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Verge Characteristics Along Unpaved Roads are not Correlated with Presence of Two Early Successional Lizard Species

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***Abstract*.—Small ectotherms such as lizards often use road corridors in forested habitats. Unpaved roads, characterized by natural soils and low traffic, are hypothesized to provide connectivity between suitable early successional habitat and unsuitable dense mature forest patches for small ectotherms. We quantified the effects of six combinations of road-adjacent vegetation and disturbance history on the occurrence and encounter frequency of the Florida Scrub Lizard and Six-lined Racerunner along unpaved roads in Ocala National Forest (Florida, USA). We also compared microhabitat characteristics in the road adjacent landscape among these habitat combinations and correlated these values to occurrence and encounter frequency of these lizards. Occurrence and encounter frequency of both species showed little variation among road adjacent habitats. Microhabitat conditions were also very similar among road adjacent habitat combinations. Occurrence and encounter frequency of the Florida Scrub Lizard was associated with a greater availability of shade, whereas occurrence and encounter frequency of the Six-lined Racerunner were associated with warmer substrates. Our data show that unpaved roads create equal opportunity for use as alternative habitat for early successional lizards regardless of vegetation structure or management history in the road adjacent landscape. Consequently, maintenance of unpaved roads may contribute to the viability of these populations in Ocala National Forest.**

Key Words.—alternative habitat; Florida scrub; Florida Scrub Lizard; lizards; Ocala National Forest; Six-lined Racerunner; unpaved roads

Introduction

As humans encroach on natural landscapes, unpaved roads have become an increasing vector of habitat modification that can precipitate changes in the biology of local species (reviewed in Rytwinski and Fahrig 2012). Roads facilitate edge effects on the immediately adjacent habitat, defined as the verge, that alter many abiotic habitat conditions (e.g., light penetration, wind movement, and humidity; Delgado et al. 2007b; Pohlman 2007; Hamberg et al. 2010). Edge effects along the verge and the creation new microhabitat conditions along the road surface can generate alternative habitat (Ries et al. 2001; Brock and Kelt 2004; Vasconcelos et al. 2006; Delgado et al. 2007a; Kaunert and McBrayer 2015) and facilitate dispersal (Bennett 1990; Brown et al. 2006) for a variety of taxonomic groups. Edge-tolerant organisms, such as the Giant Ameiva (*Ameiva ameiva*), are speculated to occur in areas that were previously considered inhospitable when unpaved roads were present (Sartorius et al. 1999), although unpaved roads can prove detrimental to some species. The Eastern Massasauga Rattlesnake (*Sistrurus catenatus*) is averse to crossing unpaved roads (Paterson et al. 2019) and may become locally isolated as a consequence of the construction of these features. Understanding how different species react to unpaved roads may help land managers construct or maintain these features in a way that maximizes management or conservation goals.

National forests in the U.S. contain thousands of kilometers of temporary and permanent unpaved roads that serve recreation and land management practices including access to recreational trails, as well as mining, logging, and application of prescribed fire (Waugh 1918). Inherent differences in vegetation structure resulting from altered land management practices may confer different effects of unpaved roads on the surrounding habitats (Chen et al. 1999). The Ocala National Forest (Florida, USA) has two predominant upland habitat types, Sand Pine Scrub (SPS) and Longleaf Pine Sandhill (LLP) that fall under different management regimes. Sand Pine Scrub is managed via clear-cut logging on an approximately 40-y cycle, whereas the majority of LLP is typically burned on a 3–5 y interval to help conserve ecologically sensitive species (https://

www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd1077276.pdf). This allows SPS to be further separated into early successional (ESS) and mature scrub (MS) habitat. The canopy of SPS is comprised primarily of Ocala Sand Pine (*Pinus clausa* var *clausa*), with a dense understory of regenerating oak shrubs (*Quercus* spp.) and palmettos (*Serenoa* spp.; Jackson 1972; Greenberg et al. 1994; Greenberg 2003; Florida Natural Areas Inventory [FNAI] 2010). Notable differences between ESS and MS include reduced availability of bare ground and increased availability of litter and vegetation including Sand Pine and other under- and midstory plants (Greenberg et al. 1994). The LLP canopy is comprised primarily of well-spaced Longleaf Pine (*Pinus palustris*), an open midstory and understory including Turkey Oaks (*Quercus laevis*), and Wiregrass (*Aristida stricta*) as groundcover (Wells and Shunk 1931; Jackson 1972; FNAI 2010). Differences in the vegetation community and management regiment between SPS and LLP result in altered abiotic environmental characteristics for small vertebrates such as lizards, including thermal opportunity (Neel and McBrayer 2018) and substrate structure (Kaunert and McBrayer 2015).

