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RESEARCH ARTICLE

Fire and Herpetofaunal Diversity in the Florida Scrub Ecosystem

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ABSTRACT: The Florida Scrub ecosystem depends on fire to sustain ecosystem function and to support resident plant and animal species. A recent study addressed the relationship between the time since last fire (TSF) and resident amphibians and reptiles in rosemary bald, one Florida Scrub habitat type. This is a parallel study in another Florida Scrub habitat type, scrubby flatwoods, at Archbold Biological Station (ABS), Lake Placid, Florida, USA. We installed 36 400-m^2 enclosures (four burn units within each of three TSF categories X 3 replicates per burn unit) at ABS. Bucket trap sampling, within and outside the enclosures, occurred during the spring and late summer in 2007 and 2008. Ten environmental variables that reflect differences in the biotic and abiotic conditions of the microhabitats associated with different TSF were surveyed. Eleven species of reptiles and six species of amphibians were captured. Three lizard species together accounted for > 95% of the reptile captures, and two toad species together accounted for > 96% of the amphibian captures. Abundance of the Florida Sand Skink (*Plestiodon reynoldsi* Stejneger) was highest in long-unburned areas, probably because of the accumulated litter; but abundances of the other two lizard species did not show a relationship with TSF. Differences in relative abundances of species between sampling years may be a function of the difference in rainfall. Despite substantial variation in sampling methods between this study and the previous one, the herpetofaunal composition of the two habitat types were found to be similar; differences in diversity between them was attributable mostly to differences in relative abundances. Species inhabiting the Florida Scrub ecosystem respond differently to TSF: the federally-listed Florida Scrub Jay (*Aphelocoma coerulescens* Bosc), for example, requires more frequent burning than appears to be the case for the Florida Sand Skink. A land management plan of stochastic return intervals and spatial variation of high-intensity fires to maintain a mosaic landscape would be ideal; but management options for maintaining the diversity of all species inhabiting the Florida scrub ecosystem are limited, because of the generally small size of remaining habitat patches.

Index terms: bucket trap sampling, enclosures, fire return interval, Florida Scrub ecosystem, herpetofaunal diversity

INTRODUCTION

Pyrogenic ecosystems, such as the Australian Mallee, Mediterranean Chaparral, and Florida Scrub depend on fire to sustain ecosystem function and to support resident plant and animal species. This study was conducted in the Florida Scrub, a globally threatened ecosystem (Myers 1990). It supports more than 30 listed plants and animals (Muller et al. 1988), among the highest concentrations of listed species in the continental United States (Turner et al. 2006). It is a xeromorphic shrubland that grows on sandy uplands of the central ridges of Florida. These ridges are a series of relict dunes oriented along the north-south axis of the central part of the peninsula that were formed during pre-Pleistocene rises in ocean levels. Different habitat types within the Florida Scrub ecosystem include rosemary bald, oak-hickory scrub, scrubby flatwoods, and oak-palmetto scrub (Myers 1990). The long isolation of the central ridges has contributed to the evolution of numerous precinctive species of plants and animals.

Fire has been shown to have profound effects on biogeochemistry, plant demography and phenology, and species diversity in the Florida Scrub ecosystem (Menges et al. 1993; Menges and Quintana-Ascencio 2004; Boughton et al. 2006). These effects are modulated by the intensity, temporal occurrence (e.g., dry versus wet season), and periodicity of burning (Menges et al. 1993). Decades of fire suppression have modified many of the pyrogenic ecosystems in the southeastern United States, including the Florida Scrub, and have led to declines (Abrahamson and Abrahamson 1996) or changes in the composition (Mushinsky and Gibson 1991) of species that are adapted to frequent and/or high-intensity wildfires. Land managers are increasingly using controlled burning to restore species composition and sustain native biotas, as well as to reduce future fire hazards to human populations. Controlled burning can be used effectively to conserve the biodiversity of ecosystems in which wildfires historically occurred at moderate to high frequencies (Mitchell et al. 2006). Ideally, controlled burning plans should be based on an understanding of how fire affects the broad variety of organisms within pyrogenic ecosystems.

Animals living in pyrogenic ecosystems

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can be affected by fire in three main ways: (1) direct mortality, (2) alteration of biotic interactions, and (3) alteration of habitat structure. Although fire and heat can kill animals, as evinced by the occasional presence of numbers of dead individuals in recently burned areas (Babbitt and Babbitt 1951; pers. observation), in most cases, it is difficult to estimate the mortality resulting from fire in the field (Russell et al. 1999). Mortality rates from fire are influenced by local topographic and microhabitat characteristics, such as the availability of burrows, substrate type, thermal conductivity, and the presence of ponds and wetlands that constitute temporary refuges (Kahn 1960; Lips 1991; Friend 1993). The effects of burning on biotic interactions are little explored, but, for example, fire might kill disproportionately more predators or competitors of a given species, or the more open habitat after a burn might favor increased predation on ground-dwelling species that require surface cover as a refuge. The effects of burning on habitat structure have received substantially more attention than either of the other effects (e.g., Mushinsky 1985; Greenberg et al. 1994; Letnic et al. 2004). Periodic high-intensity fires can maintain a mosaic landscape of vegetation structure and stand ages to which many animals are adapted (e.g., Tiebout and Anderson 1997, 2001). Several studies, particularly from Australia, suggest that reptiles, in particular, show strong responses to the changes in vegetation structure (e.g., Driscoll and Henderson 2008; Lindenmayer et al. 2008) and abiotic conditions, such as soil moisture (Trainor and Woinarski 1994), that accompany fire.

