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The Response of a Pine Savanna Herpetofaunal Community to Habitat Health and Restoration

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Abstract.—**Wildland fire is necessary for maintaining and restoring Pine Savannas in the southeastern USA, but there is disagreement on best land management regimes for herpetofaunal communities in these areas. We recreated a 2004 sampling effort in the Grand Bay National Estuarine Research Reserve (GNDNERR) and Grand Bay National Wildlife Refuge (GNDNWR), south Mississippi, USA, to assess how amphibian and reptile assemblages differ in response to prescribed fire. We used Visual Encounter Surveys (VES), minnow traps, and polyvinyl chloride (PVC) tubes in three burned and three unburned sites. As in 2004, we detected more amphibians (67% of our sample) than reptiles and found more individuals in burned than unburned treatments. We found no differences in abundance, diversity, evenness, and richness between burned and unburned treatments, though a Principal Coordinates Analysis (PCoA) indicated that burned communities were more similar to one another than to unburned communities. An Indicator Species Analysis (ISA) corroborated the PCoA findings. In both studies, we found ground-dwelling frogs such as the Oak Toad (*Anaxyrus quercicus*) and Southern Cricket Frog (*Acris gryllus*) more often in burned habitats than unburned, though occupancy analyses suggested this may be due to these species having higher detection probabilities in burned than unburned habitat. Additional surveys and different sampling methods will be needed to determine if these species can truly be indications of Pine Savanna health.**

Key Words.—community analyses; herpetofauna; Indicator Species Analysis; prescribed fire; Principal Coordinates Analysis

Introduction

In Pine Savanna habitats, fire is a necessary tool whose presence, absence, and frequency of use drive changes to the biodiversity within. With some taxa such as birds and plants, the relationships between prescribed fire and community health in these habitats are well understood (Bechtoldt and Stouffer 2005; Brockway and Lewis 1997). Conversely, there is uncertainty when it comes to the best practices for maintaining populations of amphibians and reptiles with prescribed fire (Schurbon and Fauth 2003; Means et al. 2004). Herpetofauna may also be more sensitive to negative regional impacts of habitat fragmentation and urbanization than other vertebrates as they typically occupy specific microhabitats and are poor dispersers, which makes proper management in protected, unbroken tracts of their respective ecosystems essential (Colino-Rabanal and Lizana 2012).

Specific fire ecology interactions vary across the herpetofaunal community as a whole and will often be species-specific (McLeod and Gates 1998; Perry et al. 2009; Harris et al. 2020). In addition to having species-specific responses, amphibian and reptile responses to fire are also known to vary depending on the habitat type being studied. In a mountainous pine woodland of Arkansas, USA, Perry et al. (2009) found that there was no significant difference in the majority of anuran and salamander species sampled from burned and unburned habitats, with only one species, the Western Slimy Salamander (*Plethodon albagula*), being found mostly in unrestored habitat. Other amphibians benefit from prescribed fire, and the presence of dense forest canopies inhibits larval growth in species such as the Spring Peeper (*Pseudacris crucifer*) and the Reticulated Flatwoods Salamander (*Ambystoma bishopi*), federally listed as Endangered (Skelly et al. 2002; Gorman et al. 2013). Gorman et al. (2013) found that a combination of management methods including mechanical clearing and herbicide treatment of invasive species followed by prescribed fire yielded increased herbaceous groundcover while decreasing canopy cover, and thus may be an effective method for restoring amphibian habitat in Pine Flatwoods. McLeod and Gates (1998) found that several snake species associated with leaf litter were less abundant in burned areas than in unburned areas of an Atlantic coastal plain in Maryland, USA, while Means and Campbell (1981) found no evidence of population declines for several species of herpetofauna associated with leaf litter after prescribed burns in Florida, USA. Steen et al. (2013) found that prescribed fire was effective at restoring reptile assemblages in fire-suppressed sandhills to baseline conditions over a long period of time (i.e., 15 y), and that the reintroduction of fire increased similarity between fire-suppressed and baseline site assemblages in the short-term. Gopher Tortoises (*Gopherus polyphemus*) are a fire-adapted keystone savanna species that benefit from canopy reduction resulting from fires and whose burrows provide necessary shelter to many other savanna vertebrates (Rostal and Jones 2002; Catano and Stout 2015).

Changes to herpetofauna abundance, richness, and diversity in areas that receive prescribed burns are thought to occur as indirect responses due to change in habitat over time, rather than as direct responses due to mortality from fire (Means and Campbell 1981; Perry et al. 2009). While this is intuitive for many aquatic amphibian and reptile species, the direct mortality of terrestrial reptiles from prescribed burns is also thought to be low as animals associated with pyrogenic vegetation are behaviorally adapted to resist mortality by fire (Means and Campbell 1981). In a study of 68 marked Eastern Diamondback Rattlesnakes (*Crotalus adamanteus*) in Florida, five fires during a five-year period resulted in the mortality of only two snakes (Means and Campbell, 1981). These two snakes were also noted as being mid-ecdysis at the time of the burn, which may have hindered their escape. While most other instances of reptile mortality due to prescribed fire have been anecdotal accounts, there are two previous studies that note significant direct mortality to Eastern Glass Lizards (*Ophisaurus ventralis*; Babbitt and Babbitt 1951; Means and Campbell 1981) and multiple studies that note box turtle mortality due to fire (Platt et al. 2010; Howey and Roosenberg 2013; Harris et al. 2020).

In a previous study, Langford et al. (2007) conducted surveys at the Grand Bay National Estuarine Research Reserve (GNDNERR) and Grand Bay National Wildlife Refuge (GNDNWR), hereafter referred to as the Grand Bay Reserve (GBR), to measure the effects of prescribed fire treatments on herpetofaunal communities in southern Mississippi, USA, Pine Savannas. Herpetofauna abundance was greater at burned sites than at unburned sites, though there was little to no difference in diversity, evenness, and richness between treatments. As the GNDNERR and GNDNWR were designated just prior to the 2004 surveys for the Langford et al. (2007) study (in 1999 and 1992, respectively), these surveys also provided an initial species inventory and community dataset for the area. Russell et al. (1999) notes that while there are many studies of the effects of prescribed burning on herpetofauna, those that reported differences in abundance and diversity between burned and unburned habitats lack meaning without baseline data, adequate controls, and replication. The baseline work of Langford et al. (2007), concomitant with the current Pine Savanna restoration and land acquisition activities occurring at GBR (Grand Bay National Estuarine Research Reserve 2013), has provided a unique opportunity to conduct follow-up community surveys.

