Variation In Population Densities of the Florida Scrub Lizard (sceloporus Woodi) between Managed Sand Pine Scrub And Longleaf Pine Stands in the Ocala National Forest

Matthew D. Kaunert

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by

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(Under the Direction of Lance D. McBrayer)

ABSTRACT

Population-level response to habitat fragmentation is central to applied species management and conservation. Managed landscapes are often subject to increased fragmentation and, consequently, may force once connected populations to function as metapopulations. Studies investigating metapopulations occurring over patchy, managed landscapes are of increasing importance as fragmentation is a known cause of biodiversity loss. In June-September 2012, populations of the rare, endemic Florida scrub lizard (*Sceloporus woodi*) were sampled across the Ocala National Forest (ONF) to compare abundance and density across two management types. In the ONF, sand-pine scrub is clearcut and rollerchopped whereas longleaf pine is managed via prescribed burning (2 year cycle). Lizard abundance and density was also compared between the interiors of stands to the associated natural surface roads. Ten stands of scrub (2-3 years post disturbance) and ten stands of longleaf pine (1 year post-disturbance) were sampled. To compare microhabitat conditions, vegetation and substrate data were also gathered. Lizards were more abundant in longleaf pine than scrub. Stands of scrub showed a noticeable absence of lizards. Higher encounter rates suggest that lizards are utilizing natural surface roads. Scrub and longleaf differed in several microhabitat conditions which may drive differences in abundance and density. However, variables such as patch size and isolation may play a larger role in the overall persistence of the Florida scrub lizard metapopulation.

INDEX WORDS: *Sceloporus woodi*, Sand-pine scrub, Longleaf pine, Ocala National Forest, Management, Clearcutting and rollerchopping, Prescribed burn, Metapopulation

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TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

Population-level response to habitat fragmentation is a central issue in conservation and population management (Shea et al. 1998). Fragmentation has subdivided many once-connected populations (Wiens 1995b, 1996b) and forced them to function as metapopulations (Levins 1968, 1969). Metapopulation theory has gained considerable application (Hanski and Gilpin 1997; Hanksi and Simberloff 1997) as fragmentation has become more widespread in many habitats.

Although classic metapopulation theory is guided by the processes of extinction and re-colonization (Levins 1968; Hanski and Gilpin 1991), recent empirical evidence suggests that habitat dynamics such as disturbance and succession may also act as primary drivers of long-term metapopulation persistence (Harrison and Taylor 1997; Thomas and Hanski 2004). Disturbance events such as development, landscape management, and natural disasters are archetypically considered to isolate patches of habitat (Possingham et al. 1994; Lindernmayer and Possingham 1996). For instance, populations of montane mammals have been isolated on mountaintop habitats due to changes in climate (Brown 1971). Salamander (Welsh 1990) and woodpecker (Stangel et al. 1992) species are restricted to remnant patches of fragmented old-growth forest. Thus, for many species, disturbance negatively influences population size and persistence.

However, certain species have coevolved with frequent local disturbance (Shapiro 1979; Murphy and White 1984; Thomas and Harrison 1992; Thomas and Jones 1993). Many disturbance-dependent species follow the dynamics of a non-equilibrium “habitat-tracking” metapopulation (Thomas 1994c; Hanski and Gilpin 1997). Patches within habitat-tracking metapopulations are created or destroyed by extrinsic factors, such as local disturbance (Hanski and Gilpin 1997). Therefore, instead of a balance of extinction and re-colonization driving metapopulation persistence, local populations will simply "track" the availability of recently created habitat patches. Thus, as long as rates of patch loss and renewal are roughly equal, a habitat-tracking metapopulation is likely to persist (Thomas 1994c).

Habitat-tracking models can be useful for conserving frequently disturbed, dynamic landscapes (Stelter et al. 1997, Wahlberg et al. 2002). Managed, successional landscapes vary in intrinsic microhabitat conditions and spatiotemporal dynamics, which can affect the distribution of local populations (Turner 1989; Wiens et al. 1993; Wiens 1995a, Fabry 2007). Documenting the distribution and density of habitat-tracking metapopulations occurring over managed, heterogeneous landscapes could provide a metric for measuring the success of anthropogenic habitat management practices.

Florida xeric pine forests such as sand-pine scrub (henceforth SPS) and longleaf pine-wiregrass forest (henceforth LLP) provide good examples of dynamic, managed habitats. Sand-pine 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 amidst broad areas of wiregrass (*Aristida beyrichiana*) (Wells 1928; Wells & Shunk 1931).

Sand-pine scrub and LLP are each disturbance-dependent forests. Recently disturbed SPS bears a low canopy and an abundance of open sand. Disturbed LLP typically has an intact canopy but is also characterized by an open understory. Historically, these intrinsic microhabitat conditions were naturally created via high-intensity wildfires (Greenberg et al. 1994) that occurred throughout the peninsula every 10-20 years (Myers 1990).

Many species adapted to a natural wildfire regime require an open, sandy microhabitat characteristic of recently disturbed xeric pine forest (Campbell & Christman 1982; Mushinsky 1985; DeMarco 1992; Anderson & Tiebout 1993; Anderson & Tiebout 1994). Such species are termed "xeric-adapted."

In recent decades, however, wildfire suppression has allowed for landscape-scale xeric forest maturation (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 reduction of both SPS and LLP (Frost 1993) forests. In particular, SPS 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 (≈ 1 – 3% of original range remaining; Outcalt 2000).

In the absence of wildfire, ideal open microhabitat conditions are now created primarily via silvicultural management practices (i.e. clearcutting and prescribed burning; Greenberg et al. 1994; Tiebout and Anderson 2001) in many of the remaining patches of SPS and LLP. This raises questions about how management regimes affect intrinsic microhabitat conditions, and how the spatiotemporal configuration of managed stands of forest affects the constituent populations of xeric-adapted species.

The Florida scrub lizard, *Sceloporus woodi*, is a small, terrestrial lizard endemic to the xeric pine forests of peninsular Florida (Cambell and Christman 1982; McCoy and Mushinsky 1992; Tiebout and Anderson 1997, 2001). *S. woodi* is rare (Wood 1990; McCoy and Mushinsky 1992) and has limited vagility (Jackson 1973; Tiebout and Anderson 1997; Clark et al. 1999; Hokit et al. 1999; McCoy et al. 2004). It is also as it is listed as a species of concern by the U.S. Fish and Wildlife Service (USFWS 1999) and as a species of greatest conservation need in Florida (FFWCC 2005).

S.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 SPS (DeMarco 1992; Anderson and Tiebout 1993; Greenberg et al. 1994; Tiebout and Anderson 2001). However, the species also occurs in stands of LLP habitat (Jackson 1973; Williams, 2010), but has been relatively understudied in this forest type. Today, management activities (clearcutting and rollerchopping in SPS, prescribed fire in LLP) provide the disturbance regimen, and presumably the appropriate microhabitat conditions that *S.woodi* requires (i.e. open sand; Anderson & Tiebout 1993). However, differences in microhabitat structure and scrub lizard population densities have yet to be compared between SPS and LLP.