A recent study (Ashton and Knipps 2011) addressed the relationship between the time between burns (time since last fire, TSF) and resident reptiles and amphibians in one restricted Florida Scrub ecosystem habitat type, rosemary bald (Myers 1990). Variation in TSF causes variation in vegetation structure, which, in turn, was shown to promote variation in the abundances of some resident reptile species (Ashton and Knipps 2011). No effect of TSF on herpetofaunal diversity could be demonstrated, however (Ashton and Knipps 2011). This paper describes a parallel study in a less restricted Florida Scrub ecosystem habitat type, scrubby flatwoods (Myers 1990). Scrubby flatwoods habitat has a sparse to moderate overstory dominated by slash pine (*Pinus elliottii*) and/or sand pine (*P. clausa*), and a complex midstory with several species of oak (*Quercus* spp.), and a variety of other relatively low-growing species. Although rosemary bald habitat often contains many of the same species as scrubby flatwoods habitat, it is characterized by many sandy open patches and large widely-spaced rosemary (*Ceratiola ericoides*) plants. Often, the scrubby flatwoods habitat surrounds the open rosemary bald habitat.

In this study, we present capture results for reptiles and amphibians over a two-year sampling period, and relate them to TSF. We use detailed analyses of the most common reptile species to gain insight into how TSF affects their abundances. We could not do the same for the most common amphibian species, however, because their distribution and abundance are likely to be related mostly to availability of seasonal ponds, and we did not control for distance to ponds when designing our study. We compared our results in scrubby flatwoods habitat with those from rosemary bald habitat (Ashton and Knipps 2011) to determine how general the results were for the Florida Scrub ecosystem as a whole. Similarities and differences in fire effects on resident species between habitats likely are important for developing management plans for the Florida Scrub ecosystem. Because of inherent structural differences in the vegetation of the two habitats, we were able to offer explanations for some seemingly anomalous results of the previous study.

METHODS

Our study was conducted at Archbold Biological Station (ABS), Lake Placid, Florida, USA (27º 10' 50" N, 81º 21' 00" W), located near the southern end of the Lake Wales Ridge. Biologists and land managers at this ~2100-ha natural preserve of Florida Scrub have used controlled burning during the last 40 years and maintain an inventory of all wild and prescribed fires, including their date, spatial extent, and burning intensity (Archbold Biological Station, unpubl. data). The main property of ABS is subdivided into burn units managed according to different fire return intervals (Main and Menges, unpubl. data). The fire return strategy represents the intervals intended to maintain a shifting mosaic landscape of habitat types at ABS, and are used to compile an annual burn schedule. The actual burning frequency of each unit is affected by several factors, including adverse climatic conditions during a particular year and occurrence of wildfires.

Our study was designed to avoid some of the limitations of previous controlled burning experiments, such as the lack of control for season and habitat type, too few or no replicates, inadequate sampling effort, and unaccounted variations in detectability (Means et al. 2004; Robertson and Ostertag 2004). Twelve burn units at ABS were selected by overlaying vegetation, soil type, and fire history map layers in GIS. Our goal during the selection process was to minimize environmental variation among field sites, so that differences among sites could be attributed primarily to fire history, rather than to factors associated with variation in habitat type. We first restricted our selection to the vegetation layer corresponding to Inopina Oak Scrubby Flatwoods, one of the most representative habitat types at ABS. Vegetation was comprised of sclerophyllous shrubs, dominated by clonal oaks (*Quercus inopina, Q. chapmanii, Q. geminata*); palmettos (*Seronoa repens, Sabal etonia*); ericaceous shrubs (e.g., *Befaria racemosa*); and occasional slash pines. We then restricted our selection to the soil layer corresponding to Satellite sand, a moderately- to well-drained soil type that is sandy to depths of more than 200 cm. Finally, we used the fire history layer to select burn units according to TSF, with recently burned (six or fewer years since last fire), burned at intermediate intervals (seven to 17 years since last fire), and long unburned (18 or more years since last fire) as categories. Stratified selection of burn units ensured representation of the full range of canopy closure and loss of ground cover that accompanies maturation of scrubby flatwoods habitat. Four burn units were selected within each TSF category and three locations for installing enclosures (described below) within each burn unit.

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In all, 36 400-m^2 enclosures (four burn units within each of three TSF categories X 3 replicates per burn unit) were installed at ABS. The principal purpose of the enclosures was to confine individuals of the Florida Sand Skink (*Plestiodon reynoldsi* Stejneger), a federally threatened species with a range restricted to the central ridges of Florida, so that population densities could be estimated with simulated removal trapping (Sutton et al. 1999). The enclosures were constructed of metal or vinyl flashing inserted in ~30 cm deep trenches. Three bucket traps were countersunk on the inside and on the outside of each of the four walls of an enclosure, and 16 pitfall-trap arrays were regularly spaced over the entire 400-m^2 area (Figure 1). A pitfall-trap array consisted of a 2-m long, 15-cm deep piece of flashing partially buried in the sand with two bucket traps countersunk at each extremity. Therefore, the total trapping effort per enclosure was 76 bucket traps inside and 12 bucket traps outside. Buckets were 22 cm deep, and recessed an additional 3 cm below the ground surface. A layer of sand in the bucket traps and lids supported a few cm above them served to protect captured individuals from predators and direct exposure to the sun.

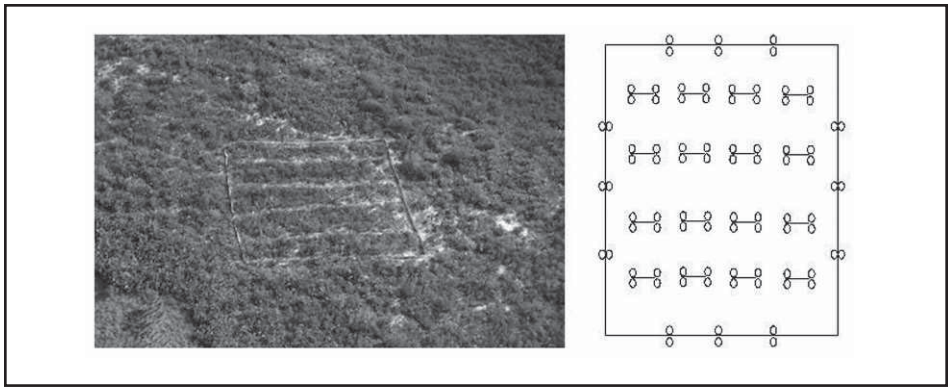


Figure 1. Aerial view of an enclosure and a schematic drawing, showing the arrangement of bucket traps inside and outside (not to scale).