Our objective was to replicate the sampling methods of Langford et al. (2007) as closely as possible to obtain a second dataset with which to make long-term comparisons of the responses of herpetofaunal communities to land management. This includes measures of species abundance, richness, diversity, and evenness among burned and unburned sites. We incorporated new land acquisitions at the GBR into our study to establish control sites (unburned since before the 2004 surveys), and to provide an updated herpetofauna inventory for the GBR by surveying areas that had not been available to survey during the Langford et al. (2007) study. Additionally, we aimed to determine if burned and unburned herpetofaunal communities were different from one another and which, if any, species of herpetofauna may be indicators of healthy Pine Savanna habitat.

Materials and Methods

Study area.—We conducted our study in the GNDNERR and GNDNWR in Jackson County, Mississippi, USA. In keeping with Langford et al. (2007), we selected three study sites that had received a prescribed burn in the year prior to our sampling (2019) and three sites that had not (Fig. 1). Our three burned sites had all been previously sampled by Langford et al. (2007) in 2004; one as burned habitat and two as unburned habitat (Fig. 2). Our three unburned sites had not been sampled in the previous study. We were unable to use the other three previously sampled sites due to land management activities that were scheduled to occur in these respective management units of the GBR during our sampling and instead incorporated sites from new, unmanaged land acquisitions in the GBR to simultaneously conduct an inventory of sections of the current GBR not sampled in 2004. While the unburned sites used in our study represent degraded habitat that had not been burned for a long period of time, the unburned sites used in Langford et al. (2007) were otherwise typical pine savanna habitats that had not been burned in over a year.

Sampling.—We sampled herpetofauna from six sites (three burned and three unburned) within the GBR from January-July 2020 (Fig. 2). We surveyed each site 23 times (once weekly) and each survey included sampling via minnow traps, polyvinyl chloride (PVC) tubes, and a 30-min-long Visual Encounter Survey (VES) along an

Figure 1. A Pine Savanna at the Grand Bay National Estuarine Research Reserve, south Mississippi, USA, approximately one week after a prescribed burn (left) and a site that has not undergone a prescribed burn in decades (right). (Photographed by Sandra Bilbo [left] and Andrew Heaton [right]).

established transect. Transects were 200 m long that we established in locations that were easily traversable by foot while still providing areas of standing water either at the terminus of or parallel to the transect, allowing for the use of minnow traps. During VES, we searched an approximately 5-m wide area of the transect, counting exposed animals and those hidden under objects such as logs, vegetation, and debris. We deployed six unbaited minnow traps at each site the day before surveying to achieve a 24 h soak time, providing a sampling effort of six trap nights per survey. We did not use these traps during periods of drought and we returned them when rainfall provided deep enough standing water for the openings of the traps to be submerged at all sites. For treefrog (*Hyla* spp.) sampling, we installed five 60 cm long × 2.5 cm interior diameter PVC tubes next to overstory trees adjacent to the transects at each site. We spaced tubes at approximately equal distances along the transect. We identified herpetofauna to species according to Powell et al. (2016). With the exception of turtles and alligators, Langford et al. (2007) sampled without replacement, either using the captured animals in a separate parasite study or re-releasing them only at the end of the study period. In this study, we sampled animals with replacement by releasing all immediately after species identification with no effort to track whether individuals were captured in multiple surveys.

Habitat description.—We measured habitat using the methods previously employed by Langford et al. (2007). We randomly placed a 10 × 10 m (100 m^2) plot adjacent to each transect. We identified the three most dominant species of trees, shrubs, and vines within each plot and estimated percentage cover for each. We averaged percentage cover of individual species across burned and unburned treatments. For the two most common tree species in each plot, we measured and averaged the diameter at breast height (DBH) for trees > 3 cm DBH. We established a 1 × 1 m plot in the southwest corner of each 100 m^2 plot to visually estimate herbaceous ground cover, woody debris, bare ground, hardwood litter, pine litter, and herbaceous litter. In each smaller

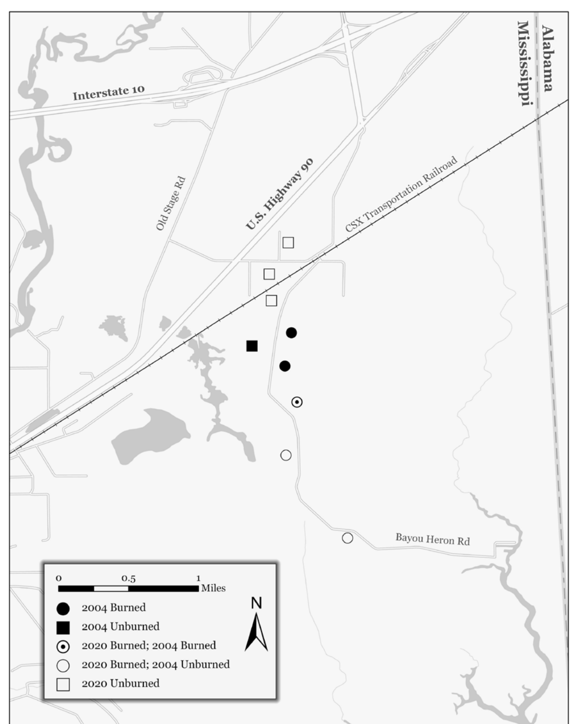

Figure 2. Location of burned and unburned sites at the Grand Bay National Estuarine Research Reserve (GNDNERR) and Grand Bay National Wildlife Refuge (GNDNWR) in south Mississippi, USA, from sampling efforts by Langford et al. (2007) in 2004 and the current study in 2020.

plot, we measured leaf litter depth to the nearest 1 cm in this smaller plot and we averaged these data across treatments. More information on the edaphic factors of the Reserve is available upon request.

Statistical analyses.—We used Microsoft Excel to calculate species richness, abundance, and Shannon diversity and evenness indices. For multivariate analyses, we retained only species with three or more captures to avoid undue influence from outliers. We excluded American Alligators (*Alligator mississippiensis*) from all analyses as a newly hatched brood of alligators was consistently present at a single site, leading to skewed occurrence values (Table 1).

Table 1. Amphibians and reptiles sampled from burned and unburned sites at the Grand Bay Reserve (GBR), Mississippi, USA. Data were collected from January to July 2020 in the current study, and from January to June 2004 during the initial survey by Langford et al. (2007) of the GBR. Burned sites had all received prescribed fire < 1 y before sampling began.

