.87"	81°48'24.35"	324,569	2
LLP3	Waterhole East	29°27'14.21"	81°48'14.31"	519,788	1.2
LLP4	Penner West	29°27'32.7"	81°27'32.7"	282,919	1.8
LLP5	Riverside West	29°25'21.72"	81°48'33.6"	551,134	3.7
LLP6	Hast_River	29°23'51.54"	81°23'51.54"	103,223	0.9
LLP7	Syracuse Island	29°22'55.7"	81°42'32.94"	395,797	2.4
LLP8	Hastings Island	29°22'46.3"	81°47'51.07"	301,132	1.8
LLP9	Salt Springs Island	29°19'32.23"	81°47'43.48"	1,405,000	3.8
LLP10	Kerr Island	29°21'44.14"	81°49'35.43"	1,185,000	1.6
FSC1	Stand 84038	29°12'01.89	81°47'32.55"	799,948	2.8
FSC2	Stand 273027	29°0'59.04"	81°40'49.02"	315,723	1.8
FSC3	Stand 271022	29°1'6.7"	81°40'22.02"	207,471	1.5
FSC4	Stand 84006	29°11'19.66"	81°48'00.2"	436,716	2.8
FSC5	Stand 85002	29°13'20.74"	81°48'38.72"	411,755	2
FSC6	Stand 84002	29°13'12.15"	81°47'49.44"	114,529	1.3
FSC7	Stand 273016	29°2'00.99"	81°41'25.65"	226,519	1.4
FSC8	Stand 273023	29°1'25.18"	81°41'23.32"	234,266	1.3
FSC9	Stand 49004	29°18'29.46"	81°48'51.49"	186,832	1
FSC10	Stand 31023	29°22'50.62"	81°44'22.17"	416,940	1.9

Appendix 2. Capture data for *Sceloporus woodi* by site (Longleaf Pine: LLP; Florida Scrub: FSC) and by capture substrate type. Site locations are found in Appendix 1. Abbreviations are: DWD - dead wood, LIT - litter, SPI - Sand Pine, OAK - oaks, LLP - Longleaf Pine, OPS - open sand, and OTV - other vegetation. Sand Pine and other vegetation were not observed in Longleaf Pine stands (dashes); likewise, Longleaf Pine was not observed in Florida Scrub stands (dashes).

	Stand interior							Natural Surface Road						
	DWD	LIT	SPI	OAK	LLP	OPS	OTV	DWD	LIT	SPI	OAK	LLP	OPS	OTV
LLP1	2	20	-	2	3	9	-	0	11	-	4	6	10	-
LLP2	0	0	-	0	1	0	-	0	2	-	0	0	1	-
LLP3	0	2	-	0	9	3	-	0	3	-	1	3	0	-
LLP4	0	1	-	0	7	1	-	0	5	-	0	6	5	-
LLP5	0	0	-	1	0	2	-	0	0	-	1	1	1	-
LLP6	0	0	-	0	1	0	-	0	2	-	0	7	0	-
LLP7	0	1	-	0	0	2	-	0	10	-	1	2	9	-
LLP8	1	2	-	2	4	2	-	1	4	-	5	2	1	-
LLP9	3	16	-	7	1	1	-	1	20	-	2	4	5	-
LLP10	0	2	-	1	17	9	-	2	11	-	5	3	10	-
FSC1	0	0	0	0	-	0	0	0	12	0	0	-	7	1
FSC2	0	0	0	0	-	0	0	0	1	0	1	-	2	0
FSC3	1	0	0	0	-	0	0	1	4	0	0	-	4	0
FSC4	0	0	0	0	-	0	0	0	0	0	0	-	0	0
FSC5	0	1	0	0	-	1	0	1	3	1	0	-	0	0
FSC6	0	0	0	0	-	0	0	0	2	0	0	-	2	0
FSC7	0	0	0	0	-	0	0	1	3	0	0	-	2	0
FSC8	0	1	0	0	-	0	1	1	0	0	0	-	0	0
FSC9	0	0	0	0	-	0	0	0	0	0	0	-	0	0
FSC10	0	0	0	0	-	0	0	0	0	0	0	-	0	0