Bucket-trap sampling, within and outside the enclosures, occurred during the spring and late summer of 2007 and 2008. These trapping seasons coincided with the major activity periods of the Florida Sand Skink. The Florida Sand Skink has a single mating period each year from February to May, and females produce a single clutch of eggs between May and June (Ashton 2005). It is during this mating period that adults are most active. The emergence of hatchlings occurs between July and October (Ashton and Telford 2006). Traps were open 14 March – 29 June and 17 August – 2 October in 2007; and 4 March – 16 June and 29 August – 30 September in 2008. Each trap was checked every three days during each trapping season.

Captured individuals of the Florida Sand Skink were transported to the laboratory for measurements and marking; and after a maximum of three days, were released near their points of capture. We recorded snout-vent length, body mass, sex, trap location, tail length, and other head and body morphometric measurements. We assigned a 6-digit identification code using visible implant elastomer (Northwest Marine Technology, Shaw Island, WA) to mark and recognize individuals (see Penney et al. 2001 for methods). Captured individuals of four other lizard species, the Florida Scrub Lizard (*Sceloporus woodi* Stejneger), a species largely restricted to scrub habitats on the central ridges; the Six-lined Racerunner (*Aspidoscelis sexlineatus* L.); the Southeastern Five-lined Skink (*Plestidon inexpectatus* (Taylor)); and the Ground Skink (*Scincella lateralis* Say), were measured and marked in the field. We recorded snout-vent length, tail length, and sex; and individually marked each individual by toe clipping. Individuals were then released near their points of capture. Abundances of these five species were estimated as both the numbers of total captures and of unique captures in all buckets, inside and outside of the enclosures, during the two trapping seasons. Other captured species were recorded but not marked or measured. Abundances of these species were estimated only as the numbers of total captures in all buckets during the two trapping seasons.

Standard indices were employed to describe herpetofaunal diversity. Three indices were selected to cover the range of sensitivity to the shapes of relative abundance distributions. The three indices were species richness, Shannon-Wiener, and Berger-Parker Dominance. Shannon-Wiener Evenness also was calculated. The indices were calculated for the complete data set and for the data from the different TSF treatment categories separately. Shapes of relative abundance distributions were compared with the Kolmogorov-Smirnoff Two-Sample Test. Some of the same methods were employed to compare our results with those of the previous study (Ashton and Knipps 2011).

We evaluated the effect of TSF on abundances of the most common reptile species with a two-way ANOVA. TSF treatment category was a fixed factor and burn unit was a random factor (burn units nested within TSF). Separate analyses were performed on data from the two years. We followed the two way ANOVAs with Tukey post hoc tests based on the observed means. Because most long unburned enclosures were clustered in the southern portion of the study area, we used Mantel tests to estimate the correlation between the geographical distance between enclosures and population density. Mantel tests were performed in program R. To determine the direct effects of fire on individuals within and outside the five burned enclosures, we used one-way repeated ANOVAs. We report the significance values for the spring and late summer densities, and the combined spring and late summer densities. All tests were performed in SPSS 17.0, unless otherwise indicated.

Because individuals of the Florida Sand Skink were marked and confined by the enclosure walls, actual densities of individuals within enclosures could be estimated as the number of unique captures inside the enclosure during spring and late

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summer trapping seasons combined. We used a robust design cohort model with closed captures (Kendall et al. 1997), in program MARK, to calculate maximum likelihood estimates of survival and capture probabilities of the Florida Sand Skink within enclosures. Akaike's Information Criterion (AIC) was used to select among competing models, and Akaike weights (w) were computed to identify the relative strength of evidence for each model. We separated individuals into two groups for this analysis: hatchlings (≤ 40 mm SVL) and sub-adults/adults (> 40 mm SVL). The global model (S(t-age)P(t-age)) estimated survival probabilities (S) within enclosures for both age groups (age) across all trapping sessions (2 trapping seasons per year X 2 years). Reduced models assumed constant survival and capture probability either among trapping sessions (SESS) or between seasons (SEAS). We introduced fire history treatment group as a covariate in some of the models.

Densities of the Florida Sand Skink were related to differences in environmental variables within enclosures. We surveyed 10 environmental variables that reflect differences in the biotic and abiotic conditions of the microhabitats associated with different TSF (McCoy et al. 1999): (1) Leaf litter samples (g/m^{-2}) were taken at 12 locations per enclosure in 0.1 m^2 quadrats. Samples were oven-dried at 60 ºC to constant weight; (2) Light measurements were taken at 12 locations per enclosure on clear, breezy days in November, between 1100 and 1330, to avoid bias from weather conditions and variations in light intensity during the day; (3) Number of palmettos was the total number of *Serenoa repens* and *Sabal etonia* within each enclosure; (4) Sand moisture was estimated from sand cores at 15-cm depth. Samples were oven-dried at 105 ºC for 24h; (5-9) Percentage of bare ground, live vegetation, dead vegetation, lichen, and woody debris were estimated as the ground surface area within 16 subplots (1 m^2) per enclosure composed of each of the categories; and (10) Canopy height was estimated as the average height of the canopy within each enclosure. A Principal Components Analysis (PCA) was performed with the environmental variables and used to separate the TSF treatment categories based on the most heavily loaded factors. We plotted the variation in environmental factors among categories in relation to the first two principal components. We conducted a backwards step-wise multiple regression using the four most heavily loaded environmental factors as independent variables and density of the Florida Sand Skink as the dependent variable.