Species	Common Name	Burned 2020	Unburned 2020	Total 2020	Burned 2004	Unburned 2004	Total 2004
Amphibians							
Acris gryllus	Southern Cricket Frog	154	20	174	84	50	134
Amphiuma means	Two-toed Amphiuma	2	16	18	1	0	1
Anaxyrus fowleri	Fowler's Toad	0	1	1	1	0	1
Anaxyrus quercicus	Oak Toad	12	0	12	105	9	114
Anaxyrus terrestris	Southern Toad	0	0	0	1	1	2
Gastrophryne carolinensis	Eastern Narrow-mouthed Toad	3	0	3	2	3	5
Hyla cinerea	Green Treefrog	4	20	24	3	2	5
Hyla femoralis	Pinewoods Treefrog	6	0	6	19	8	27
Hyla squirella	Squirrel Treefrog	11	32	43	3	1	4
Lithobates catesbeianus	Bullfrog	3	0	3	0	0	0
Lithobates clamitans	Green Frog	1	9	10	0	1	1
Lithobates grylio	Pig Frog	6	0	6	2	13	15
Lithobates sphenocephalus	Southern Leopard Frog	0	7	7	51	2	53
Pseudacris nigrita	Southern Chorus Frog	0	0	0	3	0	3
Siren intermedia	Lesser Siren	21	0	21	1	0	1
Total		223	105	328	276	90	366
Reptiles							
Alligator mississipiensis	American Alligator	1	117	118	1	0	1
Agkistrodon piscivorus	Cottonmouth	1	1	2	1	4	5
Anolis carolinensis	Green Anole	47	14	61	5	1	6
Coluber constrictor	Black Racer	3	3	6	3	2	5
Deirochelys reticularia	Chicken Turtle	0	0	0	0	1	1
Kinosternon subrubrum	Eastern Mud Turtle	2	0	2	13	2	15
Lampropeltis holbrooki	Speckled Kingsnake	1	0	1	3	0	3
Nerodia cyclopion	Mississippi Green Watersnake	7	0	7	0	0	0
Nerodia fasciata	Banded Watersnake	11	0	11	1	2	3
Ophisaurus ventralis	Eastern Glass Lizard	4	0	4	4	1	5
Pantherophis guttatus	Corn Snake	0	1	1	0	0	0
Plestiodon inexpectatus	Southeastern Five-lined Skink	2	3	5	0	2	2
Scincella lateralis	Ground Skink	1	12	13	4	1	5
Sternotherus odoratus	Musk Turtle	0	1	1	0	0	0
Terrapene carolina major	Gulf Coast Box Turtle	5	22	27	5	2	7
Thamnophis saurita saurita	Eastern Ribbon Snake	5	5	10	1	1	2
Trachemys scripta elegans	Red-eared Slider	3	7	10	0	1	1
Total		92	69	161	40	20	60

Principal Coordinates Analysis (PCoA; also known as metric multidimensional scaling) was performed in R (v. 3.6.3; R Core Team 2020) using the function pcoa within the package ape (Paradis and Schliep 2019) to compare community dissimilarity at each site. We selected this ordination approach because it offers some advantages over other similar techniques such Principal Components Analysis (PCA). PCoA is an eigenanalysis of the community dissimilarity matrix and allows for use of several options for the pre-determined distance metric compared to PCA (Kang et al. 2015). We used a Bray-Curtis distance metric in the PCoA in this study to construct the dissimilarity matrix (Hernandez-Ordonez et al. 2019) from total captures by species and site for the entire study period. To show the influence of species on site groupings, we overlaid vectors representing the most influential species in the PCoA on a biplot.

We performed Indicator Species Analysis (Dufrêne and Legendre 1997) on weekly capture data using function multipatt from the R package indicspecies (De Caceres and Legendre 2009). Due the potential for temporal autocorrelation, we restricted permutations for *P*-value calculations to the sites themselves (i.e., all 23 rows for a site were permuted together). This led to only 20 possible permutations, so we performed the *P*-value calculations on the complete permutation set. Finally, to aid in interpretation of results of the PCoA and Indicator Species Analysis, we performed Occupancy Analyses on the five species that appeared to have the largest indicator values. We converted abundances to a presence/absence matrix. We used the R packages unmarked (Fiske and Chandler 2011) and MuMIn (Barton 2020) to generate models and ranking metrics (Akaike Information Criterion, AIC, or corrected Akaike Information Criterion, AICc; weights) for each species in which habitat type (burned or unburned) was included as a covariate for occupancy, detection probability, neither, or both. We averaged models with an AIC difference of < 5 from the best model using the AICcmodavg package (Mazerolle 2020) to generate estimates and standard errors for occupancy and detection probabilities in both habitat types. There is some uncertainty in the literature about whether to use AIC or AICc (which includes a correction for small sample sizes) to rank models: Burnham and Anderson (2004) recommend using AICc except in cases of very large sample sizes, whereas MacKenzie et al. (2017) use AIC due to difficulty in determining the effective sample size needed for calculation of AICc. Here, because we were mainly interested in exploration rather than inference from these models, we used both ranking methods. The AICc-based method favored the null model (habitat type not affecting either occupancy or detection probability), whereas the AIC-based ranking included more models in the averaging, though with lower weights.

Results

We recorded 489 individuals from 29 species during our study period, of which 328 (67%) were amphibians (13 species) and 161 (33%) were reptiles (16 species). Three species, the Southern Toad (*Anaxyrus terrestris*), Chicken Turtle (*Deirochelys reticularia*), and Southern Chorus Frog (*Pseudacris nigrita*) were sighted during the 2004 surveys but not the 2020 surveys (Table 1). Four species, the Bullfrog (*Lithobates catesbeianus*), Mississippi Green Watersnake (*Nerodia cyclopion*), Corn Snake (*Pantherophis guttatus*), and Musk Turtle (*Sternotherus odoratus*) were sighted during the 2020 surveys but not the 2004 surveys. All species that were only present during one survey period were detected in low numbers (Table 1).

Since the initial surveys by Langford et al. (2007), 16 new species of herpetofauna have been found to occur at the GBR. Only four of these species were reported from the 2020 surveys, although all off-survey species sightings were confirmed by Reserve staff. Some species, such as the Dusky Pygmy Rattlesnake (*Sistrurus miliarius barbouri*) and the Musk Turtle were found in lands acquired by the GBR since 2004, which would not have been available during the initial baseline surveys.

Similar to the findings of Langford et al. (2007), VES was our most effective sampling method, detecting 26 of 29 total species and being the sole capture method for 15 (52%) of those species. Minnow traps caught 10 species, three of which were the only species not detected via VES and whose sole capture method was minnow trap: the Mississippi Green Watersnake, and our only two salamander species; the Two-toed Amphiuma (*Amphiuma means*) and the Lesser Siren (*Siren intermedia*). As expected, treefrogs were the only species detected with PVC tubes, although all three species present in our sample were also detected at lower rates during VES.