In particular, the SPS clearcutting management regime does not mimic the landscape-level scale of the natural wildfire regime. Instead, the result is a patchy network of suitably managed SPS stands. In a relatively short period of time (approximately 5 years following a disturbance event; Tiebout and Anderson 1997, 2001), natural succession deteriorates open sand microhabitat conditions for *S.woodi* in

SPS, forcing individuals to disperse to other recently disturbed stands throughout the landscape. Scrub lizards have a maximum dispersal distance of ≤ 750 meters (Tiebout and Anderson 1997; Hokit et al. 1999), and do not disperse through mature stands of scrub (Greenberg et al. 1994; Hokit et al. 1999) or other habitats that do not meet their microhabitat needs (e.g. open sand; Fernald 1989). Thus, both intrinsic microhabitat features and spatiotemporal variables such as patch size and isolation (Fabry 2007) likely affect scrub lizard dispersal, colonization, and overall metapopulation persistence (Hokit et al.1999).

Yet, scrub lizards are known to use natural surface roads, trails, and firebreaks (Fabry 2007; Anderson pers. comm.; McBrayer pers. comm.) which may provide dispersal corridors (Greenberg et. al. 1994) and/or permanent habitat (Anderson and Tiebout 2001). Therefore, it seems necessary to quantify lizard density along roads and road-like habitats. While several studies have investigated the effects of management regimes on scrub lizard habitat use (Anderson and Tiebout 1993; Greenberg et al. 1994; Tiebout and Anderson 2001; Fabry 2007), no study has compared lizard density between recently disturbed stands of SPS (Greenberg et al. 1994) and LLP. Also, no study has investigated lizard densities along natural surface road habitat.

The purpose of this study is to compare scrub lizard density between managed stands of SPS and LLP (management types). Furthermore, this study will compare lizard density between the interior area of stands and the associated natural surface road habitat (habitat types). Finally, microhabitat conditions (e.g. vegetation, substrate) will be quantified to compare differences between management types and to observe correlations with observed trends in lizard abundance within stands. Understanding the use of different management and habitat types as well as the resulting differences in intrinsic microhabitat conditions and landscape-level variables could influence future management and conservation of the Florida scrub lizard.

METHODS

Study site

The study site was the Ocala National Forest (ONF) in central peninsular Florida. The ONF contains the largest remaining contiguous patch of sand-pine scrub habitat in Florida (Greenberg et al. 1994; Tiebout and Anderson 2001). 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 2004). Within the ONF, mature stands of SPS are clearcut for wood pulp harvest (U.S. Forest Service 1985; Tiebout and Anderson 2001) on 30 to 40 year cycles (Greenberg et al. 1994). This process destroys sand-pines and other aboveground vegetation, and is typically followed by the practice of rollerchopping. 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 two-year prescribed burning cycle (K. Bronson, pers. comm.). Nearly every stand of ONF SPS and LLP has an associated road, trail, or firebreak which intersects and/or borders the stand interior (Kathy Bronson pers. comm.).

Selection of managed stands of SPS and LLP

Stands were mapped across the ONF via ArcGIS 10 software (Environmental Systems Research Institute, 2004). Spatial data were obtained from the ONF Seminole Ranger District office (K. Bronson, pers. comm.). Ten SPS and ten LLP sites were selected based on the current ONF management practices (see below), and the presence of adjacent natural surface road habitat. Stands with no natural surface road habitat, and/or stands bordering development such as paved roads were not sampled. Selected SPS stands were clearcut and rollerchopped in 2009 or 2010 (2-3 years prior to study). These stands were considered to be the most suitable for lizard populations considering the colonization window imposed by SPS understory succession (≤ 5 yrs. post-disturbance; Tiebout and Anderson 1997, 2001) and the fact that stands managed ≤ 1 year post-disturbance would have a lower probability of dispersing lizards locating and colonizing a SPS stand.

The selected LLP stands were burned in 2011 (1 year prior to study), and thus were considered to be most suitable because most ONF LLP stands are burned biennially. Stands burned in 2011 were selected because A) stands 2012 were burned only a few months prior to sampling, and B) a limited number of LLP stands were burned solely in 2009 or 2010. Hence, LLP stands burned in 2011 were considered to be the most comparable to the sampled SPS stands because they were of the most suitable age for lizard colonization and microhabitat similarities, while still representing another major forest type and management regime in the ONF.

Lizard sampling

Each sampled stand was considered to have two distinct habitat types: the interior of each stand and the associated road. The "road" was defined 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. The "interior" of each stand was the remaining area of the stand, excluding a 25-meter buffer zone extending from the edge of the road into the interior (Fig. 1). Lizards observed within the 25-m buffer zone were not included in any analyses to avoid confounding samples between habitat types. 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”), were surveyed to determine differences in lizard density between stands of managed and habitat types.

All lizard surveys took place between 0900 and 1400 hours from June to September 2012. On each survey day, several climatic variables were measured: cloud cover, soil temperature in both sun and shade, and air temperature in sun and shade approximately 1 m above the ground. All ambient temperature readings were taken with a handheld infrared temperature gun (Raytek Corporation, Santa Cruz, CA).

Lizards were captured by noose or by hand. Upon capture, the following variables were recorded: location, time of capture, body temperature, detection method, substrate used when first observed, temperature of substrate used where first observed, lighting condition where first observed, and detection distance when first observed. Detection distance was recorded to determine any differences between management and habitat types. Lizard body temperatures were taken with a cloacal thermometer (Miller and Weber Inc, Richmond, VA) within 30 s of capture.

Each lizard was given 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. All spatial data and line transects were measured using a handheld GPS device (Garmin Etrex Legend). Lizards were released at the site of capture.

Sampling effort within stand interiors

In early June 2012, preliminary data were collected from the interior of three SPS stands to estimate the needed sampling effort per stand. However, no lizards were observed in any SPS interior. Therefore, the longest diagonal transects were walked within five SPS stands; these five stands spanned the total range of area of SPS stands across the ONF. The average area covered during these transects was approximately 4.6% of the total area of the stand interior. This figure (4.6%) was used to standardize the area sampled within stand interiors.

The area of sampled stand interiors varied considerably in both SPS (range: 114,529 m^2 to 799,948 m^2), and LLP (range: 103,223 m^2 to 3,400,955 m^2). Yet, sampled stands of SPS and LLP did not significantly differ in total interior area (Fig. 2; $F = 0.9$, $p = 0.65$). Across the entire ONF, however, there was a significantly larger area of biennially burned LLP stands than SPS stands that met the management criteria for this study (Figs. 3-4; $F = 29.2$, $p < 0.0001$). Sampled stands of LLP were either discrete stands or portions of a larger stand surrounded by a natural surface road.

Line transects were used to sample lizard density in each stand interior. Total area sampled in each line-transect was calculated as a 3-m sampling width. Transects were spaced at least 25 m apart and traversed the longest distance of each stand to maximize any variation within the stand (Fig. 1). In smaller stands, at least two shorter transects (still comprising 4.6% of total interior area) were sampled to avoid sampling a single interior transect.

Sampling effort for natural surface roads

In order to compare lizard density between road and interior habitats, 100% of the area of associated road habitat was sampled. Sampling 100% of the area of stand interiors would have been logistically impossible. Roads, however, occupied significantly less area than stand interior habitat ($F = 6.3$, $p = 0.03$). Hence, 100% of the area of road habitat could be sampled rapidly. Encounter rates (lizards observed per minute sampled) were also recorded along roads and within stand interiors.

Vegetation and substrate sampling

To assess the microhabitat conditions within each stand, vegetation and substrate characteristics were recorded. Point samples were taken at 2-m increments along line transects. For each point sample, the substrate type (open sand (OS), pine litter (PL), leaf litter (LL), mixed litter (ML), coarse 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 (area void of aboveground vegetation regardless of substrate type)) were recorded. A 2.5m pole was marked at 0.5-m increments to the vegetation height, vegetation patch width, and substrate patch width.