RESULTS

We captured eleven species of reptiles (excluding turtles) and six species of amphibians in 2007 – 2008 (Table 1). Three species of lizards (Florida Scrub Lizard, Florida Sand Skink, and Six-lined Racerunner) accounted for 95% – 97% of the reptile captures and two species of toads (Eastern Narrow-mouthed Toad, *Gastrophryne carolinensis* Holbrook; and Oak Toad, *Anaxyrus quercicus* (Holbrook)) accounted for 96% – 99% of the amphibian captures in the two years. Richness was 15 species in 2007 and 12 species in 2008. The difference in richness principally was a result of the lack of snake captures in 2008. Rainfall – the only climatic variable likely to be substantially different between years – was substantially greater in 2008 than in 2007 (Figure 2). Based on total captures, the overall Shannon-Weiner diversity value was 1.56 nats and 1.54 nats, and Berger-Parker dominance was 0.25 and 0.37 in 2007 and 2008, respectively. Shannon-Weiner evenness was 0.58 in 2007 and 0.62 in 2008. The relative abundance distributions for the two years were different ($D = 0.19$, $p < 0.01$), mainly because of the high abundance of the explosively-breeding Eastern Narrow-mouthed Toad in 2008.

Herpetofaunal species richness was not strongly related to TSF. Eleven of the 17 species were captured in all three TSF categories in both years; the six species that did not were the least common species (Table 1). We could find no significant difference in species richness among fire history treatments in either 2007 ($F = 0.80$, $df = 35$, $p = 0.38$) or 2008 ($F = 0.17$, $df = 35$, $p = 0.68$). For the three most common reptile species, only the abundance of the Florida Sand Skink was related to TSF (see below). For the two most common amphibian species, total captures were related to TSF for the Oak Toad in 2007 ($F = 7.60$, $df = 35$, $p < 0.01$; 2008: $F = 2.49$, $df = 35$, $p = 0.12$). The relationship remained strong when data were placed into TSF categories ($F = 3.51$, $df = 2$, $p = 0.04$). A Post-hoc Tukey Test indicated that abundance was higher in long unburned units than in more recently burned units in 2007 ($p = 0.06$). Overall, Berger-Parker Dominance values indicated little difference among TSF categories in 2007 (0.28, 0.27, and 0.32, for recently burned, burned at intermediate intervals, and long unburned, respectively), but a greater difference in 2008 (0.46, 0.46, 0.33). The lower dominance in long unburned units in 2008 is attributable to the relative paucity of captures of the Eastern Narrow-mouthed Toad in those units (Table 1). Among reptiles alone, we found little difference among TSF categories either in 2007 (0.42, 0.41, 0.51) or 2008 (0.44, 0.52, 0.46). The somewhat higher dominance in long unburned units in 2007 is attributable to the Florida Sand Skink's higher rate of capture there (see below), and in units burned at intermediate intervals in 2008 to the Florida Scrub Lizard's change in distribution among TSF categories between 2007 and 2008 (Table 1). Among amphibians alone, the difference in dominance among TSF categories (2007: 0.65, 0.46, 0.42; 2008: 0.88, 0.88, 0.62) is attributable in both years to the Eastern Narrow-mouth Toad's higher capture rate in more recently burned units (Table 1).

Abundance of the Florida Sand Skink was related to TSF. Based on unique captures, the relationship was stronger for the 2007 data ($F = 5.33$, $df = 35$, $p = 0.03$) than for the 2008 data ($F = 2.48$, $df = 35$, $p = 0.12$). A second-order regression did not fit the data better than a linear regression. Abundance tended to display the same increase with TSF when 2007 data were placed into TSF categories ($F = 3.51$, $df = 2$, $p = 0.09$). A Post-hoc Tukey Test indicated that abundance was higher in long unburned enclosures than in more recently burned enclosures in 2007 ($p = 0.02$). Of the 692 individuals captured in 2007 – 2008, nearly half (47.7%) were captured in long unburned enclosures (Table 1). The difference between years in the distribu-

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Table 1. Total captures of reptiles and amphibians during the study period (2007 - 2008). Individual captures in parentheses, for *S. woodi, P. reynoldsi, A. sexlineata, P. inexpectatus,* and *S. lateralis*, which were marked when first captured.

Species	TSF (years)					
	2007			2008		
	≤6	7-17	≥18	≤6	7-17	≥18
Reptiles						
Sceloporus woodi	211 (143)	157 (101)	166 (109)	195 (108)	263 (151)	269 (146)
Plestiodon reynoldsi	142 (95)	128 (85)	324 (183)	143 (92)	151 (90)	319 (147)
Aspidoscelis sexlineata	98 (68)	75 (60)	90 (46)	77 (53)	73 (47)	73 (48)
Tantilla relicta	18	8	25	18	13	14
Plestiodon inexpectatus	13 (7)	5 (5)	23 (21)	8 (6)	2 (2)	13 (11)
Anolis carolinensis	11	10	1	5	2	1
Scincella lateralis	2 (2)	1 (1)	1 (1)	1 (1)	3 (3)	2 (2)
Cemophora coccinea	1	1	0	0	0	0
Diadophis punctatus	0	0	1	0	0	0
Seminatrix pygaea	1	0	0	0	0	0
Thamnophis sirtalis	1	0	0	0	0	0
Amphibians						
Gastrophryne carolinensis	160	90	199	441	482	163
Anaxyrus quercicus	82	101	169	57	57	95
Anaxyrus terrestris	4	5	21	3	4	3
planirostris	0	0	0	2	2	3
Hyla cinerea	0	0	0	1	0	0
Hyla femoralis	0	0	1	0	0	0

tion of individuals among TSF categories was small (Figure 3). More of the long unburned enclosures were located in the south of Archbold Biological Station than in the north, but the spatial effect on total abundance in 2007 – 2008 combined was not particularly strong (Mantel statistic R = 0.05, p = 0.20). The spatial effect was strong in 2007 alone, however (Mantel statistic R = 0.09, p = 0.04).