Species abundance, diversity, evenness, and richness were similar for both the burned and unburned sites in our study (Table 2). Estimates of percentage ground cover for plant species and leaf litter depth measurements showed a clear distinction between our burned and unburned sites (Table 3). Our burned habitats were defined by greater occurrence and percentage cover of forb and graminoid species, their lack of measurable leaf litter, and some presence of bare ground. Our unburned habitats were defined by their greater percentage cover of woody and herbaceous ground litter, lower graminoid percentage cover and species occurrence, and greater number of tree species. The unburned habitats used in our study occurred on lands that were recently acquired by the Reserve and are currently unrestored. In contrast to the better-managed burned sites, a number of invasive

Table 2. Mean and standard deviation (in parentheses) of amphibian and reptile abundance (mean number of amphibians or reptiles per transect), Shannon diversity and evenness indices, and species richness (number of species captured) between three burned and three unburned sites from the Grand Bay Reserve, Mississippi, USA. Data were collected from January to July 2020 in the current study, and from January to June 2004 during the initial inventory of the GBR by Langford et al. (2007). Burned sites had all received prescribed fire < 1 y before sampling began.

		Burned 2004	Burned 2020	Unburned 2004	Unburned 2020
Amphibians					
	Abundance	11.36 (4.67)	1.77 (1.67)	4.26 (3.45)	3.32 (3.17)
	Diversity	1.52 (0.69)	1.02 (0.04)	1.5 (0.61)	1.54 (0.3)
	Evenness	0.6 (0.23)	0.57 (0.02)	0.7 (0.57)	0.88 (0.13)
	Richness	7.67 (5.98)	7 (0)	4.67 (5.39)	5.67 (0.58)
Reptiles					
	Abundance	1.33 (1.58)	1.12 (1.38)	0.86 (1.36)	1.41 (1.47)
	Diversity	1.99 (0.9)	1.32 (0.47)	2.33 (1.67)	1.45 (0.22)
	Evenness	0.78 (0.81)	0.72 (0.1)	0.94 (1.15)	0.82 (0.11)
	Richness	5 (7.61)	7.67 (3.21)	5.33 (6.89)	8 (2.65)

plant species were present in these unburned areas including Chinese Tallow (*Triadica sebifera*), Chinese Privet (*Ligustrum sinense*), and Cogon Grass (*Imperata cylindrica*).

Herpetofaunal communities among burned and unburned areas showed differences. The first two axes explained 79.8% of the variance in the data (Axis 1 explained 45.2%; Axis 2 explained 34.6%). Burned sites (4, 5, and 6) grouped closely along lower levels of Axis 1 and moderate levels of Axis 2 (Fig. 3). Unburned sites 1 and 3 were associated with moderate levels of Axis 1 and high levels of Axis 2 (Site 2). Site 2 (unburned) was unique from all sites, as it was associated with high levels of Axis 1 and low levels of Axis 2. When vectors representing the most influential species were overlaid on the biplot, it was apparent that Southern Cricket Frogs (*Acris gryllus*) and Southern Leopard Frogs (*Lithobates sphenocephalus*) were important components of burned habitats while Green Tree Frogs (*Hyla cinerea*) and Squirrel Tree Frogs (*H. squirella*) were associated with the unburned Site 2. Indicator values ranged from 0.170–0.733 on a scale of 0–1. Due to restricting permutations on a small sample size (the entire time series for a site was permuted together), a *P*-value of 0.05 would have been the lowest possible outcome and no significant *P*-values resulted. Some species with high indicator values among their group, such as the Southern Cricket Frog, bolstered the results seen in ordination (Table 4). Given the impossibility of achieving low *P*-values with our restricted permutations, we performed additional occupancy and detection probability analyses on the five species that appeared to have the largest indicator values (Southern Cricket Frog, Green Treefrog, Squirrel Treefrog, Lesser Siren, and the Green Anole, *Anolis carolinensis*). Occupancy estimates were similar for burned and unburned sites, though detection probabilities differed for the Southern Cricket Frog and the Green Anole between burned and unburned sites (Table 5).

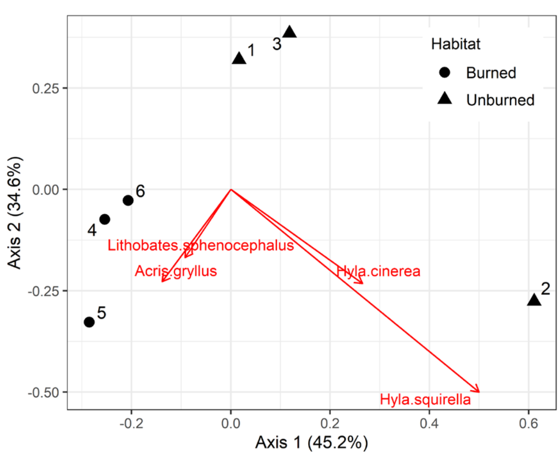

Figure 3. Principal Coordinates Analysis (PCoA) biplot comparing herpetofaunal communities of sites that have been burned recently (sites 4, 5, and 6) with sites that have no recorded burn history (sites 1, 2, and 3) within the Grand Bay National Estuarine Research Reserve, south Mississippi, USA. Vector overlays represent the species with the four largest vectors from the PCoA: Southern Cricket Frog (*Acris gryllus*), Green Treefrog (*Hyla cinerea*), Squirrel Treefrog (*Hyla squirella*), and Southern Leopard Frog (*Lithobates sphenocephalus*).

Discussion

Our study provides the first re-examination of the GBR herpetofaunal community since initial baseline surveys occurred in 2004. Russell et al. (1999) noted that while many studies of the effects of fire on herpetofauna exist, they can lack meaning without proper context and baseline data as these effects can vary by region,

Table 3. Means and standard deviations for habitat variables measured within 100 m^2 plots adjacent to three burned and three unburned sites in the Grand Bay Reserve, Mississippi, USA. Variables were measured 20 July 2020 following prescribed burns that occurred the previous year.