In the Ocala National Forest, SPS and LLP harbor two lizard species that use unpaved roads, the Florida Scrub Lizard (*Sceleporus woodi*) and the Six-lined Racerunner (*Aspidoscelis sexlineata*). The Six-lined Racerunner occurs throughout the eastern and central U.S. (Powell et al. 2016), whereas the Florida Scrub Lizard is mostly restricted to central Florida and is currently under review for federal protection (Jackson 1973; Enge et al. 2021). Both species are associated with habitat characteristics generated by recent disturbance (e.g., bare ground and sporadic vegetation for cover and shade; Mushinsky 1985; Hokit et al. 1999; McCoy et al. 2004; Ashton and Knipps 2011), and become isolated when surrounded by long undisturbed habitat (Heath et al. 2012; Ragsdale et al. 2016; Miller et al. 2023). The Six-lined Racerunner, however, can tolerate a wider array of environmental characteristics (Clark 1976; Mushinsky 1985) and is more capable of dispersing, especially through less suitable habitat (Schrey et al. 2011; Lyn Branch et al., unpubl. report). Both species can persist in long-undisturbed habitats, provided they contain suitable availability of bare ground interspersed within vegetation (Menges and Hawkes 1998; McCoy et al. 2012, 2013). The density of each species is greatly diminished in the interior of MS, which contains minimal bare ground (Greenberg et al. 1994). The lack of vegetation and debris on unpaved road surfaces paired with cover provided by road adjacent vegetation, however, may mimic the early successional conditions that these species prefer (Enge et al. 2021).

The Florida Scrub Lizard occurs more frequently along unpaved roads than adjacent stand interiors in ESS and LLP (Kaunert and McBrayer 2015). Enge et al. (2021) encountered the Florida Scrub Lizard along unpaved roads in long undisturbed habitats but did not survey in Ocala National Forest. Additionally, no studies have explored the effects of unpaved roads on the Six-lined Racerunner. It is also still unclear whether occurrence and abundance of these two species along unpaved roads bordered by long undisturbed habitat is similar to those bordered by recently disturbed habitat. Finally, it is unknown how occurrence and abundance of these two species are affected by all possible combinations of the main verge types in Ocala National Forest (ESS, MS, and LLP).

We quantified whether verge habitat is related to the occurrence and encounter frequency of the Florida Scrub Lizard and the Six-lined Racerunner along unpaved roads bordered by all possible combinations of ESS, MS, and LLP in Ocala National Forest. We also investigated how temperature and substrate characteristics along unpaved roads are affected by verge type. Finally, we tested these microhabitat characteristics for relationships with the encounter frequency and occurrence of each species. We tested two competing hypotheses concerning how encounter frequency and occurrence of both lizard species are affected by verge type.

One hypothesis is that unpaved roads do not significantly modify the adjacent habitat and that lizard encounter frequency and occurrence across verge combinations reflect historical habitat associations. Based on this hypothesis, we predict that lizards will show greater encounter frequency and occurrence along unpaved roads when verges are comprised more of early successional habitat (ESS and LLP). Our alternative hypothesis is that unpaved roads do significantly modify the adjacent habitat and there will be uniform road edge effects and the removal of vegetation and debris consistently creates the favored microhabitat characteristics of the species. Based on this hypothesis, we predict that lizard encounter frequency and occurrence across verge combinations will be uniform.

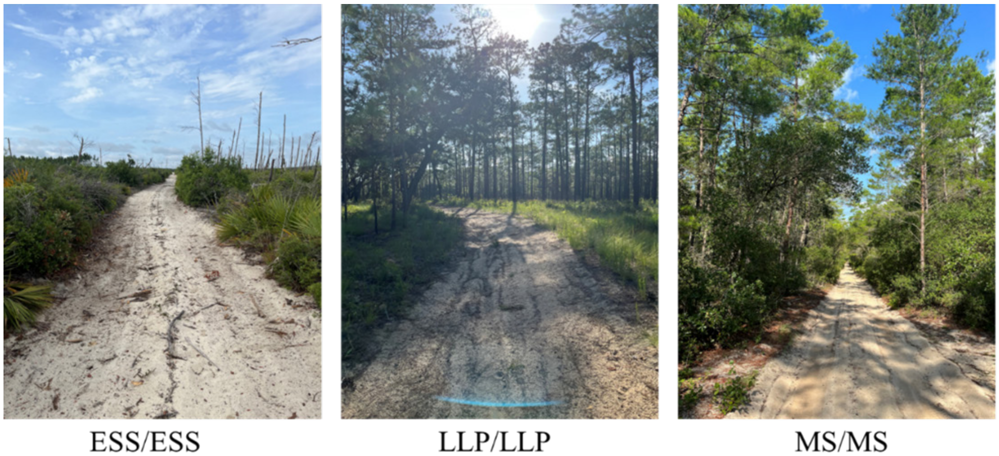

Figure 1. Photographs of roads bordered on both sides by three dominant habitats of the Florida Scrub Lizard (*Sceloporus woodi*) and the Six-lined Racerunner (*Aspidoscelis sexlineata*) in the Ocala National Forest, Florida, USA. Verge habitats (LLP = Longleaf Pine, ESS = early successional scrub, MS = mature scrub) are shown for either side of the road.