A restricted version of the global mark-recapture model fit the Florida Sand Skink data with higher likelihood than the other models (Table 2). The best model was (S(sessXage)P(seas-age)), with survival and capture probability varying with age and season, and an interaction between age and season, The robust design cohort model comparisons indicated that survival of hatchlings is significantly lower than the survival of adults and that survival does not differ between seasons. A model including TSF treatment category was not well supported, indicating that survival did not vary with TSF.

Values of environmental variables differed among the three treatment groups. The PCA analysis (Figure 4) showed that long unburned enclosures were distinct from recently burned enclosures, and that the enclosures burned at intermediate intervals were intermediate between them. The factors loading most heavily on the first principal component were leaf litter biomass (+), canopy height (+), amount of dead vegetation (+), amount of bare ground (-), light intensity (-), and amount of live vegetation (-). The first principal component (PC1) explained 44.9% of the variation, and the second principal component (PC2) explained 18.2%. The multiple regression analysis showed that leaf litter biomass had the strongest correlation with absolute density of the Florida Sand Skink in both 2007 ($R^2 = 0.46$, p = < 0.01) and 2008 ($R^2 = 0.29$, p = 0.04).

Abundances of the Florida Scrub Lizard and Six-lined Racerunner could not be shown to be related to TSF. For the Florida Scrub Lizard, we could find no significant difference among fire history treatments in either 2007 (F = 1.49, df = 2, p = 0.30) or 2008 (F = 0.07, df = 2, p = 0.96). The distribution of individuals among TSF categories shifted from a predominance in recently burned enclosures in 2007 to a predominance in enclosures burned less frequently in 2008 (Figure 3). Significant differences among the replicates within burn units occurred in 2008 (F = 3.42, df = 6, p = 0.01), but not in 2007 (F = 1.44, df = 6, p = 0.24). Likewise, for the Six-lined Racerunner, we could find no significant difference among fire history treatments in either 2007 (F = 1.43, df = 2, p = 0.31) or 2008 (F = 1.33, df = 2, p = 0.67). The

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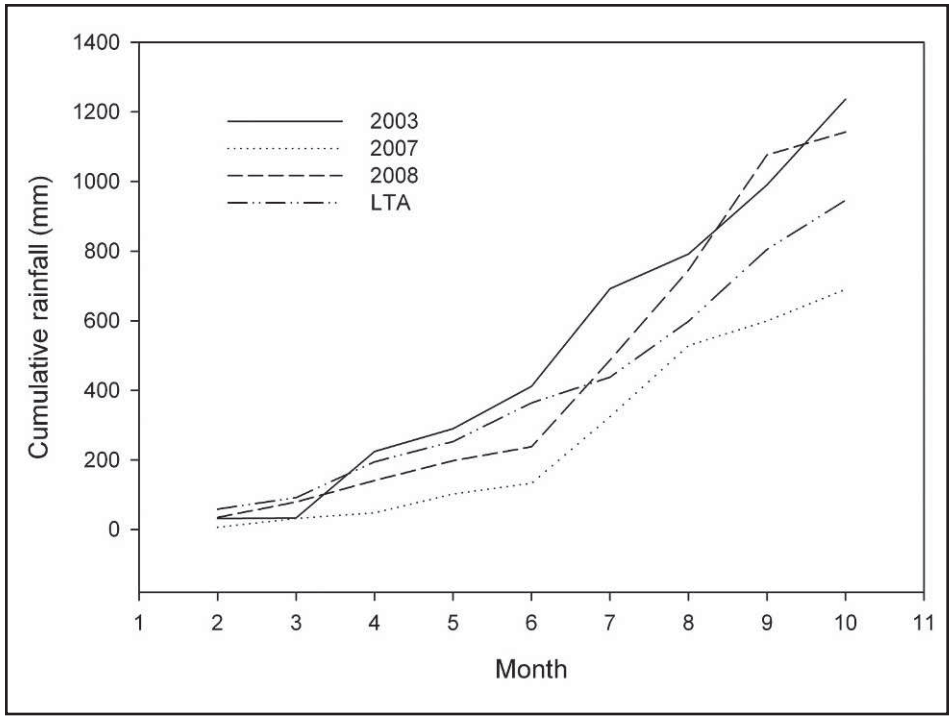


Figure 2. Rainfall data for 2003 [Ashton and Knipps' (2011) principal sampling year] and 2007 and 2008 (our sampling years). Data from the same weather station at ABS. The long-term (1932-2011) averages for the weather station are presented for comparison.

difference between years in the distribution of individuals among TSF categories was small (Figure 3).

DISCUSSION

The herpetofaunal assemblage of the Florida Scrub ecosystem shows remarkable consistency between the scrubby flatwoods and rosemary bald habitat types. Of the ten relatively common species (= ten or more total captures) that we captured in the scrubby flatwoods habitat, nine also were captured in the rosemary bald habitat (Ashton and Knipps 2011). The exception was the Ground Skink, which rarely ventures out of leaf litter. The Ground Skink is found in deciduous mesophytic forests, pine woods, and wooded fields–generally in areas with sufficient moisture, cover, and food (Brooks 1967). Likewise, of the nine common species captured in the rosemary bald habitat (Ashton and Knipps 2011), we also captured eight in the scrubby flatwoods habitat. The exception was the Bluetail Mole Skink (*Plestiodon egregius lividus* Mount), which has an extremely patchy and unpredictable distribution and is known from only 34 locations on the Lake Wales Ridge (USFWS 1999). The species has never been collected in scrubby flatwoods habitat at Archbold Biological Station. Ashton and Knipps (2011) also did not collect it in rosemary bald habitat at ABS. The seven species common in both habitats were similar in rank order of abundance, with the principal exceptions of the Southern Toad (*Anaxyrus terrestris* Bonnaterre), which was relatively more abundant in the rosemary bald habitat, and the Eastern Narrow-mouthed Toad, which was relatively more abundant in the scrubby flatwoods habitat. The Southern Toad often moves through open areas, such as rosemary bald habitat, especially after rain (pers. observation). The Eastern Narrow-mouthed Toad tends to attain its greatest abundance near seasonal ponds, but also can be found relatively far from ponds (pers. observation). The differences in relative abundances of these ubiquitous species between the two habitats probably are a consequence of local, unmeasured factors.