Habitat Variable	Burned	Unburned
Dominant tree (% cover)		
Slash Pine (*Pinus elliottii*)	5 (± 3.1)	4.5 (± 0.4)
Loblolly Pine (*Pinus taeda*)	0	10 (± 0)
Pond Cypress (*Taxodium ascendens*)	5 (± 0)	0
Water Oak (*Quercus nigra*)	0	1 (± 0)
Chinese Tallow (*Triadica sebifera*)	0	6.3 (± 2.3)
Dominant shrub (% cover)		
Inkberry (*Ilex glabra*)	30 (± 4.1)	2 (± 0.8)
Yaupon Holly (*Ilex vomitoria*)	3.5 (± 1.22)	2.7 (±1.1)
Wax Myrtle (*Morella cerifera*)	3.5 (± 1.2)	5 (± 0)
Chinese Privet (*Ligustrum sinense*)	0	6 (± 0)
Dominant vine (% cover)		
Common Dewberry (*Rubus flagellaris*)	3 (± 1.6)	2 (± 0.7)
Saw Greenbrier (*Smilax bona-nox*)	0	1 (± 0)
Peppervine (*Ampelopsis arborea*)	0	5 (± 0)
Virginia Creeper (*Parthenocissus quinquefolia*)	0	5 (± 0)
Poison Ivy (*Toxicodendron radicans*)	0	2.5 (± 0.4)
Dominant herb (% cover)		
Wiregrass (*Aristida stricta*)	10 (± 0)	0
Broomsedge (*Andropogon virginicus*)	27.5 (± 10.2)	0
Elliott's Beaksedge (*Rhynchospora elliottii*)	5 (± 0)	0
Witchgrass (*Dichanthelium* sp.)	20 (± 4.1)	0
Horsetail Spikerush (*Eleocharis equisetoides*)	35 (± 0)	0
Grass-leaved Goldenrod (*Euthamia graminifolia*)	15 (± 0)	0
Cogongrass (*Imperata cylindrica*)	0	10 (± 0)
Hairy Primrose-willow (*Ludwigia pilosa*)	40 (± 0)	0
Path Rush (*Juncus tenuis*)	0	2 (± 0)
DBH (stems > 3 cm)		
Slash Pine (*Pinus elliottii*)	21.9 (± 5.5)	12.9 (± 6.3)
Loblolly Pine (*Pinus taeda*)	0	15.3 (± 7.3)
Pond Cypress (*Taxodium ascendens*)	4.4 (± 0)	0
Water Oak (*Quercus nigra*)	0	20.3 (± 0)
Chinese Tallow (*Triadica sebifera*)	0	8.4 (± 2.6)
Ground cover (%)		
Pine litter	5 (± 0)	75 (± 15.4)
Hardwood litter	0	7.5 (± 2.0)
Herb litter	4 (± 0.8)	18.3 (± 13.3)
Bare ground	18.3 (± 5.4)	0
Woody debris	6 (± 3.3)	5 (± 0)
Litter depth (cm)	0	5.8 (± 1.3)

Table 4. Indicator Species Analysis of the herpetofaunal community sampled at three burned and three unburned sites of the Grand Bay Reserve, Mississippi, USA, from January-July 2020. Species are listed under the habitat with which they have more of an association. Indicator values are on a scale of 0–1. *P*-values were calculated using restricted permutations (see text) and the threshold for significance was $P \leq 0.05$.

Treatment	Group	Species	Common Name	Indicator value	*P*-value
Burned	Amphibians	*Acris gryllus*	Southern Cricket Frog	0.733	0.085
		Siren intermedia	Lesser Siren	0.434	0.440
		Lithobates grylio	Pig Frog	0.295	0.385
		Hyla femoralis	Pinewoods Treefrog	0.269	0.440
		Anaxyrus quercicus	Oak Toad	0.241	1.00
		Gastrophyrne carolinensis	Narrow-mouthed Toad	0.209	0.440
		Lithobates catesbeianus	Bullfrog	0.170	1.00
	Reptiles	*Anolis carolinensis*	Green Anole	0.569	0.085
		Nerodia fasciata	Banded Watersnake	0.341	0.085
		Nerodia cyclopion	Mississippi Green Watersnake	0.269	1.00
		Ophisaurus ventralis	Eastern Glass Lizard	0.241	0.085
Unburned	Amphibians	*Hyla squirrella*	Squirrel Treefrog	0.482	0.425
		Hyla cinerea	Green Treefrog	0.433	0.085
		Amphiuma means	Two-toed Amphiuma	0.421	0.180
		Lithobates clamitans	Green Frog	0.273	0.085
		Lithobates sphenocephalus	Southern Leopard Frog	0.241	0.385
	Reptiles	*Scincella lateralis*	Ground Skink	0.402	0.085
		Terrapene carolina major	Gulf Coast Box Turtle	0.401	0.600

habitat, and species. This long-term re-sampling effort has provided us with a comparative dataset, mixed evidence of current species-specific responses based on management treatments, and a more complete species inventory for the GBR.

Langford et al. (2007) found that while herpetofauna abundance was greater in GBR wet Pine Savannas that were recently burned, diversity, evenness, and richness indices showed no differences based on fire. When repeating the methods of Langford et al. (2007), community indices (abundance included) between burned and unburned habitats were similar, with high standard deviations. In terms of individual captures, both our dataset and the Langford et al. (2007) dataset showed that more amphibians and reptiles total were found in burned habitats than unburned habitats at the GBR. The presence of four new species brings the total number of species known to occur on GBR lands to 47. These new species sightings are likely due to surveying new areas of the Reserve, and an updated census of all reptile and amphibian species known to occur at the Reserve is included (Appendix Table).

In the 2004 dataset, Langford et al. (2007) noted that Oak Toads (*A. quercicus*) and Southern Cricket Frogs were found more often near clumps of Wiregrass (*Aristida stricta*) in burned habitats, which may be due to the fact that the grass provides filtered sunlight, a thermal gradient, and the high hydration levels required by both species (Hamilton 1955; Walvoord 2003). Our burned habitats included the bunchgrasses Wiregrass and Broomsedge (*Andropogon virginicus*), which would provide greater refuge for these species than our unburned habitats, which had no detected ground cover of bunchgrasses, and whose pine and herbaceous ground litter cover would be consumed as fine fuels during a fire. We also found Southern Cricket Frogs and Oak Toads more often in burned habitats, but occupancy modeling of Southern Cricket Frogs suggests this is due to higher probability of detection in these habitats rather than increased occupancy of this species. While our smaller sample size of Oak Toads did not warrant occupancy analyses (it was not prominent in ISA/PCoA results), as a small, ground-dwelling species, greater detection probability may also play a role in its increased sightings in GBR savannas. One potential explanation for the smaller sample of Oak Toads in our study is a shelter-in-place order issued for the state of Mississippi due to the COVID-19 pandemic, which prevented

Table 5. Results of occupancy analysis on major species from Principal Coordinates Analysis (PCoA) and Indicator Species Analysis output, showing predicted probability with standard error in parentheses. Four models were fit for each species: psi(.)p(.) indicates constant occupancy and detection probability in the model; psi(b)p(b) includes habitat type (burned/unburned) as a covariate affecting both occupancy and detection; psi(.)p(b) includes habitat type as a covariate affecting only detection probability; psi(b)p(.) includes habitat type as a covariate affecting only occupancy. The Included Models and Weights column indicates which of the four candidate models were included in weighted model-averaging (based on Akaike Information Criterion, AIC) to produce the occupancy and detection probabilities. Estimates from AICc-based ranking were similar to those shown but, except for two species, were based only on the null model, psi(.)p(.). The *A. gryllus* estimates used only the psi(.)p(b) model. The *A. carolinensis* estimates included the null model with weight 0.84, and the model psi(.)p(b) with weight 0.16.