Materials and Methods

Study site.—Formed from Pliocene and Pleistocene era sea level changes, the Ocala National Forest (Florida, USA) is situated atop the Mount Dora Sand Ridge and represents one of the largest contiguous patches of the globally imperiled Florida scrub ecosystem (Myers 1990; U.S. Fish and Wildlife Service 1999; Whitney et al. 2004; FNAI 2010). Much of the remaining Florida scrub is managed as small preserves (Christman and Judd 1990), however. The Ocala National Forest contains the largest remaining contiguous patch of Florda scrub (FNAI 2010) and, consequently, represents one of the last remaining strongholds of habitat for many endemic species. The forest contains several scrub communities, but SPS is the most prevalent (https://www.fs.usda.gov/detail/ocala/landmanagement/?cid=STELPRDB5190567). The forest also contains several large stands of LLP sandhill that exist as habitat islands amid the surrounding scrub. Average minimum and maximum daily temperatures range from 20° to 32° C for April-October and 11° to 23° C from November to March. Rainfall is highly variable, but averages about 1,300mm/y, with much of the rainfall occurring June-September (Aydelott 1966; Brooks 1972, as cited in Kalisz and Stone 1984). Elevations in the forest range from 2–49 m above sea level (Aydelott 1966; Brooks 1972, as cited in Kalisz and Stone 1984).

Commercial logging has replaced fire as the dominant form of disturbance in Ocala National Forest scrub patches but stands of LLP are maintained by prescribed fire, typically on a 3–5 y interval (https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd1077276.pdf). Logging practices, coupled with extensive firebreaks and off-road vehicle trails, result in the creation of many permanent and temporary sand roads to transport goods and machinery. This includes a grid (about 256-ha [640-ac] cell size) of low use unpaved roads throughout the majority of the forest. The U.S. Forest Service also recognizes nearly 450 km of off-road vehicle trails in the forest (https://www.fs.usda.gov/recarea/florida/recarea/?recid=83528#:~:text=OHV%20Riding%20%26%20Camping&text=With%20nearly%20200%20miles%20of,top%20destination%20for%20off%2Droading), not including many kilometers of similar features such as unsanctioned trails and firebreaks. From 2020–2021, nearly 90 km of unpaved roads were serviced to act as fire breaks by either clearing with bulldozers or by discing (https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd1077276.pdf). Because nearly every forest stand is intersected or bordered by such roads (Kathy Bronson, pers. comm.) and they are so ubiquitous throughout the forest, any ecological effects imposed by these features may have large-scale implications.

Road selection.—We obtained management history of stands within the Ocala National Forest from the Seminole Ranger District office of the Ocala National Forest (Kathy Bronson, pers. comm.). We surveyed only single-lane forest management roads (e.g., those used to transport goods/machinery during logging) and off-highway vehicle roads (i.e., those used for dirt bikes, all-terrain vehicles, etc.) due to their similarity in width, substrate, and traffic volume (pers. obs.). We surveyed roads bordered by six verge type combinations based on the road adjacent habitat (henceforth verge habitat one/verge habitat two). The verge combinations are ESS/ESS, ESS/MS, LLP/ESS, MS/MS, LLP/LLP and LLP/MS (Fig. 1). We surveyed each verge combination at eight locations, except for LLP/ESS, which only existed in four locations. All location/verge type combinations were only surveyed one time. We suspect the low prevalence of LLP/ESS roads is due to the limited availability of LLP reducing the likelihood of an adjacent patch being recently logged. All surveys of the same verge combination took place in separate stands as delineated by U.S. Forest Service. We classified early successional SPS as stands ≤ 5 y post disturbance, and MS as ≥ 30 y post disturbance. We did not survey stands 6–29 y post disturbance. The Florida Scrub Lizard and Six-lined Racerunner experience the greatest difference in environmental pressures between recently and long-undisturbed habitats (Tevs et al. 2023b). By surveying only recent and long-undisturbed forest patches, we highlight the capacity for unpaved roads to facilitate lizard occurrence in areas with distinctly different adjacent habitats. We did not control for fire history in LLP because time since the last fire at surveyed sites ranged from 1–3 y (i.e., within the same time since disturbance range as ESS). Also, because LLP is limited in availability, attaining sufficient replication within fire history categories would be infeasible.

Visual encounter surveys.—We estimated lizard encounter frequency and occurrence using Visual Encounter Surveys (Kaunert and McBrayer 2015). We conducted surveys from 2 June to 13 August 2021 and again between 6 June to 7 July 2022. We sampled only during the summer because we expected the warmer temperatures to increase lizard activity and abundance (Paulissen 1988; Enge et al. 2021). We recorded sex and age structures only during 2022 surveys. Because sex and age data were limited, we did not include these data in analyses. Males of both species exhibit vibrant blue coloration along their ventral scales, allowing for rapid sex determination without the need for capture (Powell et al. 2016). We did not capture any lizards to confirm sex but have observed 100% accuracy with this method in other studies (unpubl. data). To avoid variation in encounter frequency and occurrence due to daily temperature fluctuations affecting lizard activity levels (Neel and McBrayer 2018), we conducted all surveys between 0830 and 1300 and with < 50% cloud cover. We conducted surveys with two observers walking in parallel along one of the two road edges in tandem for 10 min. To correct for variation in walking speed among surveys and calculate sampling effort more accurately, we also recorded coordinates for the starting and stopping points of the survey. We defined the start of the road edge as the point of contact where disturbed, bare sand from vehicle tires touches vegetation. We measured road width at the start of each survey as the distance between the two road edges. Each surveyor scanned for the Florida Scrub Lizard and the Six-lined Racerunner along the road as well as the respective verge to their left or right. We assumed any lizard that could be reliably identified from the road edge was using some aspect of the road and was counted in the survey. When we heard a lizard before visual observation, we stopped until that individual could be visually identified. If we could not identify that individual within 3 min of audible detection, we did not count it, and the survey was resumed.