Line transects were chosen at random within the interior of each stand. To maximize variation in microhabitat characteristics, transects were divided into four 50 meter transects. The total transect length (200m) was chosen after preliminary sampling determined this asymptotic value closely approximated where each vegetation and substrate category leveled off (n = 3 stands of SPS and LLP).

Statistical Analyses

Lizard density data were analyzed using a split-plot ANOVA with management type as the main plot, habitat type as the subplot, and sampled stand as the random effect. Correlation analyses and non-parametric alternatives (Spearman's Rank tests) were used to examine relationships between lizard abundance within stands and microhabitat characteristics as well as with total stand area. One–way ANOVAs, matched pair tests and non-parametric alternatives (Mann-Whitney U-test, Wilcoxon signed rank test) were used to compare encounter rate, detection distance, microhabitat conditions, and total area between management and habitat types.

RESULTS

Do management and habitat types affect lizard density?

Lizard density was significantly higher in LLP than in SPS (Fig. 5A-B; $F = 10.2$, $p = 0.01$). All LLP stand interiors and roads were occupied by scrub lizards. However, 70% of SPS stand interiors, 30% of SPS roads were devoid of lizards; when combining road and interior habitats, 30% of all SPS sites surveyed were devoid of lizards.

Lizard density was significantly higher along road habitat than within stand interior habitat (Fig. 5C-D; $F = 31.3$, $p < 0.0001$). There was a significant interaction between management and habitat type ($F = 7.41$, $p = 0.01$). There was no significant effect due to sampled stand ($F = 1.12$, $p = 0.42$).

Encounter rate & detection distance

Encounter rates were significantly higher along roads than within stand interiors in both LLP (Fig. 6A; $t = 3.74$, $p = 0.01$) and SPS (Fig. 6B; $S = -13$, $p = 0.03$). Detection distance of lizards did not differ between all management and habitat comparisons. There were no significant differences in detection distance between LLP and SPS stands ($Z = 1.08$, $p = 0.28$) or between the roads surrounding LLP and the roads surrounding SPS ($Z = 0.1$, $p = 0.92$). There were also no differences in detection distance between the interior of LLP and the roads surrounding LLP ($Z = 0.94$, $p = 0.35$), or between the interior of SPS and the roads surrounding SPS ($Z = 1.3$, $p = 0.19$).

Lizard captures by substrate type

Lizard microhabitat use differed between management and habitat types (Fig. 7). In LLP, lizards used trees (37%) and litter (37%) more than open sand (23%) or downed wood (3%). In SPS, lizards used litter (50%) and open sand (33%) more than downed wood (9%), trees (4%), or other vegetation (4%). Within stand interiors (SPS + LLP), lizards used trees (48%) and litter (27%) more than open sand (20%), downed wood (4%), or other vegetation (0.8%). Along roads (SPS + LLP), lizard used litter (45%), and open sand (27%) more than trees (24%), downed wood (4%) or other vegetation (0.4%).

Microhabitat conditions

Sand pine-scrub had significantly more open sand (Fig. 8A; $F = 45.8$, $p < 0.0001$), coarse woody debris (Fig. 8A), oaks (Fig. 8B; $F = 168.8$, $p < 0.0001$), and open ground (Fig. 8D; $Z = 2.7$, $p < 0.006$). Longleaf pine had significantly more litter (Fig. 8A; $Z = -3.7$, $p < 0.0002$), turkey oaks (Fig. 8B; $Z = -3.1$, $p = 0.01$) and wiregrass (Fig. 8D).

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 ($r = 0.78$, $p = 0.01$) and negatively correlated with litter ($r = -0.78$, $p = 0.01$). The abundance of lizards found within SPS 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 (Spearman's = 0.68, $p = 0.03$). The abundance of lizards found within SPS stands was not correlated with the total area of SPS interior (Spearman's = -0.07, $p = 0.85$).

DISCUSSION

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

Scrub lizard abundance is known to be 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 than SPS. 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). Yet, lizard abundance within LLP stands was positively correlated with open sand and negatively correlated with litter. This suggests that lizards within LLP still use, or even depend on, terrestrial open sand habitats, despite the lower relative proportions of open sand in LLP.

The importance of litter in LLP is reflected in scrub lizard microhabitat use. In LLP, litter and trees were used more than any other substrates, while in SPS, litter and open sand were the most used substrates (Fig. 7A). These results are similar to Williams (2010) in that scrub lizards favor trees and understory debris (litter + downed wood) in LLP (Fig. 7). Hence, *S. woodi* has different microhabitat preferences between SPS and LLP.

In LLP, trees may allow lizards to avoid wiregrass, which dominates the LLP understory (40%; Table 2; Wells 1928; Wells & Shunk 1931) and is absent from SPS. Wiregrass is a poor refuge from thermal extremes and predators (Burrow et. al. 2001; Green 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 SPS (Williams, 2010). Litter and downed wood represented the warmest substrates in LLP (Williams, 2010). Hence, scrub lizards may selectively use litter and trees for thermoregulation during different parts of the day (Adolph 1990; Adolph & Porter 1993, 1996; Smith & Ballinger 2001). However, further comprehensive studies are needed to compare differences in microclimate and microhabitat use between SPS and LLP.

Despite lower lizard density, SPS may still harbor high density of scrub lizards if managed in proximity to other occupied stands of managed SPS or LLP. A small (approx. 147,000 m^2) SPS stand was sampled using the same protocols described above in May 2013. This stand is located along a road with a history of sequential SPS clearcutting and rollerchopping management and has high connectivity with neighboring SPS stands. Many of these neighboring stands have historically yielded high lizard abundances over the past ten years (R.A. Anderson, unpublished data). Fourteen lizards were observed within this stand's interior, which is the highest density of any SPS stand surveyed in this study. Therefore, while there is likely a limiting threshold for suitable intrinsic microhabitat conditions in both SPS and LLP, population connectivity among managed stands is likely a better predictor of Florida scrub lizard density (Hokit et al. 2001; Fabry 2007) than microhabitat conditions alone.

Because scrub lizards can occupy the conditions present in both SPS and LLP management types, larger spatial and/or temporal differences between management types may explain the higher lizard density in LLP (Fabry 2007). Longleaf pine management in the ONF is currently on a biennial burning cycle. This cycle reduces the possibility for litter buildup and succession that results in cluttered understory. Instead, an open habitat is steadily maintained (K. Bronson pers. comm.). Conversely, SPS stands are typically clearcut once and then allowed to undergo natural succession, without any subsequent management for 30-40 years (Greenberg et al. 1994). Often within five years after clearcutting and rollerchopping, regeneration of sand pines and the extensive shrubs and other understory has almost completely covered the once plentiful patches of open sand (McBrayer pers. comm.; Tiebout and Anderson 1997, 2001). The current SPS management schedule limits the available time for dispersing lizards to locate, colonize, and proliferate in the open sand microhabitat of SPS. Whereas, in LLP, once a suitable stand is located and colonized, the higher frequency fire disturbance maintains the suitable microhabitat conditions needed for populations to increase in size and persist (Fabry 2007).

Longleaf pine management also results in larger patch size and higher connectivity of managed stands. Large stands of LLP are often separated into sections and managed by alternating the burning year of adjacent sections (Fig. 4; sections burned in 2008, 2010, 2012 (gray), versus those burned 2009, 2011, and 2013 (black)). Given the biennial burning schedule, portions of larger LLP stands are burned every year, which maintains or increases total LLP patch area. More importantly, doing so also increases the connectivity of adjacent LLP stands. This differs considerably from the current SPS management regime which results in smaller, more isolated stands of SPS.