		Occupancy		Detection	
Species	Included Models and Weights	Burned	Unburned	Burned	Unburned
Acris gryllus Cricket Frog	psi(.)p(b): 0.73; psi(b)p(b): 0.27	1 (0.004)	1 (0.004)	0.638 (0.058)	0.217 (0.05)
Hyla cinerea Green Treefrog	psi(b)p(.): 0.49; psi(b)p(b): 0.22; psi(.)p(.): 0.2; psi(.)p(b): 0.09	0.655 (0.209)	0.683 (0.201)	0.216 (0.044)	0.217 (0.043)
Hyla squirrella Squirrel Treefrog	psi(.)p(b): 0.3; psi(.)p(.): 0.25; psi(b)p(b): 0.24; psi(b)p(.): 0.21	0.831 (0.156)	0.836 (0.152)	0.294 (0.045)	0.297 (0.044)
Siren intermedia Lesser Siren	psi(b)p(.): 0.52; psi(.)p(.): 0.21; psi(b)p(b): 0.19; psi(.)p(b): 0.08	0.348 (0.208)	0.319 (0.2)	0.282 (0.067)	0.283 (N/A)
Anolis carolinensis Green Anole	psi(.)p(b): 0.73; psi(b)p(b): 0.27	1 (0.002)	1 (0.002)	0.42 (0.059)	0.145 (0.042)

any surveys from occurring in April 2020 and that caused our sample period to include 23 survey weeks between January-July, as opposed to the 23 survey weeks between January-June as done by Langford et al. (2007). Newly metamorphosed Oak Toads began to appear in our surveys of burned habitats in May 2020, and as mortality is high for young frogs, if they had been present in these habitats as of April 2020, the number of Oak Toads possible to detect on a survey may have already decreased significantly due to predation or other mortality by May.

Greater numbers of Southern Leopard Frogs and Eastern Mud Turtles (*Kinosternon subrubrum*) were detected in the 2004 surveys than in 2020, while greater numbers of Green Anoles, Lesser Sirens, Two-Toed Amphiumas, Banded Watersnakes, and Mississippi Green Watersnakes were detected in 2020. Green Anoles were detected in burned habitat more than unburned habitat in both 2004 and 2020 (albeit at lower numbers in 2004), while Two-Toed Amphiumas, Lesser Sirens, Mississippi Green Watersnakes, and Banded Watersnakes were all detected in low (three or less) numbers in 2004 and had no observable preference for one habitat treatment or the other. It is unclear why Eastern Mud Turtles and Southern Leopard Frogs were not detected as often in our surveys as they were in the 2004 surveys. While many Southern Leopard Frog or Green Frog tadpoles were found in minnow traps in our burned and unburned habitats, these were not included in our analyses. This suggests that these adults probably occur in these habitats at higher levels than were detected. Langford et al. (2007) found 13 Eastern Mud Turtles in burned habitat and two in unburned habitat, but also noted that an additional 30 Eastern Mud Turtles were found in burned habitat and an additional three were found in unburned habitat, and that these were not included in their survey total as they evaded physical capture. Our finding of only two Eastern Mud Turtles in burned habitat over our entire sampling period is a steep decline from the 48 turtles seen in 2004. The lack of turtle species in our herpetofaunal community sample (only four species were detected of the nine turtle species known to occur in the GBR), and the low number of individuals counted for species that were detected (with 10 Red-eared Sliders, *Trachemys scripta elegans,* being the most of any aquatic turtle species), suggests that sampling methods beyond VES will need to be included in future surveys of the Reserve to better study this underrepresented reptile assemblage. While sites surveyed in this study all contained adjacent wetlands with shallow water, there are areas of the GBR that contain permanent ponds, oxbows, bays, bayous, and even portions of the Escatawpa River that may be used to monitor species beyond those found in these surveys.

Our burned habitat variables were generally similar to those found in 2004 (e.g., a large percent cover of graminoid species, little to no leaf litter depth, and with pines (*Pinus* spp.) as the dominant tree), though there are important distinctions to be noted between the unburned habitats used in Langford et al. (2007) and in our study. In 2004, the unburned sites surveyed were areas of otherwise healthy Pine Savanna habitat that had not been burned as recently (> 1 y prior to sampling) as the burned sites (< 1 y prior to sampling). This is evident as *Pinus* and *Aristida*, species who are together indicative of Pine Savanna habitat, were dominant in the percent cover of their respective categories of the unburned sites while the leaf litter depth was much greater than at burned sites (Langford et al. 2007). The unburned sites chosen for our 2020 surveys were areas located further north in the GBR, which had been more recently acquired by the Reserve. While these sites were historically Pine Savanna habitat, and plant species typical of savanna habitat can still be found in them to a lesser degree, in recent decades they have been residential areas. The houses and other anthropogenic material have been removed from these lands in recent years, though the habitats themselves are as of yet unrestored. These sites differ from the 2004 unburned sites by having no savanna graminoid species detected in our percent cover measurements and by the presence of invasive plant species. We detected more overall amphibians and reptiles total in unburned habitats in 2020 than in 2004, though our lower counts of Southern Cricket Frogs and Pinewoods Treefrogs (*Hyla femoralis*) may be due to either the degraded nature of these sites or differences in detection probabilities. The observed differences in species counts among regularly burned areas (burned sites 2004, 2020), areas not burned as recently (unburned sites 2004), and degraded, unmanaged sites (unburned 2020) provide possible insight into the effects of burn frequency as a gradient for change among herpetofaunal communities.