Microhabitat sampling.—We collected microhabitat characteristics along each transect via five, 1-m^2 plots spaced equidistantly along each survey transect. Because these are small lizards (mean snout-vent length < 65 mm; Witz 2001; Tevs et al. 2023a), we concluded this plot size was adequate to represent variation in microhabitat conditions they would experience in their home ranges. We chose five plots per survey because this was the maximum number we could logistically perform given time constraints associated with this and other research we were conducting. Average transect length across all verge combinations was 630 m, resulting in an average distance of 158 m between plots. We placed plots randomly on either road edge and we extended each plot perpendicular to the road surface (randomly 1–10 m determined by a random number generator) towards the stand interior. Sampling within 1–10 m from the road edge encapsulated the smallest reported mean home range for either species (Florida Scrub Lizard: 400 m^2; Lyn Branch et al., unpubl. report). We used stratified random sampling to assign plots to each side of the road by flipping a coin five times and assigning heads or tails to either the left or right side of the road. If we assigned more than three plots to one side of the road, we re-flipped the coin for all five plots until this criterion was met. Within each plot, we estimated the proportion of full sun, dappled sun, and full shade at ground level, as well as the proportion of three substrate types: open sand, litter, and course woody debris. We also estimated the proportion of coverage by herbaceous and woody vegetation. We measured the surface temperature of each substrate/light combination (e.g., litter in full shade) using an infrared thermometer. We made all estimates from eye level of the same principal observer (DRT). We estimated vegetation proportions based on the horizontal area covered by foliage/stems. In instances where vegetation covered part of the plot but did not alter the availability of substrate (e.g., large, overhanging palmetto fronds), the proportion of vegetative cover did not detract from the substrate proportion. In such cases, we estimated the light availability at ground level under overhanging vegetation.

Statistical analysis.—We used the statistical software JMP (ver. 16) to perform all statistical analyses. Because road width and transect length may affect lizard encounter rates independently of verge characteristics, we first sought to determine if these characteristics were similar between verge combinations. We compared road width and transect length between verge combinations using Kruskal-Wallis tests. We then used two analytic approaches to compare occurrence and encounter frequency of the Florida Scrub Lizard and the Six-lined Racerunner along road verges. Because transect length but not road width varied among verge types, we first used Logistic Regression to verify transect length did not affect occurrence (i.e., presence/absence) of both species (see results below). We then tested whether occurrence of the Florida Scrub Lizard and the Six-lined Racerunner differed among verge combinations using G tests and adjusted α for the number of tests on each species/verge type combination (Bonferroni alpha = 0.01). Second, we tested for variation in encounter frequency of each species among verge types using Scheirer-Ray-Hare tests. Because transect length differed among verge combinations, we used transect length-corrected residuals of the number of encounters per species among verge types. We performed surveys along different verge combinations within the same forest stand, so we also included sampling location as a random effect in each Scheirer-Ray-Hare Test.

To test how microhabitat characteristics varied among verge types, we estimated the mean proportion of each substrate, light, and vegetation type, as well as mean substrate temperature contained in all five 1-m^2 sampling plots corresponding to a specific survey. We calculated substrate temperature as the weighted average of all substrate/light combinations based on the mean proportion of space each occupied in the plots belonging to each survey. We used Principal Components Analysis (PCA) to condense all microhabitat conditions estimated in the road adjacent habitat into axes that described major variation in each microhabitat condition among all verge combinations. We included the following microhabitat conditions in the PCA: (1) the proportion of open sand; (2) litter; (3) course woody debris; (4) full sun; (5) dappled sun; (6) full shade; (7) herbaceous vegetation; (8) woody vegetation; and (9) substrate temperature.

We used a series of Logistic Regressions and Spearman's Ranked Correlations to determine the relationship between microhabitat conditions and lizard occurrence and encounter frequency. We also used transect length-corrected residuals for the encounter frequency of each species in these Spearman's Ranked Correlations. Due to the number of tests, we corrected alpha for each series of Logistic Regressions and Spearman's Ranked Correlations using the Bonferroni correction (α = 0.006).

Results

Surveys resulted in 73 observations of the Six-lined Racerunner and 71 observations of the Florida Scrub Lizard (Table 1). Transect length (H = 12.21, df = 5, P = 0.032) but not road width (H = 3.561, df = 5, P = 0.614) differed among verge types. Transect length was not correlated with lizard occurrence (i.e., presence/absence along surveys; Florida Scrub Lizard: G = 0.73, df = 1, P = 0.392; transect length: X^2 = 0.71, P = 0.399; intercept: X^2 = 1.73, P = 0.188; Six-lined Racerunner: G = 2.67, df = 1, P = 0.102; transect length: X^2 = 2.33, P = 0.127; intercept: X^2 = 0.99, P = 0.319; Table 1). We detected differences in the percentage occurrence of the Florida Scrub Lizard between only two verge types (Fig. 2). The Florida Scrub Lizard occurred most frequently along MS/MS roads and least frequently along LLP/MS roads (G = 6.904, df = 1, P = 0.009), but we detected no difference in occurrence rates among all other verge combinations. Occurrence of the Six-lined Racerunner did not significantly vary among any verge combinations (Fig. 2). Encounter frequency of the Florida Scrub Lizard (verge type: H = 4.084, df = 5, P > 0.050; sampling location: H = 35.27, df = 35, P > 0.050) and the Six-lined Racerunner (verge type: H = 6.212, df = 5, P > 0.050; sampling location: H = 32.40, df = 35, P > 0.050) also did not differ between verge types (Fig. 3).