Patch size and isolation are accurate predictors of scrub lizard patch occupancy (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 SPS stands (Hokit and Branch 2003), as well as increasing genetic diversity (Branch et al. 1999; Clark et al. 1999). *S. woodi* genetic differentiation is higher among fragmented patches of suitable habitat (Clark et al. 1999; Branch et al. 2003; Hokit et al. 2010) and lower in highly connected habitat (Heath et al. 2012). Therefore, patch area and isolation are key factors that influence the genetic diversity and extinction probability for *S. woodi* (Hokit and Branch, 2003; Fabry 2007).

This study supports earlier hypotheses that scrub lizards use ONF natural surface roads extensively (Anderson pers. comm.; McBrayer pers. comm; Greenberg et al. 1994; Anderson and Tiebout 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 species like *S.woodi*, roads increase connectivity between suitable habitat patches and food resources (Huey 1941; Getz et al. 1978; Forman et al. 2003; Fabry 2007), albeit the current high degree isolation of many ONF stands make actual dispersal events highly unlikely if not impossible. The microhabitat of natural surface roads with low traffic volume provides *S.woodi* and other xeric-adapted species with additional permanent habitat (Anderson and Tiebout 2001) and/or dispersal corridors (Greenberg et al. 1994; Brehme et al. 2013).

Additional research should investigate both the use of natural surface roads by *S. woodi* as well as any differential use of SPS and LLP stands. Studies should attempt to elucidate the role that ONF roads play in lizard habitat use, as well as the underlying mechanism of scrub lizard dispersal. Also with many low-use natural surface roads being decommissioned across the ONF (K. Bronson, pers.comm.), the effects of road habitat removal on scrub lizard habitat use should be investigated. Differences in demography between SPS and LLP could determine if population growth rates, recruitment, and persistence is indeed higher in LLP. Finally, future research should be devoted to the fire management of SPS. Managing SPS more similarly to LLP via biennial burning of selected stands should result in larger area of suitable habitat, and greater connectivity among suitable patches for scrub lizard populations.

Management Suggestions and Conclusions

This study shows that stands of managed LLP and natural surface roads are more important to the ONF scrub lizard metapopulation than previously appreciated. Also, previous assumptions about the importance of open sand habitat within clearcut and rollerchopped stands of SPS may be misleading, unless applied in the broader context of landscape scale metapopulation dynamics.

Due to the higher connectivity and frequency of local disturbance (Fabry 2007), LLP stands tend to have dense populations of scrub lizards, whereas SPS stands do not. As such, LLP stands are likely to serve as extinction-resistant source populations. Long leaf pine stands could permit dispersal to neighboring SPS sinks, which will deterministically become extinct (Pulliam 1988; Pulliam and Danielson 1991) within five years 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 SPS. However this hypothesis is untestable. Conversely, the current management regimen may be creating more suitable and/or more connected habitat in LLP, while SPS management is not doing so. This hypothesis could be tested by clustering managed SPS stands in a particular spatial (≤ 750 meters) and temporal (≤ 5 yrs. post-disturbance) pattern. Such management should increase dispersal, interpatch 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). Thus, the ideal relationship between SPS, LLP, and natural surface roads should follow a composite of "habitat-tracking" and "source-sink" metapopulation dynamics.

Due to its restricted range, habitat specialization, and low vagility, it is not suprising that S. woodi in an imperiled species. However, given the species need for frequent disturbance and the current variety of ONF landscape management practices, the ONF provides a unique opportunity for the objectives of conservationists and land managers to align.

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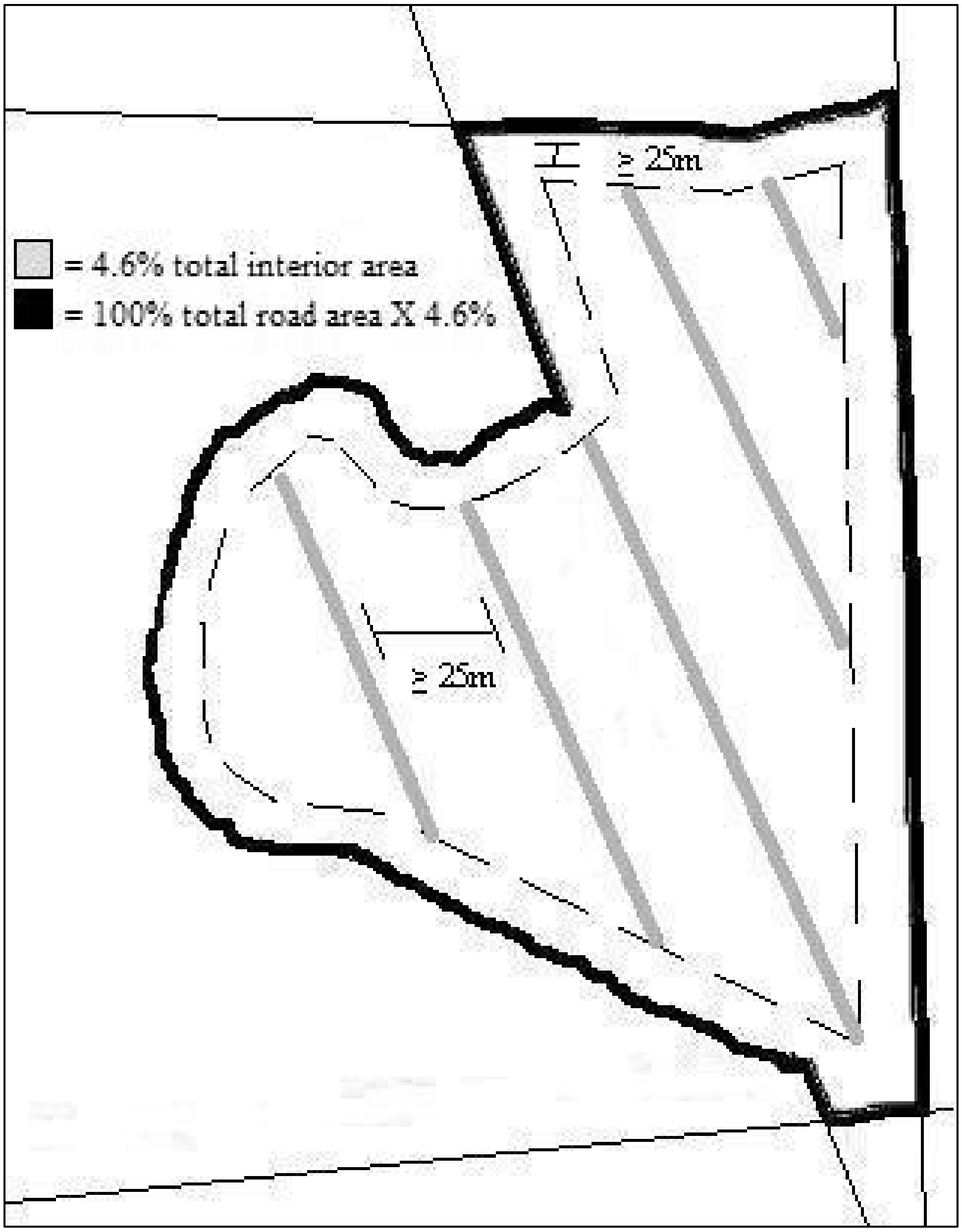

Figure 1. Model of sampling methods and calculations for stand interior and associated roads. **Interior-**Line transects were used to sample 4.6% of the total area of stand interiors (gray). Line transects were separated by 25 meters. **Roads-**100% of the area of associated road habitat was sampled. A 25 meter buffer zone separated interior samples from road samples.