The total species richness recorded in rosemary bald habitat (17; Ashton and Knipps 2011) is identical to the total spe-

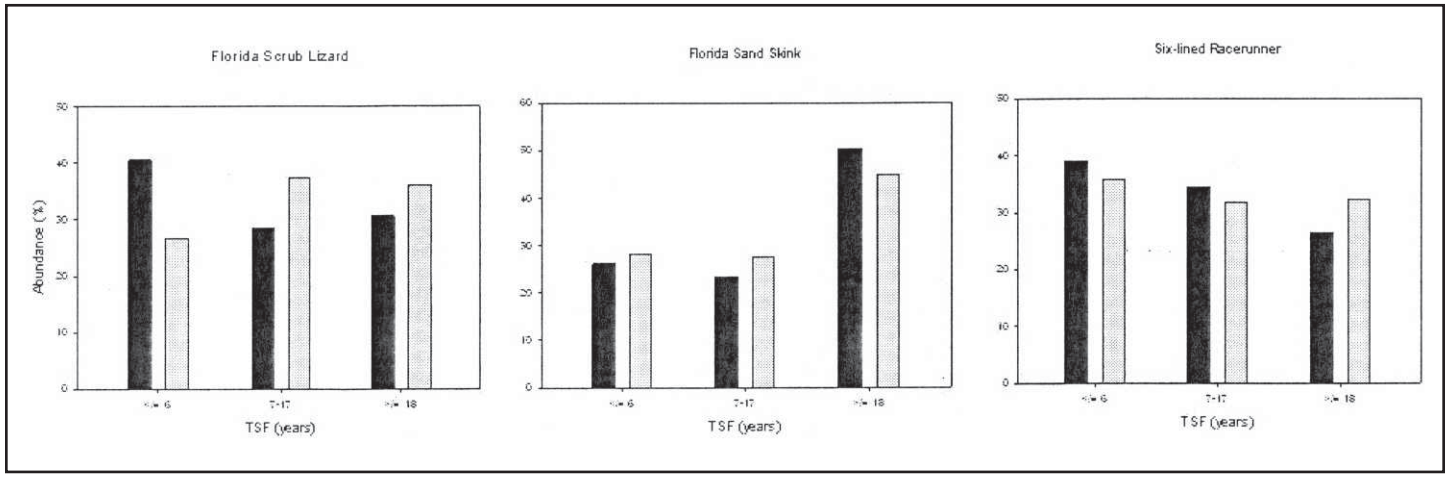


Figure 3. Relative abundance of the Florida Scrub Lizard, Florida Sand Skink, and Six-lined Racerunner during 2007 (darker bars) and 2008 (lighter bars) within TSF categories.

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Table 2. Mark-capture model selection for the Florida Sand Skink. Survival (S) and capture probability (P) were allowed to vary among trapping sessions (sess), among times (t), and between seasons (seas).

	Delta AICc	AICc weight	Likelihood	Deviance
S(sessXage)P(seas-age)	0.0	0.51631	1.0	3065.346
S(sess-age+age(age))P(seas-age)	1.5456	0.23839	0.4617	3064.821
S(t-age)P(t)	1.8809	0.20159	0.3904	3056.831
S(t)P(t)	5.5377	0.03239	0.0627	3056.298
S(sess-age+age(age))P(t)	7.6398	0.01132	0.0219	3056.298
S(seasXage)P(seas-age)	61.5107	0.0	0.0	3128.920
S(sessXage,TSF)P(seas-age)	64.5395	0.0	0.0	3127.815
S(seas-age)P(seas-age)	87.0753	0.0	0.0	3156.548
S(sess-age)P(sess-age)	87.1393	0.0	0.0	3154.551

cies richness that we found in scrubby flatwoods habitat. Only 14 species were recorded from rosemary bald sites at ABS, however. Fewer species recorded from rosemary bald habitat than scrubby flatwoods habitat at ABS may simply reflect sampling effort. Based on array-days, the effort was 516–528 in rosemary bald habitat at ABS, but 4896–5508 in scrubby flatwoods habitat at ABS. On the other hand, only 12 species were recorded from scrubby flatwoods habitat in 2008, when rainfall amount was more typical. Overall Berger-Parker Dominance in rosemary bald habitat (0.41 for all sites, 0.36 for ABS) is similar to that in scrubby flatwoods habitat (0.25 in 2007, 0.37 in 2008). Comparison of relative abundances could be affected by the difference in sampling techniques between the two studies. All individuals were marked in the rosemary bald study, but only individuals of selected species in the present study. The difference in marking between the studies does not appear to have affected the comparison substantially: estimated numbers of unique captures from total captures, based on the relationship between unique captures and total captures for those species we did mark, changed relative abundances little (unpubl. data). A difference in the spread of TSF values between the studies also could affect the comparison. Four of the rosemary bald sites were unburned for longer periods than any of the scrubby flatwoods sites, but one would need to do a more detailed comparison than is presently possible to determine how important the extra 8+ years is in influencing relevant habitat structure. A difference in environmental conditions at the times of sampling could affect the comparison. We demonstrated the effect that variable rainfall amounts, for example, could have on herpetofaunal abundances. The difference in location of sampling sites is yet another factor that could affect the comparison, and we explore this difference below.