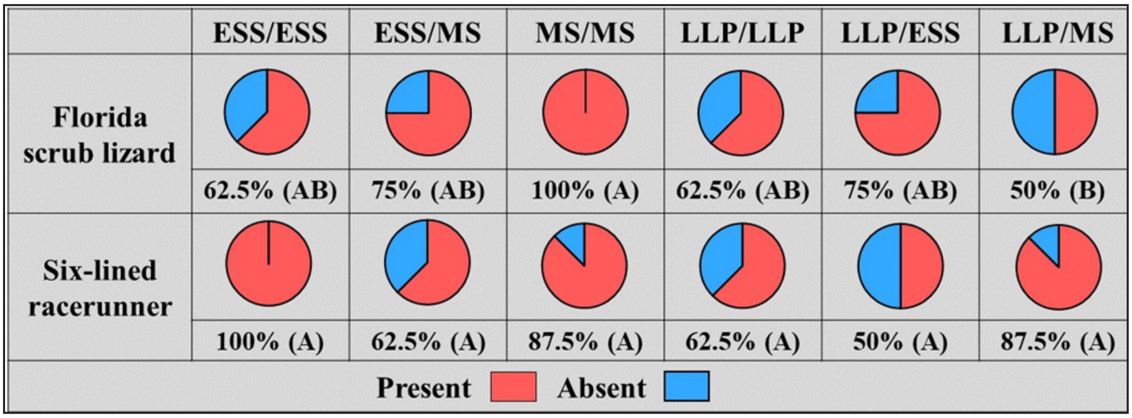

FIGURE 2. Pie charts representing the occurrence of the Florida Scrub Lizard (*Sceloporus woodi*) and the Six-lined Racerunner (*Aspidoscelis sexlineata*) among verge combinations (LLP = Longleaf Pine, ESS = early successional scrub, MS = mature scrub) on either side of a road. Red indicates the proportion of surveys on which we detected lizards. Blue indicates the proportion of surveys from which lizards were absent. Percentages correspond with the proportion of surveys within a particular verge combination where a species was present. Comparisons were only made within species across verge combinations. No comparisons were made between species within verge combinations. Shared letters (whether alone or paired) indicate no significant difference in occurrence of that species between verge combinations after Bonferroni correction.

Four PCA axes had eigenvalues > 1.0 that described variation in microhabitat among all verge types (Table 2). Principal Component (PC)1 had a gradient of increasing woody vegetation and shade and a decreasing availability of sun. PC2 had increasing substrate temperature and decreasing availability of open sand and course woody debris. PC3 had a gradient of increasing substrate temperature and availability of sand, and a decreasing availability of herbaceous vegetation, and PC4 had increasing herbaceous vegetation and decreasing availability of dappled sun. Density ellipses representing 95% confidence intervals for each verge combination (Fig. 4) show large areas of overlap along the first two principal components for all verge combinations, however, these areas of overlap appear greater for verges combinations comprised of multiple habitat types.

We detected several correlations between microhabitat conditions and lizard encounter frequency and occurrence. The number of Florida Scrub Lizard encounters was positively correlated with shade ($\rho = 0.448$, $P = 0.002$) and litter ($\rho = -0.420$, $P = 0.005$), and negatively correlated with full sun ($\rho = 0.412$, $P = 0.005$). The Florida Scrub Lizard was also more likely to occur along surveys with a greater availability of shade ($G = 10.942$, df = 1, $P = 0.001$; proportion shade: $X^2 = 7.56$, $P = 0.006$; intercept: $X^2 = 3.47$, $P = 0.062$) and a lower availability of full sun ($G = 7.683$, df = 1, $P = 0.006$, proportion full sun: $X^2 = 6.02$, $P = 0.014$; intercept: $X^2 = 8.99$, P = 0.003). The number of Six-lined Racerunner encounters was

TABLE 1. Summary of survey characteristics and encounters across verge types of the Florida Scrub Lizard (*Sceloporus woodi*) and the Six-lined Racerunner (*Aspidoscelis sexlineata*) in the Ocala National Forest, Florida, USA. Road width and survey length columns display mean ± standard deviation. Total column for each species shows the combined number of observations of that species for both 2021 and 2022. Sex and age distributions of each species were only available for 2022 data. Verge habitats (LLP = Longleaf Pine, ESS = early successional scrub, MS = mature scrub) are listed for either side of the road. Abbreviations are RW = road width, SL = survey length, M = male, F = female, J = juvenile, and U = adult of unknown sex.