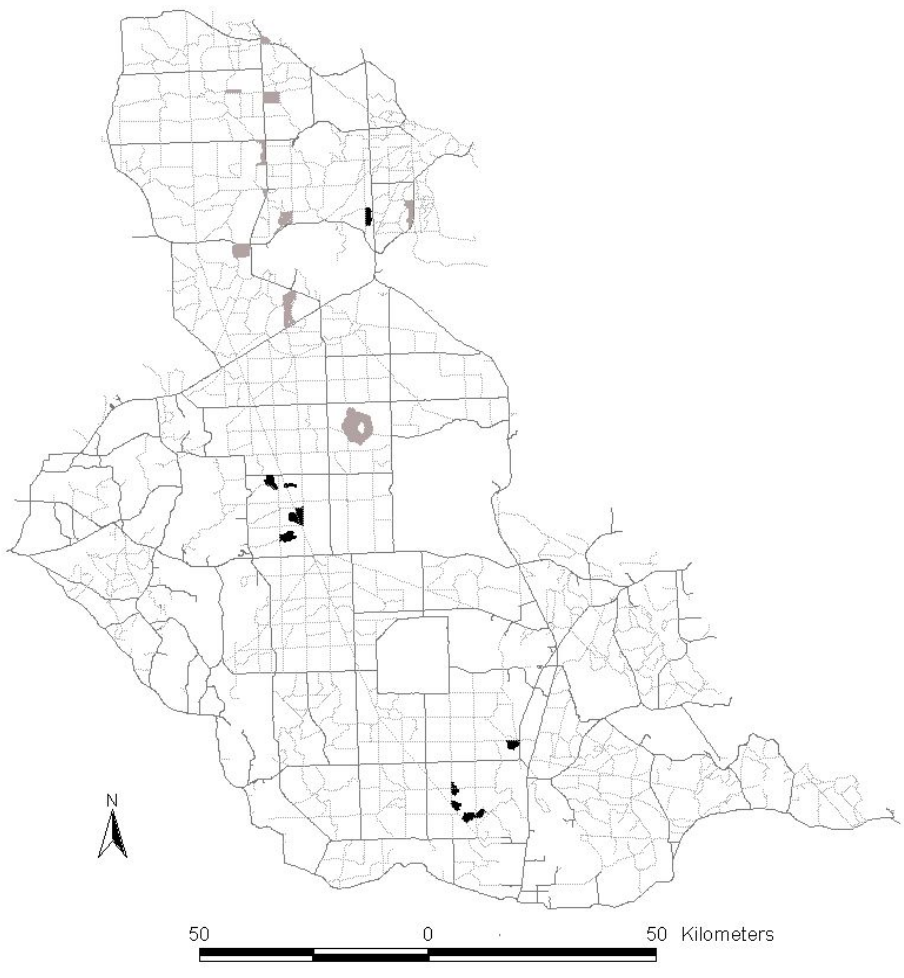

Figure 2. Map of sampled SPS (black) and LLP (gray) stands. The total area of the selected SPS and LLP stands did not significantly differ (One-way ANOVA; $p = 0.65$).

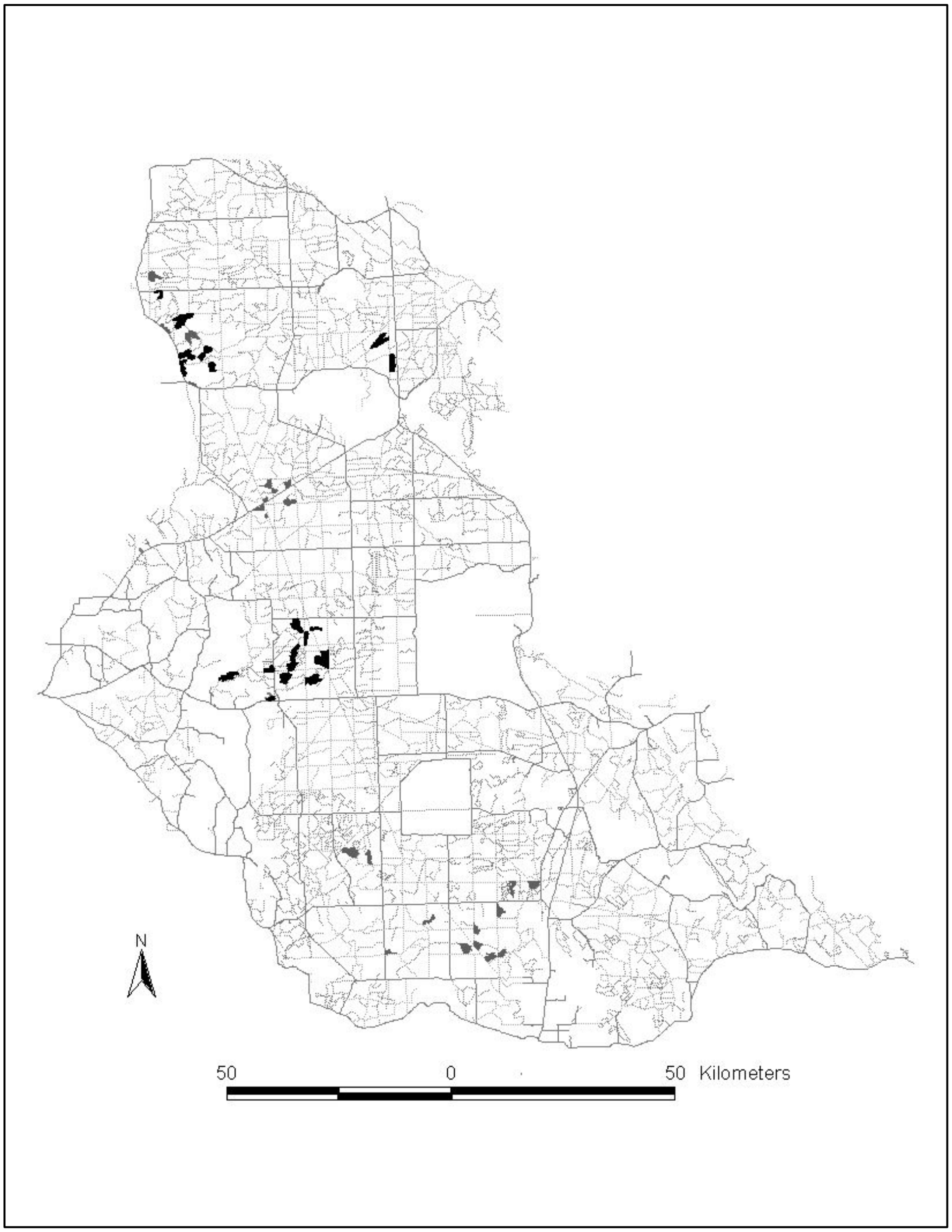

Figure 3. Map of all 2009 (gray) & 2010 (black) clearcut and rollerchopped SPS stands present across the ONF. 26% of available stands meeting the management criteria were sampled. Total area of 2009 and 2010 clearcut and rollerchopped SPS is significantly less than area of biennially burned LLP (One-way ANOVA; p-value < 0.0001).