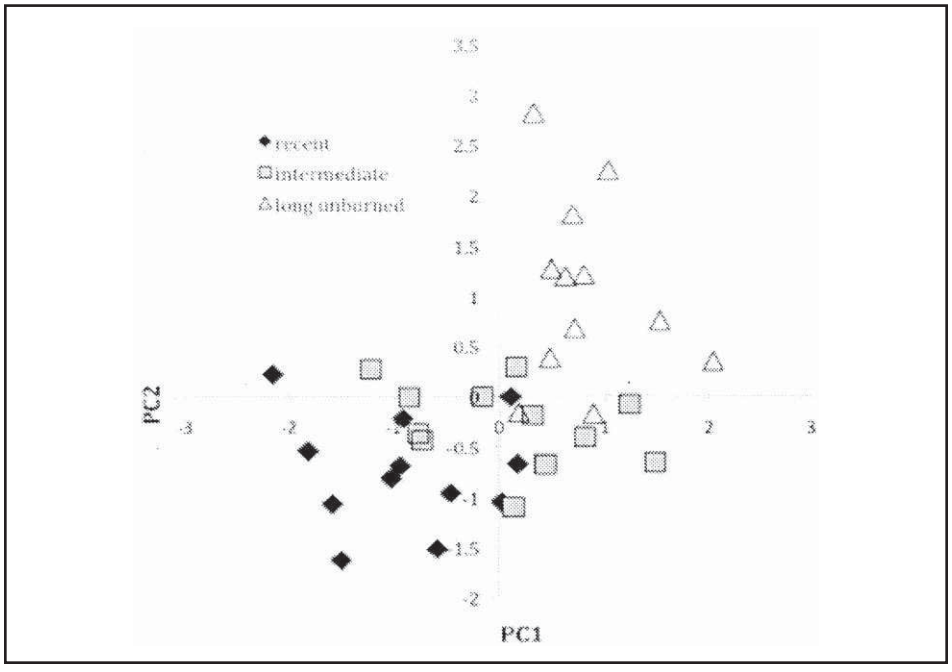


Figure 4. Principal components analysis of the environmental variables measured in 36 enclosures divided into three TSF categories.

The rosemary bald study (Ashton and Knipps 2011) used six sites at ABS and six isolated scrub sites, whereas the sites used in the present study all were at ABS. We can use the data from Ashton and Knipps (2011) to examine differences between abundances of species at the ABS rosemary bald sites and at the isolated rosemary bald sites. If we assume, based on the identical sampling effort, that abundances should be equal for the two groups of sites, then we can rank species by their proportional deviation from equality. The abundant species (= ten or more total captures) common to both rosemary bald and scrubby flatwoods

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habitats rank: Oak Toad (+0.58 at ABS), Six-lined Racerunner (+0.19), Southern Toad (-0.15), Florida Scrub Lizard (-0.23), Eastern Narrow-mouthed Toad (-0.25), Florida Sand Skink (-0.52), and Ring Crowned Snake (*Tantilla relicta* Telford) (-0.88). These differences indicate that only ABS data should be used to compare abundances recorded in the two studies. For the five lizard species for which we have unique capture data, we can use the difference in sampling effort (see above) to determine expected abundances in scrubby flatwoods habitat from abundances in the rosemary bald habitat at ABS. Based on this procedure, we can rank species by proportional deviation from the expected value. For the 2008 data, these species rank: Ground Skink (> +0.75 at ABS), Southeastern Five-lined Skink (+0.42), Florida Sand Skink (-0.18), Six-lined Racerunner (-0.29), and Florida Scrub Lizard (-0.78). At least some of the species for which we do not have unique capture data also could be analyzed in this way, but we will not do so here. A portion of the negative deviation for the Six-lined Racerunner and Florida Scrub Lizard may result from the inherent non-linearity between unique captures and sampling effort. Nevertheless, this analysis indicates that an important difference between the two habitat types is in the relative abundances of species. It also indicates that a more sophisticated model, including both within- and between-habitat metrics, might be needed to tease out the effects of TSF on herpetofaunal diversity.

The Florida Sand Skink displayed a strong relationship to TSF in both habitat types; specifically, it had a tendency toward higher abundance in areas not burned for relatively long time periods (more than 17 years in the scrubby flatwoods habitat). The difference in abundance between long-unburned areas and the other types was approximately twofold in the scrubby flatwoods habitat, but much greater in the rosemary bald habitat (Ashton and Knipps 2011). The greatest microhabitat difference among TSF categories in the scrubby flatwoods habitat was in leaf litter biomass. Abundance of the Florida Sand Skink was correlated positively with leaf litter biomass, even more strongly than with TSF.

The results for the Florida Sand Skink implicate the importance of cover, particularly leaf litter ground cover, in influencing its relative abundance among areas varying in TSF. The importance of leaf litter has been suggested by several previous studies (e.g., Telford 1959; Moler 1992), and a recent study of the species' diet (McCoy et al. 2010) indicated that prey items available in the litter are an important food resource. Long unburned areas that accumulate fallen twigs, pine needles, oak leaves, and logs may present a greater abundance of prey than more recently-burned areas. This finding would seem to contrast with the general impression that the Florida Sand Skink prefers microhabitats with loose sand and sunny exposures (Christman 1992; but, see McCoy et al. 1999) and not those with extensive litter layers (Collazos 1998; Christman 2005). We are currently addressing this seeming contradiction with a meta-analysis of the microhabitat preference (*en sensu,* Railsback et al. 2003) of the Florida Sand Skink (Rizkalla et al., unpubl. data).