Verge type	Number of Surveys		RW (m)	SL (m)	Florida Scrub Lizard		Six-lined Racerunner	
	2021	2022			Total (2021-2022)	M-F-J-U (2022)	Total (2021-2022)	M-F-J-U (2022)
ESS/ESS	3	5	2.74 ± 0.27	602.13 ± 42.95	12	5-2-0-3	16	7-1-1-3
LLP/LLP	4	4	2.67 ± 0.28	627.88 ± 97.06	13	1-1-0-1	10	2-1-0-3
MS/MS	3	5	2.53 ± 0.32	674.88 ± 60.92	18	3-3-0-2	9	4-0-0-1
ESS/MS	6	2	2.79 ± 0.45	527.88 ± 128.83	15	0-1-0-0	10	0-1-0-2
LLP/ESS	3	1	2.80 ± 0.32	599.25 ± 87.94	5	0-0-0-0	9	0-0-0-0
LLP/MS	4	4	2.69 ± 0.38	734.38 ± 178.78	8	0-1-0-0	19	4-4-0-1

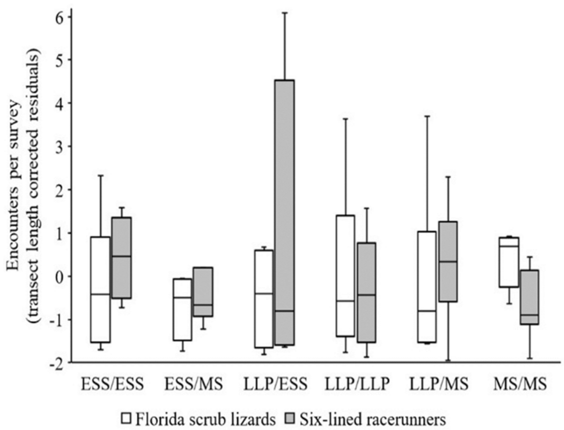

Figure 3. Encounter frequency (mean encounters/survey) of the Florida Scrub Lizard (*Sceloporus woodi*) and the Six-lined Racerunner (*Aspidoscelis sexlineata)* across verge combinations (LLP = Longleaf Pine, ESS = early successional scrub, MS = mature scrub) along roads in Ocala National Forest, Florida, USA. Boxes display inter-quartile range, central lines represent median values, and whiskers display the range of values. No significant differences were detected between any comparisons.

positively correlated with substrate temperature (ρ = 0.428, P = 0.004) and occurrence was more likely in areas with warmer substrates (G = 9.52, df = 1, P = 0.002; substrate temperature: X^2 = 6.50, P = 0.011; intercept: X^2 = 4.83, P = 0.028). We failed to detect correlations among all other microhabitat variables and encounter frequency or occurrence of either species.

Discussion

Results support our hypothesis that road edge effects and the removal of vegetation and debris consistently creates the favored microhabitat characteristics of the Florida Scrub Lizard and Six-lined Racerunner. Occurrence and encounter frequency of both species were uncorrelated with verge type. We also observed little variation in the distribution of different microhabitat characteristics among verge types. This suggests that edge effects resulting from unpaved roads may homogenize substrate and vegetation structure (Greenberg et al. 1994; Greenberg 2003; Kaunert and McBrayer 2015) and thermal characteristics (Neel and McBrayer 2018) that are suggested to differ between ESS, MS, and LLP interiors. Similar results have been described in relation to urbanization of multiple habitat types, where consistency in development practices homogenize abiotic characteristics that differ prior to urbanization (Reviewed in Groffman et al. 2014).

Near equal occurrence and encounter frequency of the Florida Scrub Lizard among verge combinations suggests unpaved roads allow this species to occur in MS, which was historically considered unsuitable for this species (Greenberg et al. 1994). Historical associations between the Florida Scrub Lizard and early successional habitat characteristics (Greenberg et al. 1994; Hokit et al. 1999; Tiebout and Anderson 2001), suggest this species would occur more frequently and in higher abundance along roads bordered by ESS or LLP. Yet, the Florida Scrub Lizard was present along all MS/MS surveys and was equally abundant across all verge combinations. Roads with MS/MS verges were most strongly delineated from other verge combinations based on increasing availability of shade, and Florida Scrub Lizard encounter frequency and occurrence were also both associated with a greater availability of shade. These patterns align with previous accounts of the Florida Scrub Lizard selecting shaded sand over other substrate/light combinations (Tiebout and

Table 2. Mean ± standard deviation of microhabitat characteristics across verge combinations (LLP = Longleaf Pine, ESS = early successional scrub, MS = mature scrub) in Ocala National Forest, Florida, USA. Except for substrate temperature, all values represent the proportion of space occupied in 1 m^2 plots.

Microhabitat characteristic	Verge type					
	ESS/ESS	LLP/LLP	MS/MS	ESS/MS	LLP/ESS	LLP/MS
Open Sand	37.50 ±18.76	4.63 ± 3.96	2.75 ± 6.61	18.57 ± 11.47	27.25 ± 17.40	9.33 ± 13.81
Litter	56.55 ± 21.07	68.33 ± 11.92	84.75 ± 15.19	62.71 ± 14.66	51.25 ± 25.67	73.18 ± 16.63
Course woody debris	2.95 ± 2.06	0.50 ± 1.07	3.50 ± 2.62	4.29 ± 2.21	9.50 ± 6.86	3.13 ± 3.44
Full sun	41.45 ± 24.75	53.83 ± 19.61	14.08 ± 15.34	36.38 ± 8.47	49.15 ± 16.86	43.08 ± 20.93
Dappled sun	9.70 ± 5.53	15.70 ± 9.31	23.95 ± 8.66	18.88 ± 6.51	18.15 ± 6.19	13.03 ± 6.64
Full shade	48.83 ± 23.80	29.95 ± 17.23	61.83 ± 15.56	45.25 ± 12.16	32.65 ± 20.13	42.63 ± 19.72
Herbaceous vegetation	12.85 ± 10.28	29.88 ± 12.29	17.73 ± 15.13	14.80 ± 7.62	28.25 ± 12.80	25.68 ± 16.28
Woody vegetation	44.58 ± 17.19	11.10 ± 8.03	47.38 ± 22.61	38.03 ± 12.69	9.65 ± 12.24	29.40 ± 14.01
Substrate (°C)	36.33 ± 5.45	35.94 ± 5.06	32.77 ± 5.56	32.05 ± 5.60	30.15 ± 6.46	36.99 ± 5.75