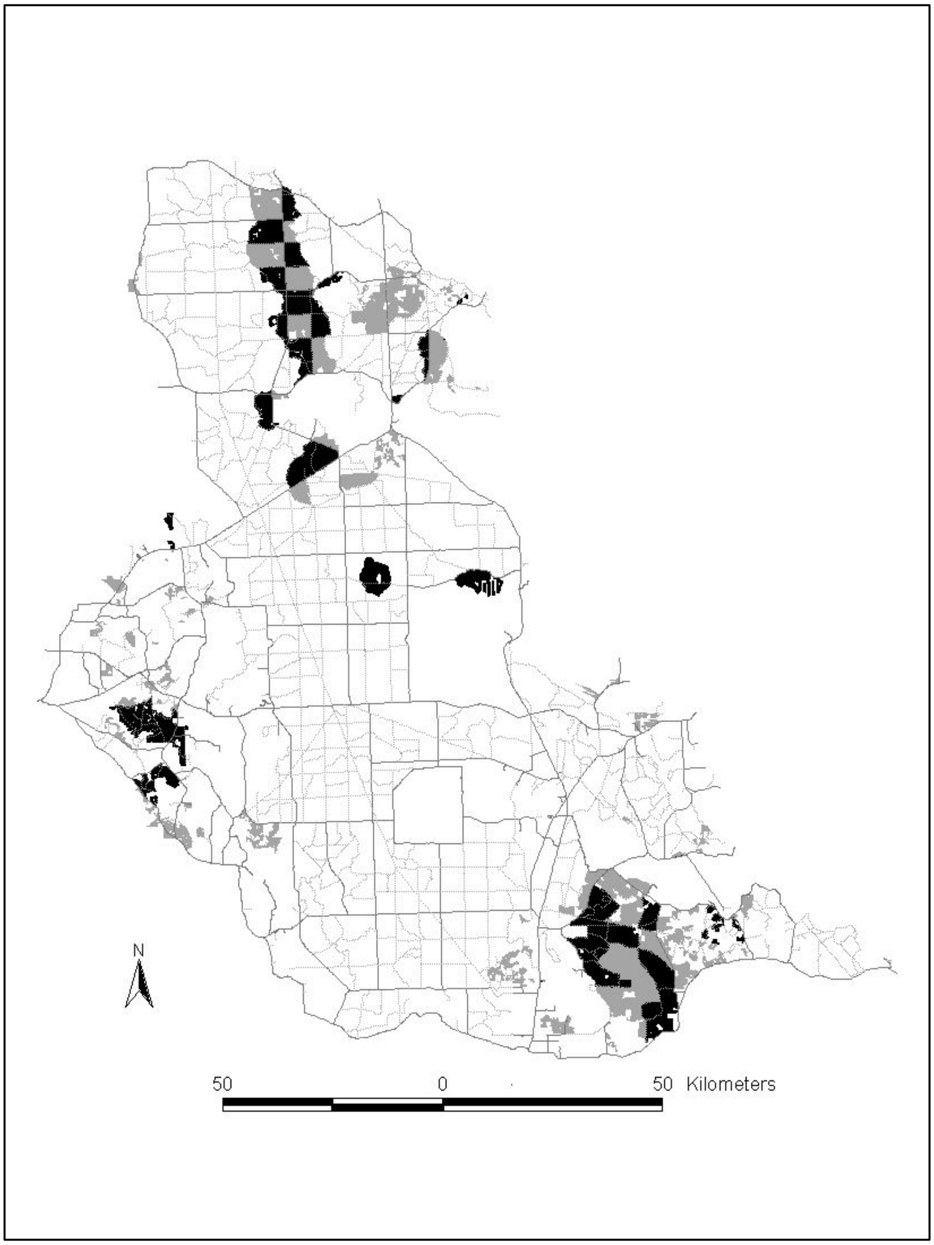

Figure 4. Map of all biennially burned LLP stands across the ONF. Black stands are burned in 2009, 2011, 2013, etc. Gray stands are burned in 2008, 2010, 2012, etc. Total area of biennially burned LLP is significantly higher than area of 2009 and 2010 clearcut and rollerchopped SPS (One-way ANOVA; p-value < 0.0001).

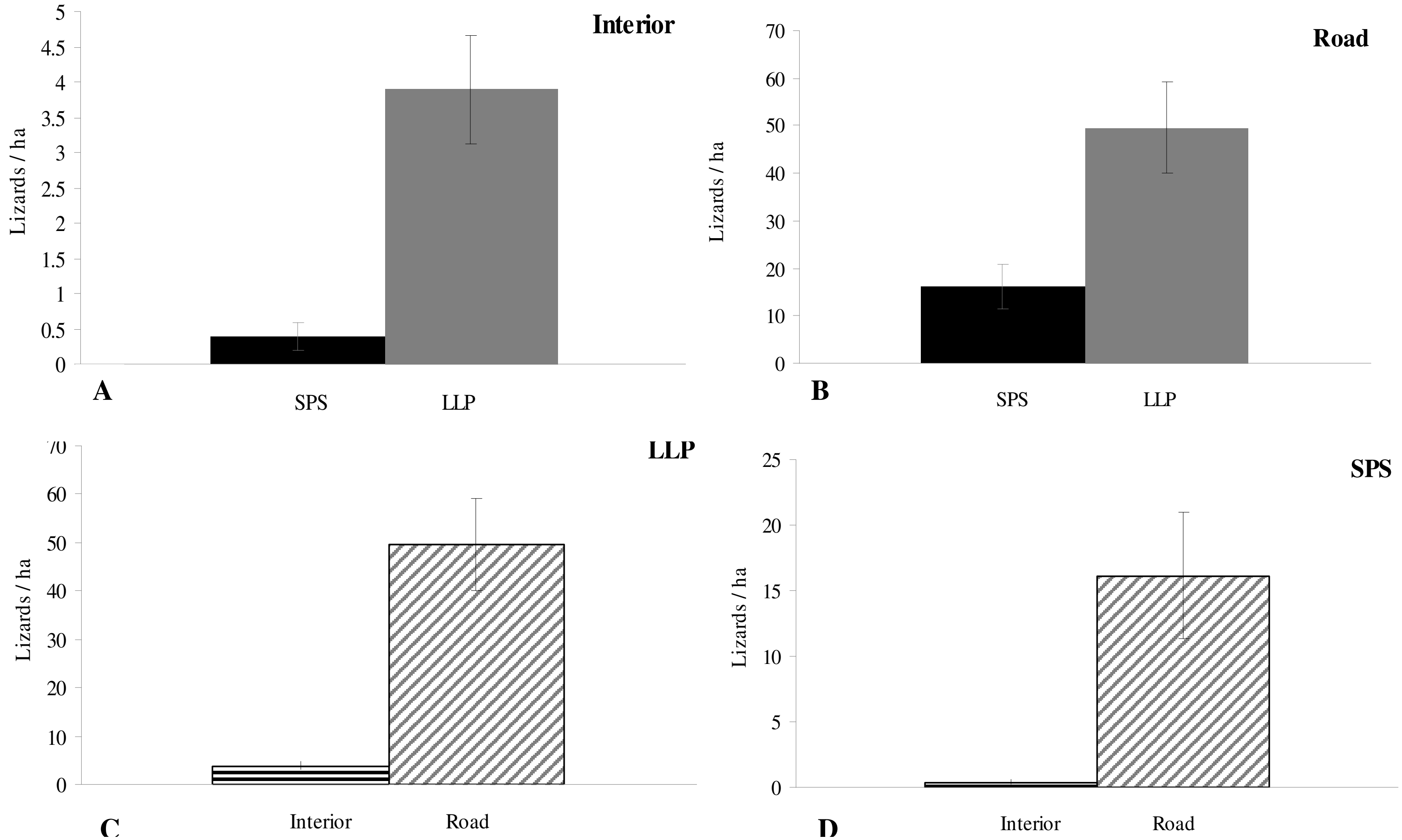

Figure 5. Lizard densities ± 1 S.E. Scrub lizard densities were significantly higher in LLP than SPS both (A) within stand interiors and (B) along roads. In both (C) LLP and (D) SPS, lizard densities were significantly higher along roads than stand interiors.