The clear grouping of burned sites was the most evident result of the PCoA analysis. One species, the Southern Cricket Frog, was prominently associated with the burned sites in vector overlays. Occupancy modeling showed, however, that Southern Cricket Frogs were likely to occupy both burned and unburned sites but was more likely to be detected at burned sites (detection probability 0.638 versus 0.217). The use of AIC or AICc did not make a substantial difference in estimated occupancy or detection probabilities for the tested species in our study. As AIC and AICc results were similar, we chose to report only AIC-based results as a means to convey our results with more information on model weights. A second noteworthy result was the uniqueness of Site 2, which had abundant Gulf Coast Box Turtles and Squirrel Treefrogs relative to other sites. Our indicator species analysis suggested that 11 species were more associated with regularly burned Pine Savanna habitat while seven species were associated with degraded, more densely canopied habitat at the GBR; however, due to the low number of sites and the applied permutation restrictions, this analysis did not have statistical power to allow us to declare any of these species to be indicators. Instead, we have interpreted the associations and indicator values returned from our indicator species analysis in tandem with the results of our PCoA ordination. The preference of Southern Cricket Frogs and Pinewoods Treefrogs for open canopied habitats and their association with the habitat variables present in these burned habitats has been previously documented (Walvoord 2003; Mohrman et al. 2005; Langford et al. 2007). While there may be no direct effects of burning on the habitat preferences and requirements of watersnakes (*Nerodia* spp.), we suggest that secondary effects driven by their dietary preferences may be the cause of their association with regularly burned savannas at the GBR. Watersnakes are dietary generalists who undergo ontogenic changes, often mainly feeding on small fish and tadpoles as juveniles and mainly feeding on frogs and some larger fish as adults, depending on the habitats they occupy (Gibbons and Dorcas 2004; Vincent et al. 2006; McKnight et al. 2014). The greater number of frog species such as Bullfrogs, Pig Frogs, and Southern Cricket Frogs in our burned habitat surveys are possible driving factors behind the preference of Banded Watersnakes and Mississippi Green Watersnakes for burned habitats at the GBR.

Previous studies have found that detection probabilities and movement rates of some species of herpetofauna were higher after fires, and we cannot rule out the possibility of increased detection probability in burned habitats influencing our observation rates of species who were primarily observed through VES, such as the Green Anole (Chelgren et al. 2011; Brown et al. 2014). Of the species whose burned/unburned habitat preferences were prominent enough to receive further occupancy analyses in our study, Green Anoles and Southern Cricket Frogs both showed significant differences in detection probability between burned and unburned sites, but no differences in occurrence. These were also species who were only detected through VES. We used VES to attempt to recreate previous survey efforts at the GBR as closely as possible, but this method relies on observer detection that could potentially bias data for species that are not observed through more regimented, trap-based sampling where the efforts are clearly the same between sites. While it is accurate to say that species such as Southern Cricket Frogs, Oak Toads, and others are found in healthy, regularly burned pine savannas more often in the GBR, further work will be needed to elucidate if this was a difference in abundance or detection probability.

The three hylid species present in our study are known to benefit from open-canopy habitats due to larval success and prey availability (Horn et al. 2005; Mohrman et al. 2005; Binckley et al. 2007). Despite this, mixed effects are reported in current literature on the presence and abundance of Green Treefrogs and Squirrel Treefrogs in open and closed canopy sites, or between burned and unburned sites. Observations of Green Treefrogs in Indiana, USA, have shown that occurrence is dependent on open-canopied breeding sites, while a study in South Carolina, USA, found greater Green Treefrog occurrence and insect biomass in open canopy, suggesting that they also benefit from prey availability in areas of dense ground vegetation (Horn et al. 2005; Lodato et al. 2014). Conversely, a study by Schurbon and Fauth (2003) of 15 temporary ponds with varying burn histories suggested that fire had significant negative effects on amphibian abundance and richness, with Green Treefrogs being predominantly found in habitat that had not been burned in > 12 y and Squirrel Treefrogs showing no clear preference, being found in habitat burned < 1 and > 12 y prior. Our results suggest that Green and Squirrel Treefrogs are both associated with unburned habitats with denser canopies at the GBR, though our occupancy modeling does not suggest differences in occurrence or detection between burned and unburned sites. There may also be regional differences that drive the preference, or lack thereof, of treefrogs to open canopy habitats as warmer climates would not require open canopies to create favorable thermal conditions on the ground. There is less ambiguity in our finding of the association of Pinewoods Treefrogs with regularly burned habitat, as all sampled individuals were present in burned sites and available literature supports the association of this species with open-canopy or regularly burned habitat (Schurbon and Fauth 2003; Mohrman et al. 2005; Langford et al. 2007).

We did not detect any terrestrial salamanders in our surveys, and we do not believe that the observed differences in aquatic salamanders between burned and unburned habitats are important to our study as they would not be influenced by burning. The occurrence of sirens and amphiumas across a landscape is determined primarily by physical factors such as hydroperiod and distance to nearest wetland, and secondarily by biological interactions and competition (Gibbons and Semlitsch 1991; Snodgrass et al. 1999). While sirens and amphiumas are aquatic, they can survive periods of drought through aestivation, burrowing into the substrate and secreting mucous from their skin to form a protective layer that prevents water loss and desiccation (Gehlbach et al. 1973). These species are known to have poor overland dispersal ability, and colonization of new wetland sites likely occurs only when periods of heavy rainfall create temporary aquatic connections with nearby habitat. The low rates of co-existence between sirens and amphiumas at the same sites in our study is likely due to competition, as the wet Pine Savannas at the GBR experience regular flooding.

Box turtles are known to be negatively affected by prescribed burning, and the association of Gulf Coast Box Turtles (*Terrapene carolina major*) with unburned habitats in the GBR supports this (Platt et al. 2010; Howey and Roosenberg 2013; Harris et al. 2020). Of all herpetofauna species surveyed, the box turtle has the most recorded instances of direct mortality due to fire in current literature, and it does not have the refuge or ease of movement as many aquatic and arboreal species present in our study do. Harris et al. (2020) found that box turtle survival was lower for individuals who experienced prescribed burns than those who did not, and that survivorship was negatively correlated with fire intensity, fire temperature, and leaf litter depth. Two of the five turtles we found in burned habitat exhibited fire-scarring on their carapace. The association of box turtles with unburned habitat in the GBR is intuitive and may be the only case of a species whose direct mortality drives their habitat occupation and detection probability, as opposed to secondary effects of land management maintaining or changing habitat over time.

While using the methods employed by Langford et al. (2007) provided us with a valuable comparative dataset, it is clear from the results of the 2004 and 2020 survey years that additional sampling methods will need to be included in future herpetofaunal monitoring efforts at the GBR to better detect reptiles. Reptiles only comprised 33% of our total sample, and many species that were detected occurred in low numbers. Only four of nine turtle species known to occur at the GBR were detected, and species of conservation interest like the Alabama Red-bellied Cooter (*Pseudemys alabamensis*) and the Gopher Tortoise were not represented. To better detect these species in future surveys different areas than those used in this project will need to be surveyed, such as nearby ponds, bayous, marshes, and the Escatawpa River for aquatic turtle species and upland habitats of the Reserve known to include Gopher Tortoise burrows.