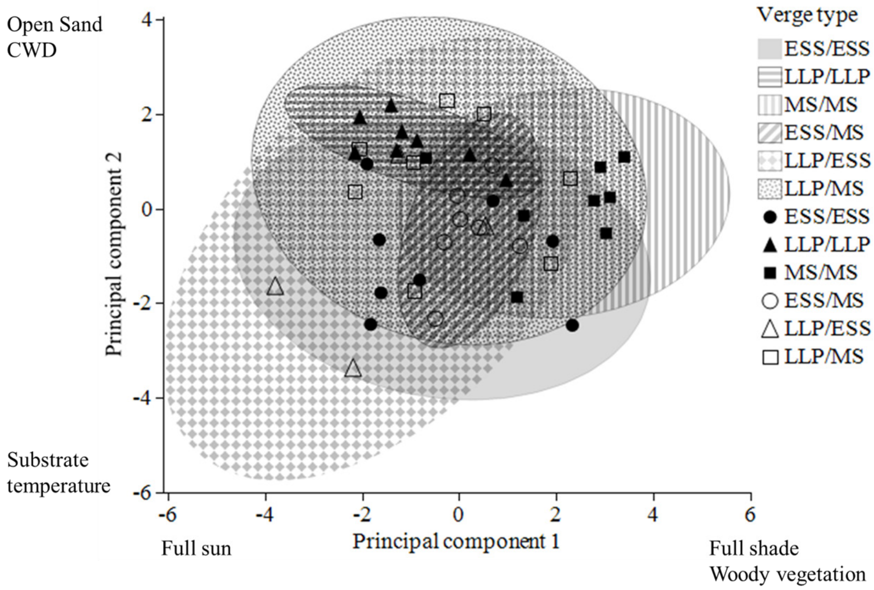

FIGURE 4. Plot of the first two principal components on microhabitat characteristics among all verge combinations (LLP = Longleaf Pine, ESS = early successional scrub, MS = mature scrub) for either side of a road. Density ellipses represent 95% confidence intervals for each verge type. Primary positive and negative loadings for principal components one and two are included at ends of each axis. Except for substrate temperature, each loading represents the proportion of space occupied in one-meter square plots.

Anderson 2001). While MS/MS verges harbored intermediate amounts of sand, road surfaces are typically comprised entirely of sand (pers. obs.). Consequently, we suggest current road maintenance practices that remove vegetation and debris from the road surface (i.e., bulldozing and discing) are sufficient to allow the Florida Scrub Lizard to occur in MS.

The Six-lined Racerunner also had equal occurrence and encounter frequency among verge combinations; however, this result was less surprising, as that for the Florida Scrub Lizard. Because the Six-lined Racerunner can persist in and disperse through a wider array of habitats (Carpenter 1959; Clark et al. 1999; Schrey et al. 2011), we suspect it requires a lower magnitude of habitat modification to occur in MS. We note the presence of a positive correlation between Six-lined Racerunner encounter frequency and substrate temperature and an increased likelihood of occurrence in areas with warmer substrates. The Six-lined Racerunner is more active at warmer temperatures (Paulissen 1988); thus, we expect these patterns are more indicative of periods increased activity and detectability. Yet, given reports of lower Six-lined Racerunner density in MS (Greenberg et al. 1994), we propose that unpaved roads in these habitats provide suitable habitat for the Six-lined Racerunner and the Florida Scrub Lizard.

We acknowledge that not accounting for detection probability between verge combinations may confound interpretations of these results. We think these data are valid, however, for several reasons. First, we detected much overlap in abiotic conditions among verge types. This suggests variation in detection probability attributable to such conditions (e.g., vegetation density and temperature; Ruiz de Infante Anton et al. 2013; Falaschi 2021) is minimal. Additionally, we suspect the little variation we did observe in abiotic conditions would reduce detection probability along MS/MS roads. For example, these areas are more densely vegetated than other verge combinations, which may obstruct the view of lizards by surveyors (Ruiz de Infante Anton et al. 2013). We also suspect the correlation between activity and temperature would reduce Six-lined Racerunner detectability in MS (Falaschi 2021), which had intermediate temperatures and high shade. Consequently, encounter rates along MS/MS roads may be disproportionately underestimated compared to other verge combinations. This strengthens our confidence in our interpretation that MS/MS roads harbor a similar number of lizards as other verge combinations, if not more.