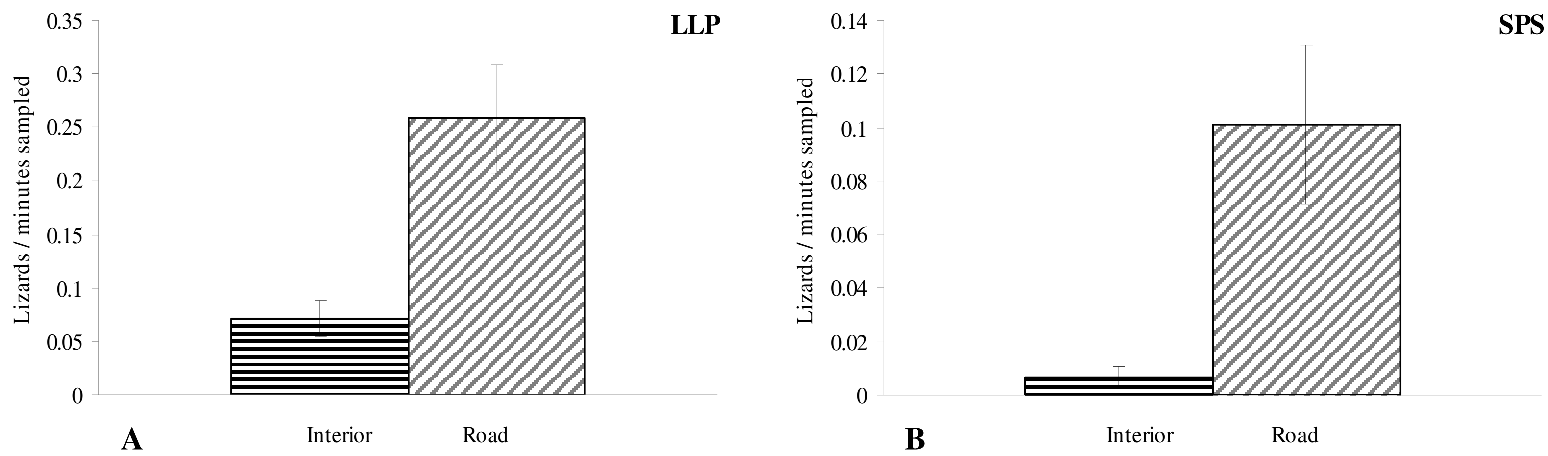

Figure 6. Encounter rates ± 1 S.E. In both (A) LLP and (B) SPS, encounter rates (lizards observed per minute sampled) were significantly higher along roads than within stand interiors.

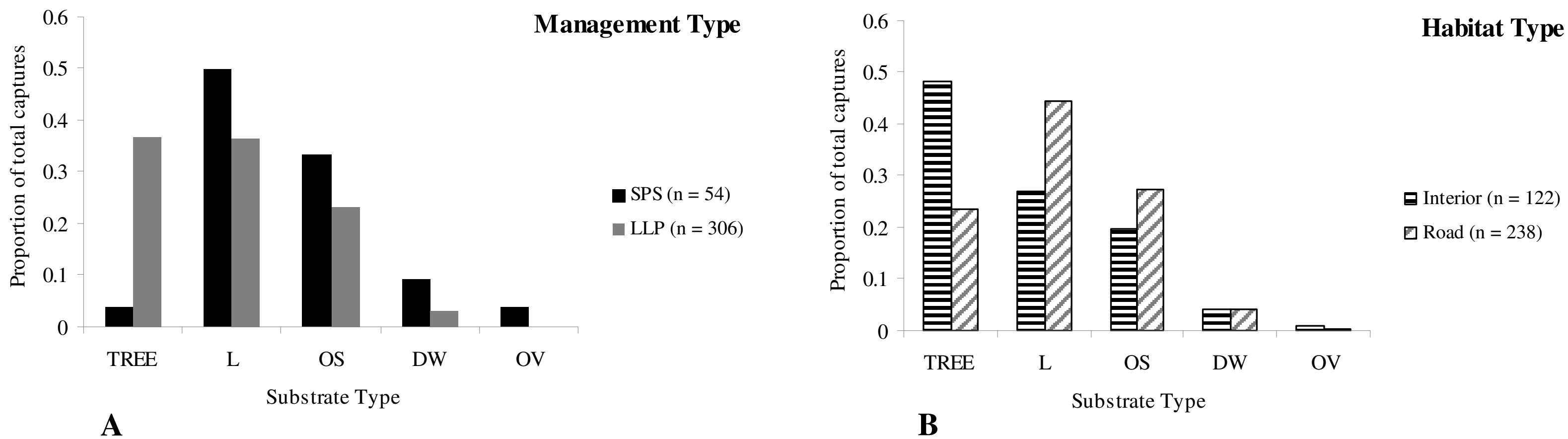

Figure 7. Lizard captures by substrate type. Scrub lizard substrate use by (A) management type and (B) habitat type. (L = litter, OS = open sand, DW = dead wood (i.e. coarse woody debris,