The fact that the Florida Sand Skink is most abundant where fire has been absent for relatively-long periods of time does not eliminate the importance of periodic burning for the species. A study of the genetic response of the Florida Sand Skink to burning at ABS (Schrey et al. 2011b) suggests that individuals generally remain in place at long-unburned sites but move in response to burning. Genetic differentiation was positively correlated with geographic distance in long unburned units, but not in recently- and intermediately-burned units. Simulations indicated that demographic changes in local populations could have generated this observed difference. Changes in local populations attributable to burning appear to diminish after about 10 years. A reasonable conclusion is that, although the Florida Sand Skink may benefit from infrequent burning of its habitat at ABS, more frequent burning may be disruptive. Individuals may find it difficult to find places where apparently preferred environmental conditions, such as a relatively deep litter layer, exist. Furthermore, too frequent burning may reduce genetic diversity, because it may take multiple generations for local populations to recover from the burn (Schrey et al., 2011a,b). Interestingly, the need for accessible areas of preferred microhabitat within the general Florida Scrub habitat shown for the Florida Scrub Lizard (Tiebout and Anderson 1997, 2001; Heath et al. 2012) also seems to be the case for the Florida Sand Skink. The difference between the species is that the first prefers areas of recently-burned habitat, while the second prefers the opposite.

No effect of TSF on the abundance of the Florida Scrub Lizard could be shown in either scrubby flatwoods or rosemary bald habitats or on the abundance of the Six-lined Racerunner in scrubby flatwoods habitat. The Six-lined Racerunner displayed higher abundances in areas burned at intermediate intervals in the rosemary bald habitat (Ashton and Knipps 2011). These results are somewhat surprising, as a preference for more open habitat is well established for both species (Jackson 1973; Mushinsky 1985; Hokit et al. 1999). One possible explanation for these results is that factors other than TSF influenced abundance, such as degree of isolation and patch size of suitable habitat surrounding sites (Hokit et al. 1999; Hokit and Branch 2003). The scrub at ABS, for example, is highly fragmented and interspersed with seasonal ponds and cutthroat grass communities, which may limit the interchange among sub-populations. Because we did not standardize the distance to ponds and other unsuitable habitat, lizard populations may have been influenced by their proximity to low quality habitat patches. Some evidence for this possibility comes from a controlled burn in 2009 occurring in five of the burn units. Although one of the burn units contained three enclosures, we observed a substantial (20+ more individuals captured in 2009 than in either 2007 or 2008) increase in captured individuals of the Florida Scrub Lizard in only one of them. This enclosure was located near the middle of the burn unit, whereas the other two enclosures were near the edge, which abutted a roadway. Another possibility is that the conclusions that have been drawn previously about habitat preferences of these species are not general, but rather reflect differences among studies in scrub type, soil type, and vegetation layers. For example, the

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Six-lined Racerunner may indeed show a relative preference for more open areas, but with some thicker patches in which it can shelter. In other words, individuals may be seeking some preferred balance between open and closed spaces. In the rosemary bald habitat, individuals may not find such balance in very recently-burned areas, but might in the different vegetation structure in the scrubby flatwoods habitat.

The direct effects of frequent fires do not appear to have an important effect on herpetofaunal diversity, at least in scrubby flatwoods habitat. Immediately after the controlled burn of 2009, we conducted pedestrian surveys for dead individuals. One dead individual, of the Florida Sand Skink, was found after burning; and no appreciable negative effects of the fall fires on population densities, either in the following spring or a year later, were evident (unpubl. data). We assume that individuals of species living in this pyrogenic habitat can avoid fires by various means. For instance, individuals of the Florida Scrub Lizard and Six-lined Racerunner are able to move quickly enough and/or to find adequate shelter to avoid the localized fires. The prescribed burning took place during a period of relative inactivity for the Florida Sand Skink, when the sequestering of individuals in refuges may have reduced mortality (cf., Griffiths and Christian 1996). The Florida Sand Skink may be found at depths of at least 8 cm at this time (Christman 1992), and peak fire temperatures measured at a depth of 5 cm ranged only between 21 ºC and 44 ºC, with most locations displaying temperatures consistent with ambient temperature profiles under non-fire conditions (unpubl. data).

Our findings, coupled with those of Ashton and Knipps (2011), have some important management implications. Both studies documented relatively high abundances of the Florida Sand Skink in long-unburned areas. Although the species prefers long-unburned areas, we cannot say that it absolutely requires them. The species has shown itself to be resilient to many perturbations, even occupying agricultural lands with suitable soils (e.g., Pike et al. 2008). Nevertheless, its apparent reliance on litter indicates the need for areas that provide this resource. More research on how well habitat preference reflects species' requirements is needed. Other federally-listed species, particularly the Florida Scrub Jay, require more frequent burning to maintain suitable habitat, however (Snyder 1992). The potential difference in burning requirements among species in the Florida Scrub ecosystem support a land management plan of stochastic return intervals and spatial variation of high-intensity fires to maintain a mosaic landscape of vegetation structure and stand ages to which many species are adapted (Mushinsky and Gibson 1991; Menges 2007). Such a plan likely is unrealistic in many places other than ABS, Ocala National Forest, and a few other relatively large reserves; it would be difficult, if not impossible, to implement in the small patches that constitute much of the remaining Florida Scrub ecosystem (Turner et al. 2006). The problem is not easily solved. One possibility is to substitute mechanical methods for fire in small patches, as they are easier to control and do not cause a fire danger or a smoke problem for surrounding human habitation. The small amount of research on this possibility suggests that the differences between the consequences of burning and mechanical manipulation of the Florida Scrub ecosystem may be too great to justify substitution (McCoy et al., unpubl. data; Menges and Gordon 2010). Of particular concern for the Florida Sand Skink is the soil compaction that accompanies mechanical manipulation. In the end, the risks of burning patches too frequently or not frequently enough may outweigh any good that management is intended to do. The remaining options seem: to be either to manage particular patches for particular species, an unattractive option; to set aside larger intact areas of scrub habitat, but few such areas remain; and/or to establish a program of habitat restoration, especially in places where the soils have not been disturbed excessively.

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