Many studies have speculated that unpaved roads bisecting stands of mature forest may act as dispersal corridors for the Florida Scrub Lizard and the Six-lined Racerunner (Greenberg et al. 1994; Tiebout and Anderson 1997; Tucker et al. 2014; Kaunert and McBrayer 2015; Orton et al. 2020). The Florida Scrub Lizard exhibits population structure among localities separated by several hundred meters of MS (Clark et al. 1999; Heath et al. 2012; Miller et al. 2023), suggesting unpaved roads could be of critical importance for this species in the fragmented landscape of Ocala National Forest. We suspect MS/MS roads could enhance connectivity of the Florida Scrub Lizard because MS/MS roads allow individuals to directly move between patches of early successional habitat and these roads allow small populations to persist in the landscape between patches of early successional habitat and act as so-called stepping-stones for gene flow to connect large populations. Similar patterns of stepping-stone connectivity have been observed in a variety of systems, including corals (Miller and Gunasekera 2017), birds (Saura et al. 2014), and mollusks (Crandall et al. 2012). Thus, we propose a similar phenomenon may take place among populations of the Florida Scrub Lizard connected by MS/MS roads in the Ocala National Forest.

While unpaved roads appear to be suitable for the Florida Scrub Lizard and the Six-lined Racerunner, the value of these features for other wildlife is variable both inside and outside the Ocala National Forest. In the Ocala National Forest, the Gopher Frog (*Lithobates capito*) uses unpaved roads in LLP as movement corridors during seasonal breeding migrations (Roznik and Johnson 2009). Unpaved road edges, however, may also facilitate persistence of non-native grass species within the forest (Gordon et al. 2005). Also in the Ocala National Forest, Black Bears (*Ursus americanus*) experience increased vehicle collision rates along paved roads at points of intersection with unpaved roads (McCown et al. 2004), likely due to using unpaved roads as movement corridors that inevitably cross paved roads. Dirt roads at the Roy Shipley Multi-Species Reserve in California, USA, facilitate movement of the endangered Stephen's Kangaroo Rat (*Dipodomys stephensi*), suggesting these features may provide critical dispersal corridors for this species throughout the landscape, although this study also showed that gravel roads may prove detrimental to dispersal of this species (Brock and Kelt 2004). This variation in the benefits and risks of unpaved roads highlights the importance of multi-species and multi-habitat studies examining the effect these features have on local wildlife.

Understanding how other road characteristics (e.g., road width and orientation) affect the presence of these species in MS may help land managers better plan unpaved roads in a way that satisfies both management and conservation goals. Gap size (here, road width) and orientation to the sun can influence how edge effects manifest in the surrounding environment (Pohlman et al. 2007; Laurence et al. 2009). We took care to ensure road widths were consistent across verge combinations but were unable to test for effects of road orientation due to low replication. Future studies may seek to understand what conditions are necessary to allow these species to occupy MS and to verify that lizards are less abundant in MS interiors compared to MS/MS roads. For example, hiking trails and fallen trees may create sufficient gaps in MS to allow lizards to occur. Also, larger, two-lane unpaved roads may affect the likelihood of occurrence or encounter frequency of lizards. Future studies may also seek to understand whether individuals occurring along MS/MS roads are dispersing through these habitats, or are using these roads as residents and persist in the middle of MS. *Sceloporus* lizards typically display male biased dispersal (Massot et al. 2003; Gifford et al. 2017) and the Florida Scrub Lizard has very small dispersal distances (up to about 500 m, but often < 200 m; Hokit et al. 1999; Enge et al. 2023). Yet our limited data show equal numbers of males and females along MS/MS, which may suggest these adults are resident individuals. More extensive sampling is needed to affirm this idea, particularly later in the season when juvenile lizards may be more prevalent.

In conclusion, unpaved roads provide suitable habitat for populations of the Florida Scrub Lizard and Six-lined Racerunner regardless of the habitat type bordering the verge. We demonstrated that unpaved roads bisecting stands of MS offer viable habitat, despite the previous view that unhospitable conditions within MS negatively affect the density of these species (Greenberg et al. 1994). These results indicate that unpaved roads homogenize landscape features necessary for lizard occurrence, likely by offsetting the lower quality habitat imposed by MS for these and possible other species. Consistent maintenance of the habitat features unpaved roads provide in MS likely improves the connectivity of populations inhabiting ESS and thus enhance their viability in the Ocala National Forest.

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Appendix Table. Principal component loadings and eigenvalues corresponding to the proportion of each microhabitat characteristic among all verge combinations along roads in the Ocala National Forest, Florida, USA. Bold values represent the primary loadings for each component.

Microhabitat characteristic	PC1	PC2	PC3	PC4
Open Sand	-0.24703	**-0.48237**	**0.43993**	0.09505
Litter	0.37076	0.37607	-0.07122	-0.21591
CWD	-0.17097	**-0.42901**	-0.29085	-0.3978
Full sun	**-0.51841**	0.19872	0.12798	-0.15745
Dappled sun	0.28192	0.22894	0.05148	**-0.50656**
Full shade	**0.44491**	-0.30432	-0.16248	0.37424
Herbaceous vegetation	-0.18515	0.21184	**-0.54025**	**0.49781**
Woody vegetation	**0.42116**	-0.15866	0.39483	0.14188
Substrate temperature	-0.12021	**0.43276**	**0.47287**	0.31099
Eigenvalue	3.0691	2.0108	1.3766	1.0104
Percent	34.101	22.342	15.295	11.227
Cumulative percentage	34.101	56.443	71.738	82.965

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