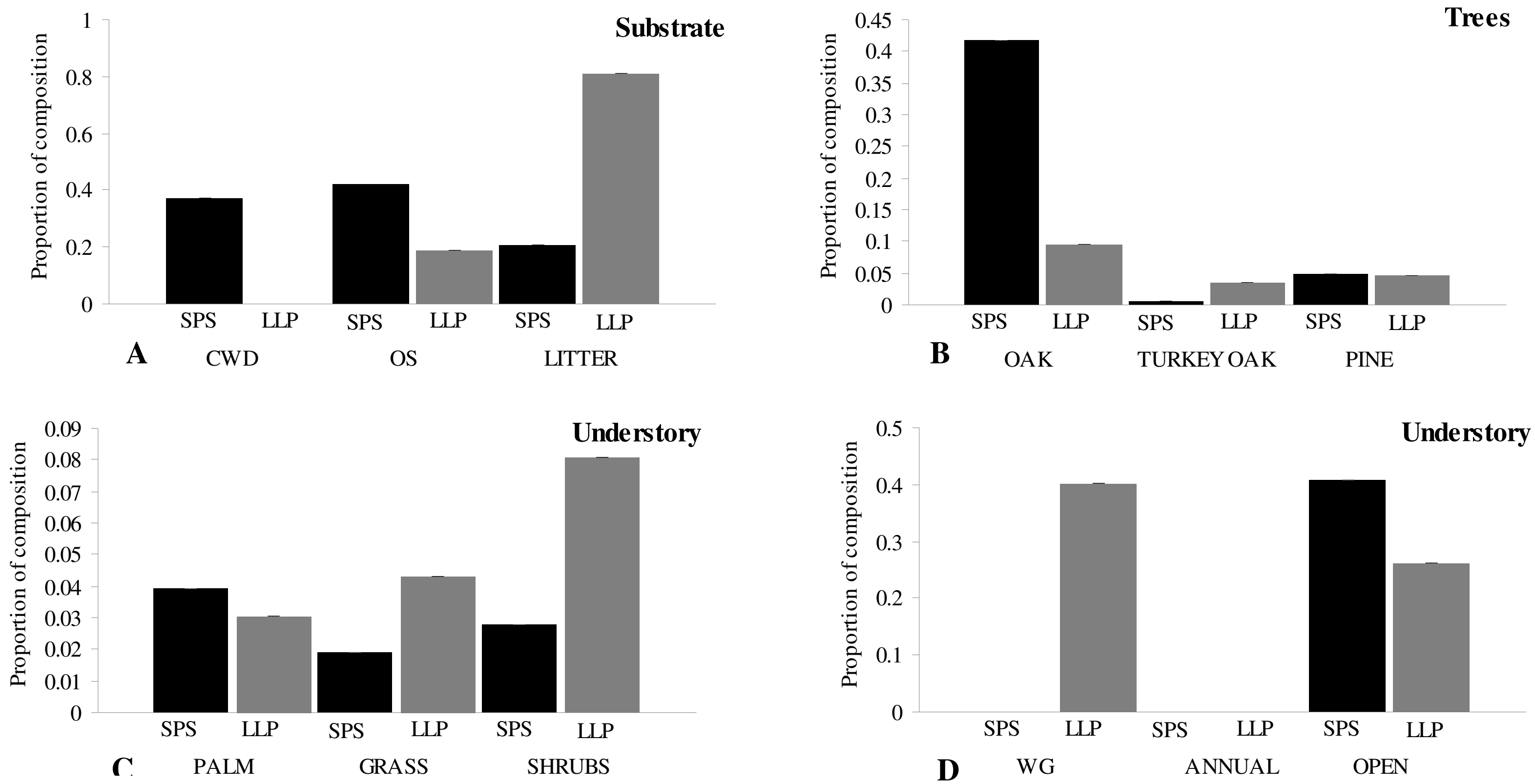

Figure 8. Vegetation and substrate composition ± 1 S.E. Management types differed significantly in terms of coarse woody debris, open sand, litter, oaks, turkey oaks, and openness. (CWD = coarse woody debris, OS = open sand, PALM = palmetto, WG = wiregrass, Open = no aboveground vegetation).

APPENDIX A

Table 1.) Means +S.E units. Means sharing the same underline did not significantly differ between habitat types. Means denoted with different letters significantly differed between management types.

	SPS (n = 54 lizards)		**LLP (n = 305 lizards)**	
	Interior (4.6% area)	**Road (100% area)**	**Interior (4.6% area)**	**Road (100% area)**
Area sampled (m^2)	15535.11 ± 2736.02	2864.63 ± 298.32	39267.9 ± 13744.96	4055.55 ± 749.27
Density (liz / ha)	0.39 ± 0.2 (a)	16.15 ± 4.77 (a)	3.89 ± 0.78 (b)	49.5 ± 9.53 (b)
Encounter rate (liz / min)	0.007 ± 0.004	0.10 ± 0.03 (a)	0.07 ± 0.016	0.26 ± 0.05 (b)
Detection distance (m)	2.76 ± 0.33	2.12 ± 0.17	2.28 ± 0.13	2.12 ± 0.09

APPENDIX B

Table 2. Longleaf pine vegetation and substrate composition. Proportions of line transects composed of different substrate and vegetation categories. (CWD=coarse woody debris, OS= open sand, Open= no aboveground vegetation).

LLP		Substrate			Vegetation								
Stand	Abundance	CWD	OS	Litter	Oaks	Turkey Oaks	Pines	Palmettos	Grasses	Shrubs	Wiregrass	Annuals	Open
LLP-1	1	0.00	0.15	0.85	0.06	0.01	0.05	0.12	0.00	0.34	0.39	0.00	0.04
LLP-2	9	0.00	0.14	0.86	0.07	0.02	0.04	0.10	0.08	0.12	0.41	0.00	0.17
LLP-3	14	0.00	0.18	0.82	0.04	0.00	0.06	0.01	0.02	0.00	0.67	0.00	0.20
LLP-4	1	0.00	0.12	0.88	0.13	0.03	0.07	0.04	0.07	0.04	0.40	0.00	0.22
LLP-5	29	0.00	0.38	0.63	0.15	0.06	0.05	0.01	0.13	0.06	0.32	0.00	0.23
LLP-6	3	0.00	0.15	0.85	0.11	0.04	0.04	0.01	0.05	0.09	0.44	0.00	0.23
LLP-7	7	0.00	0.21	0.79	0.01	0.07	0.05	0.01	0.03	0.14	0.44	0.00	0.25
LLP-8	29	0.00	0.23	0.77	0.11	0.04	0.05	0.01	0.02	0.03	0.42	0.00	0.33
LLP-9	14	0.00	0.16	0.84	0.08	0.07	0.03	0.01	0.04	0.00	0.38	0.00	0.39
LLP-10	11	0.00	0.17	0.83	0.22	0.03	0.05	0.00	0.01	0.00	0.13	0.01	0.55
	Mean	0.00	0.19	0.81	0.10	0.04	0.05	0.03	0.04	0.08	0.40	0.00	0.26
	S.E	0.00	0.02	0.02	0.02	0.01	0.00	0.01	0.01	0.03	0.04	0.00	0.04

APPENDIX C

Table 2. Sand-pine scrub vegetation and substrate composition. Proportions of line transects composed of different substrate and vegetation categories. (CWD=coarse woody debris, OS= open sand, Open= no aboveground vegetation).

SPS		**Substrate**			**Vegetation**								
Site	**Abundance**	**CWD**	**OS**	**Litter**	**Oaks**	**Turkey Oaks**	**Pines**	**Palmettos**	**Grasses**	**Shrubs**	**Wiregrass**	**Annuals**	**Open**
SPS-1	0	0.51	0.31	0.17	0.49	0.02	0.02	0.08	0.02	0.00	0.00	0.00	0.38
SPS-2	0	0.25	0.43	0.32	0.43	0.00	0.07	0.06	0.02	0.01	0.00	0.00	0.40
SPS-3	0	0.44	0.56	0.00	0.34	0.00	0.10	0.13	0.02	0.02	0.00	0.00	0.39
SPS-4	0	0.35	0.41	0.24	0.39	0.00	0.08	0.01	0.03	0.01	0.00	0.00	0.39
SPS-5	2	0.37	0.40	0.23	0.44	0.01	0.02	0.02	0.02	0.04	0.00	0.00	0.44
SPS-6	0	0.27	0.51	0.22	0.37	0.00	0.08	0.01	0.01	0.03	0.00	0.00	0.39
SPS-7	2	0.35	0.45	0.20	0.39	0.01	0.04	0.02	0.02	0.03	0.00	0.00	0.46
SPS-8	0	0.47	0.31	0.22	0.46	0.00	0.02	0.03	0.03	0.05	0.00	0.00	0.41
SPS-9	1	0.33	0.38	0.30	0.47	0.00	0.04	0.03	0.01	0.03	0.00	0.00	0.34
SPS-10	0	0.38	0.44	0.18	0.39	0.01	0.03	0.02	0.02	0.07	0.00	0.00	0.46
	Mean	0.37	0.42	0.21	0.42	0.00	0.05	0.04	0.02	0.03	0.00	0.00	0.41
	S.E	0.03	0.02	0.03	0.01	0.00	0.01	0.01	0.00	0.01	0.00	0.00	0.01