Studies that use historic data or replication for context to examine the effects of prescribed fire on herpetofauna are rare, and the land acquisition and Pine Savanna restoration efforts currently ongoing at the GBR provided us with a unique opportunity to re-sample savanna sites that had been used 16 y prior and to sample control sites of degraded savanna habitat that have not been burned since long before the previous survey (Langford et al. 2007; Grand Bay National Estuarine Research Reserve 2013). As these degraded sites are restored to their historical conditions in the coming years, we will be able to further monitor the change over time of this herpetofaunal community with baseline data from degraded habitats and comparative data from healthy habitats. Additionally, the use of these new lands in our study has allowed us to further inventory species of herpetofauna known to occur in the GBR (47 known species as of 2020), which can be important for future land management considerations and for designing future studies. Based on our statistical analyses and 2004/2020 count data, we can see that there are some community and species-level differences such as the grouping of burned sites in ordination, and larger vectors and burned habitat abundance for species such as Southern Cricket Frogs and Oak Toads. Occupancy Modeling suggests that detection probability is higher for some species in burned than unburned habitats, so results from other analyses must be interpreted with caution until more data can be collected. Many reptiles, as well as other ground-dwelling amphibians like the Eastern Narrow-mouthed Toad (*Gastrophryne carolinensis*), may also be underrepresented with the methods presented in our study and Langford et al. (2007). These methods should be used in the future for drawing comparisons with the presented data, particularly for examining changes in Oak Toad and Southern Cricket Frog occurrence over time, though we believe that hoop nets and passive sampling methods such as coverboards and drift fences should also be used in future monitoring efforts at the GBR. By employing sampling efforts that do not rely on observer detection in VES, these passive sampling methods will allow us to determine whether the differences observed in prior survey efforts are truly due to relative abundance and habitat preferences, or if instead they are simply driven by variation in detection probability. A future study that uses these different sampling methods, in tandem with comparable effort, site selection, and similar statistical analyses, will allow us to determine the best benchmarks for gauging Pine Savanna health through the status of the herpetofaunal community within.

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Jonathan L. Pitchford is a graduate of Auburn University (B.S.), Auburn, Alabama, USA, Appalachian State University (M.S.), Boone, North Carolina, USA, and West Virginia University (Ph.D.), Morgantown, USA. He has been involved in a variety of ecological research projects during his career including development of species distribution models, ecological studies of protected species, and examining the effects of climate change. At Grand Bay National Estuarine Research Reserve, Mississippi, USA, Jonathan coordinates long-term monitoring of estuarine resources in response to sea level rise, evaluating the effects of estuarine restoration, and broad-scale wet Pine Savanna and flatwoods restoration and monitoring. (Photographed by Jay McIlwain).

Appendix Table. Total inventory of herpetofauna species known to occur at the Grand Bay Reserve (GBR), Mississippi, USA, as of 2020. Initial 2004 inventory data are reported from Langford et al. (2007), while all sightings and new additions since have been confirmed by Reserve staff. Four new additions to the Reserve species inventory are reported in the 2020 surveys of the GBR: *Lithobates catesbeianus*, *Nerodia cyclopion*, *Pantherophis guttata*, and *Sternotherus odoratus*.

Species	Common Name	2004	2004-2020
AMPHIBIANS			
Acris crepitans	Northern Cricket Frog		x
Acris gryllus	Southern Cricket Frog	x	
Amphiuma means	Two-toed Amphiuma	x	
Anaxyrus quercicus	Oak Toad	x	
Anaxyrus fowleri	Fowler's Toad	x	
Anaxyrus terrestris	Southern Toad	x	

Appendix Table (continued). Total inventory of herpetofauna species known to occur at the Grand Bay Reserve (GBR), Mississippi, USA, as of 2020. Initial 2004 inventory data are reported from Langford et al. (2007), while all sightings and new additions since have been confirmed by Reserve staff. Four new additions to the Reserve species inventory are reported in the 2020 surveys of the GBR: *Lithobates catesbeianus*, *Nerodia cyclopion*, *Pantherophis guttata*, and *Sternotherus odoratus*.

Species	Common Name	2004	2004-2020
Gastrophryne carolinensis	Eastern Narrow-mouthed Toad	x	
Hyla cinerea	Green Treefrog	x	
Hyla femoralis	Pine Woods Treefrog	x	
Hyla gratiosa	Barking Treefrog		x
Hyla squirella	Squirrel Treefrog	x	
Lithobates catesbeianus	Bullfrog		x
Lithobates clamitans	Green Frog	x	
Lithobates grylio	Pig Frog	x	
Lithobates sphenocephalus	Southern Leopard Frog	x	
Pseudacris nigrita	Southern Chorus Frog	x	
Siren intermedia	Lesser Siren	x	
REPTILES			
Agkistrodon piscivorous	Cottonmouth	x	
Alligator mississippiensis	American Alligator	x	
Anolis carolinensis	Green Anole	x	
Chelydra serpentina	Snapping Turtle		x
Coluber constrictor priapus	Southern Black Racer	x	
Deirochelys reticularia	Chicken Turtle	x	
Farancia abacura	Mud Snake		x
Gopherus polyphemus	Gopher Tortoise		x
Hemidactylus turcicus	Mediterranean House Gecko		x
Kinosternon subrubrum	Eastern Mud Turtle	x	
Lampropeltis holbrooki	Speckled Kingsnake	x	
Liodytes rigida	Glossy swampsnake		x
Malaclemys terrapin pileata	Mississippi Diamondback Terrapin	x	
Nerodia clarkii clarkii	Gulf Saltmarsh Snake	x	
Nerodia cyclopion	Mississippi Green Watersnake		x
Nerodia erythrogaster	Plain-bellied Watersnake		x
Nerodia fasciata	Banded Watersnake	x	
Opheodrys aestivus	Rough Green Snake	x	
Ophisaurus ventralis	Eastern Glass Lizard	x	
Pantherophis guttata	Corn Snake		x
Plestiodon inexpectatus	Southeastern Five-lined Skink	x	
Pseudemys alabamensis	Alabama Red-bellied Cooter		x
Rhadinaea flavilata	Pine Woods Littersnake		x
Scincella lateralis	Ground Skink	x	
Sistrurus miliarius barbouri	Dusky Pygmy Rattlesnake		x
Sternotherus odoratus	Musk Turtle		x
Storeria dekayi	Dekay's Brown Snake		x
Terrapene carolina major	Gulf Coast Box Turtle	x	
Thamnophis saurita	Eastern Ribbon Snake	x	
Trachemys scripta elegans	Red-eared Slider	x	